Temporal Precision Necessitates Wingbeat-Call Asynchrony in Actively Echolocating Bats

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Abstract. I present a unified theory and empirical analysis showing that temporal precision, rather than energetic efficiency or mechanical synchrony, is the primary axis guiding echolocation call timing in flying bats. While classic hypotheses posited that coupling call emission to wingbeat and respiration cycles is optimal, my field data and mathematical modelling demonstrate that such synchrony is only maintained when sensory–motor demands are minimal. As bats approach a target or encounter complex, dynamic environments, synchrony is frequently and necessarily broken: I show that the strict temporal constraints imposed by the call–echo–response loop require bats to decouple vocal output from wing motion whenever echo delays become short or as circumstantial demands for information updates enforce. Using a simulation framework grounded in first principles, I reveal that wingbeat–call synchrony is possible only within a narrow physiological window, bounded by wingbeat frequency and amplitude. When these limits are exceeded, asynchrony reliably emerges as the only viable strategy to maintain real-time sensory feedback. Both my empirical data and theoretical model predict and explain the universal emergence of a hyperbolic relationship between interpulse interval and call rate—across all behavioural and environmental contexts—demonstrating that closed-loop, echo-guided timing is a fundamental, conserved feature of bat biosonar. Patterns such as sonar sound groups arise not as discrete modules, but as visible signatures of the feedback-driven system flexibly adapting to heightened uncertainty or unpredictability. I further discuss how species-specific morphological and aerodynamic constraints set the boundaries for synchrony flexibility, explaining interspecific diversity in echolocation behaviour. Altogether, these findings demonstrate that wingbeat-call asynchrony is an adaptive, mathematically inevitable solution for temporal precision in active echolocation, unifying previously disparate empirical observations and providing a predictive foundation for future research in sensory–motor coordination, flight control, and biosonar.

Keywords: Echolocation, Wingbeat-call synchrony, Temporal precision, Sensory-motor coordination, Flight control, Aerodynamic Constraints

1 INTRODUCTION

Echolocating bats generate high-frequency calls to sense their surroundings and coordinate rapid motor responses. Because call production, respiration, and wing motion all share biomechanical and physiological pathways, it has long been presumed that these systems operate in synchrony, particularly during flight. Classic studies demonstrated a tight coupling between wingbeat and respiratory cycles, suggesting that echolocation calls—expelled on the wingbeat-associated expiratory pulse—may be inherently bound to the mechanics of flight [1].

This presumed synchrony forms the basis for a commonly held belief: that coupling echolocation calls with wingbeats confers energetic efficiency. Specifically, it is assumed that vocal production, piggybacking on the thoracic mechanics of flapping, reduces metabolic cost while maintaining effective sonar output [2]. However, recent work challenges the universality and

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functional necessity of this synchrony. Across multiple species and behavioural contexts, studies have now observed deviations from wingbeat–call coupling, particularly at high call rates or during specific phases of behaviour such as prey pursuit or target approach.

SUMMARY. Bats navigate the world by emitting high-frequency calls and listening for echoes that reveal their surroundings—an ability crucial for tracking fast-moving prey and avoiding obstacles in flight. For this system to work, each call must be precisely timed so that the returning echo can be heard and processed before the next call is sent. While it was long believed that bats synchronise their call timing with their wingbeats to maximise efficiency, I now know this synchrony is not always maintained—and, in fact, breaking it is essential for a successful hunt.

In this study, I investigate why bats must sometimes decouple their wing motion from call production. By combining field data with mathematical modelling, I show that strict call–wing synchrony only works when sensory demands are low. As bats approach prey or navigate unpredictable environments, the window for echo processing shrinks and the need for rapid information updates intensifies. Under these conditions, I find that bats are forced to prioritise the timing of their calls—even if that means calling out of sync with their wingbeats.

My simulations and analysis reveal that this asynchrony is not a sign of failure, but rather an adaptive strategy that allows bats to maintain the split-second timing needed for successful hunting and navigation. The model explains how bats flexibly adjust their wingbeat speed or amplitude to keep up with the demands of the environment, but inevitably reach a point where only asynchrony can maintain precise echo-guided behaviour. Factors like wind, air resistance, and sudden prey movement further challenge the system, making timing—not rhythm—the critical factor.

This work shows that bats' ability to break synchrony is a smart, evolved solution to the challenges of rapid, real-world sensing. It helps us understand why echolocation is so effective, and provides new directions for studying how animals adapt their movements and timing in complex and changing environments.

For example, Wong and Waters (2001) [3] found that in *Eptesicus fuscus*, calls were often synchronised with the upstroke phase of the wingbeat during cruising flight, but this relationship weakened during feeding buzzes. Stidsholt et al. (2021) [4] further demonstrated that wild bats briefly decouple sound production from wingbeat in cluttered environments, where more flexible call timing improves echo reception. Similarly, Xia et al. (2022) [5] showed that while wingbeat–call coupling is common at low duty cycles, it breaks down in flight phases requiring increased call rates, revealing phase flexibility and call insertion at non-expiratory phases.

Most notably, Jakobsen et al. (2025) [6] analysed the echolocation behaviour of aerial hawking vespertilionid bats and showed that call rate closely tracks target approach velocity—independent of the respiratory or wingbeat rhythm. The bats modulate their call timing in a way that preserves a constant sensory update rate per unit distance travelled. However, Jakobsen et al. (2025) [6] propose that bats exhibit a dual convergence in their sonar sampling—preserving both a constant distance per call and a stable time window to traverse their sonar range by modulating call rate in direct proportion to velocity. I examine their dual-convergence claim under the framework presented here and draw comparision between the results

to show that temporal precision emerges as the principal axis of adaptation, with spatial parameters flexibly modulated according to task demands, environmental context, and behavioural strategy. My field data show that source level does not co-vary with distance per call, and that bats do not appear to compensate acoustically for speed-related changes in spatial sampling.

Together, these studies reveal that although synchrony between call emission and wingbeat is prevalent in many contexts, it is neither obligatory nor consistent. A key commonality among them is that synchrony breaks down when call rates exceed a certain threshold—a point at which sensory demands appear to override the mechanical and energetic constraints of coupling.

Yet despite this evident pattern in results from the studies, a unifying explanation has remained elusive. Existing interpretations often treat decoupling as incidental or adaptive in narrow ecological niches, without offering a generalised account of *why* the breakdown occurs or *what principles govern its emergence*. In particular, no current framework quantitatively links the breakdown of synchrony to the need for preserving temporal fidelity in sensory processing.

The prevailing explanation appeals to energetic efficiency [1]. Synchronising call emission to the wingbeat makes intuitive sense, given the role of pectoral muscles in both vocal and locomotor systems. However, the fact that synchrony fails precisely when duty cycles are high and call rates increase—and yet the echolocation system continues to function effectively—challenges the sufficiency of this energetic explanation. Successful prey interception without synchrony casts doubt on the assumption that synchrony is necessary or even optimal for biosonar function.

This invites a reinterpretation: synchrony at low duty cycles and low call rates may not be functionally enforced, but merely serendipitous—a by-product of mechanical or physiological convenience, not behavioural necessity. When timing constraints tighten, as during pursuit or target localisation, informational demands override energetic preferences.

Thus, the breakdown of synchrony is not a failure of coordination, but an active switch in priority: from energy-saving rhythmicity to temporally precise sensing. This insight forms the basis for the theoretical framework presented here, in which I formalise the conditions under which asynchrony becomes essential, using the timing relationships derived from my responsivity framework [7] and the biomechanical constraints of flapping flight.

I build on this reinterpretation by providing a generalised, mechanistic model that unites empirical observations from field and laboratory studies under a common theoretical framework. By integrating mathematical modelling, high-resolution field data, and comparative analyses, I show that strict temporal precision in the call–echo loop is not merely a feature, but a fundamental constraint that governs bat echolocation behaviour. In my results, this temporal constraint explains not only when and why synchrony with the wingbeat is relinquished, but also how bats flexibly and adaptively modulate motor output to preserve sensory integrity across a range of ecological scenarios.

Through simulation and data analysis, I demonstrate that wingbeat–call synchrony is maintained only so long as it does not conflict with the overriding need for precise sensory updating. When the timing demands imposed by echo delay, target approach velocity, or environmental unpredictability outpace the mechanical possibilities of rhythmic coupling, asynchrony emerges as a mathematically necessary solution (see Figure 1). This shift can be viewed as an adaptive reordering of priorities, with timing precision as the principal axis of control. My framework thus establishes the breakdown of synchrony as an inevitable and predictable response to closed-loop sensory–motor demands, offering a new lens for interpreting flexibility and diversity in bat

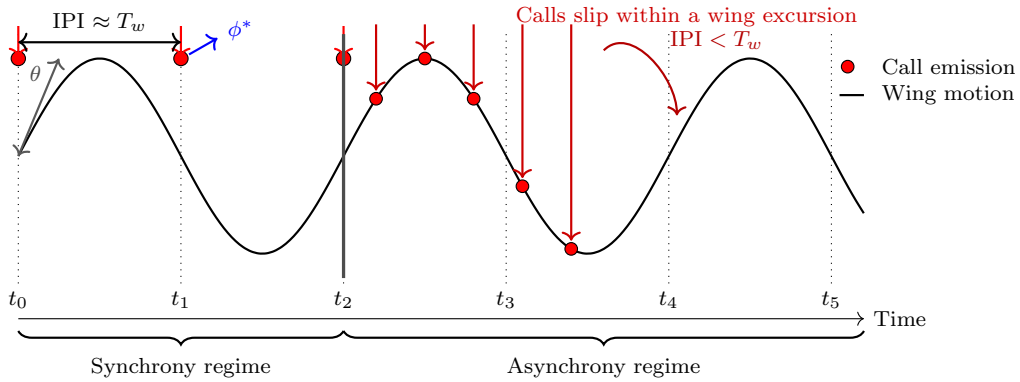


Figure 1: Schematic illustration of the transition from wingbeat–call synchrony to asynchrony in echolocating bats. The sine wave depicts wing motion over time, with red dots marking call emissions. In the *synchrony regime* (t_0–t_2), calls are phase-synched to a point in the wingbeat cycle (IPI $\approx T_w$). As echo-processing demands rise, the interpulse interval (IPI) becomes shorter than the wingbeat period (T_w), initiating the *asynchrony regime* (t_2–t_5) where calls slip in phase and are no longer strictly tied to the wingbeat. The schematic demonstrates that synchrony is only possible when timing constraints are met; as demand increases, asynchrony emerges as a necessary, adaptive solution for maintaining temporal precision.

biosonar behaviour.

2 METHODS

2.1 Call Data Analyses

The field data analyses and the computational simulation and in this study build directly on the methods and codebase established in my previous work [7], where the primary simulation tool, informally named *Vespertillio numeralis*, was developed and validated.

Field data consisted of synchronised four-channel microphone array recordings in natural settings, with bat trajectories localised by time-difference-of-arrival (TDoA) analyses [8, 9]. Custom MATLAB classes and scripts were developed to process the recordings to extract bat positions, call timings, sound levels, and all other call parameters. The distances, velocities, and interpulse intervals (IPIs) were calculated using call sequence timestamps and 3D positions. For the plots shown in Figure 2, the time intervals were derived from measured velocity and distance data, while call rate was computed directly from call event timestamps. Full experimental and analytical details can be found in [7]. Further, I analysed the calls for duration and source level paramters. I calcualted the duration for 95% call energy relative to 20μPa. The true source level calculations included corrections for attenuation as follows.

2.1.1 Calculation of Source Level

To estimate the true source level (SL) of each call, I corrected the received signal at the microphone array for both geometric spreading and frequency-dependent atmospheric attenuation, following established procedures (cf. Bass et al. (1995)) [10, 11]. The process comprised the following steps:

- **Atmospheric attenuation:** I first calculated the attenuation coefficient (α, in dB/m) using the Bass et al. (1995) [10, 11] approximation, which incorporates temperature (T_C), relative humidity (h), atmospheric pressure (P), and signal frequency (f). This method

computes the relaxation frequencies for oxygen (fr_O) and nitrogen (fr_N), and applies their respective terms to yield the total attenuation:

$$\alpha = 8.686\, f^2 \left[1.84 \times 10^{-11} P^{-1} \sqrt{T_K} + \frac{0.01275 \exp(-2239.1/T_K)}{fr_O + f^2/fr_O} + \frac{0.1068 \exp(-3352/T_K)}{fr_N + f^2/fr_N}\right]$$

where $T_K = T_C + 273.15$ is the temperature in Kelvin.

- **Transmission loss:** The total transmission loss (TL_{total}, in dB) was computed as the sum of spherical spreading loss and atmospheric attenuation:

$$TL_{\text{spherical}} = 20 \log_{10} \left(\frac{d}{d_{\text{ref}}}\right)$$

$$TL_{\text{attenuation}} = \alpha \cdot (d - d_{\text{ref}})$$

$$TL_{\text{total}} = TL_{\text{spherical}} + TL_{\text{attenuation}}$$

where d is the distance from the bat to the reference microphone, and d_{ref} is the reference distance (typically 0.1 m).

- **Source level estimation:** For each call, the received level at the microphone was corrected for TL_{total} to yield the estimated source level (SL) at 10 cm from the bat:

$$SL_{10\,\text{cm}} = RL_{\text{mic}} + TL_{\text{total}} \tag{1}$$

where RL_{mic} is the measured received level at the microphone, and all levels are referenced to 20 μPa.

This approach allowed me to compare call intensities across different distances and environmental conditions, accounting for both geometric and atmospheric propagation losses.

In the present work, I extended the simulation framework of [7] by implementing the theoretical model described in Section 2.2. This enhancement enabled me to simulate not only the spatiotemporal structure of call sequences, but also the mechanistic coordination (or breakdown thereof) between call emission and wingbeat motion, as described in Section 2.3.1. Each simulation run was parameterised as described below, and outputs included both call sequence metrics and wingbeat synchrony calculations.

2.2 Theoretical Framework

2.2.1 Overview

The moment-to-moment behavioural decisions in active echolocation tasks depend on the precise control of the sonar parameters. A defining feature of this sensory modality is its temporal structure: calls must be precisely timed to allow echoes to return and be processed before a subsequent call is issued. This requirement for precision was the central theme of my earlier responsivity model [7], which revealed that the capacity for echolocation-based action is constrained by the time taken to receive and respond to echo information.

In that framework, each call event is modelled as a temporal segment comprising four components:

$$[t_i, t_{i+1}, \ldots, t_N] = \sum_{n=1}^{N} [T_a, T_p, T_r, T_l]_n \tag{2}$$

where T_a is the echo delay, T_p is neural processing time, T_r is the reaction time, and T_l is an optional lag. This formulation treats call timing as a cumulative outcome of response latency components. Other than T_a , all other time delays may be grouped into one termed biological reation time T_b, derived as a k_r multiple of T_a, where k_r is a dimensionless scaling constant representing sensory-motor demands, defined by Umadi & Firzlaff [7].

The theoretcial curve fit to call event series–with ever descreasing intervals as the target nears–is a hyperbola of the form $y = a/(x + b)$, which follows a hyperbolic inverse relationship between the call rate and event intervals.

2.2.2 Timing Constraints in Echolocation

Let $d(t)$ be the instantaneous distance to the target, Δs is the distance travelled by the bat before the onset of echo reception, and c the speed of sound. The echo delay is given by:

$$T_a(t) = \frac{2d(t) - \Delta s}{c} \tag{3}$$

After emitting a call, the bat must wait for the echo to return (T_a), and also allow sufficient time for neural processing, motor reaction, and any additional decision lag—together defined as the biological reaction time, T_b. Thus, the minimal time interval between successive calls, or the interpulse interval (T_c), is constrained by:

$$T_c(t) \geq T_a(t) + T_b(t) \tag{4}$$

where

$$T_b(t) = T_p + T_r + T_l \tag{5}$$

with T_p as neural processing time, T_r as motor reaction time, and T_l as an optional lag.

Alternatively, using the dimensionless biological reaction constant, or responsivity parameter, k_r (with $k_r \in \mathbb{R}^+$)) to scale the echo delay, we can write:

$$T_c(t) = k_r \cdot T_a(t) \tag{6}$$

where k_r encompasses the cumulative sensory–motor and decision demands required for effective echo processing and response [7].

2.2.3 Wingbeat Frequency, Velocity, and Distance per Wingbeat

Let $f_w(t)$ denote the wingbeat frequency and $v(t)$ the bat's instantaneous velocity relative to the target. The *distance travelled per wingbeat*, denoted $\lambda(t)$, is defined as:

$$\lambda(t) = \frac{v(t)}{f_w(t)} \tag{7}$$

where $v(t)$ may reflect either airspeed or ground-relative velocity, depending on experimental context.

This parameter, $\lambda(t)$, quantifies how far the bat moves during each wingbeat cycle, and thus sets the spatial interval between consecutive echo updates. To satisfy the echo processing and sensory–motor timing constraints described above, $\lambda(t)$ must not exceed a context-dependent maximum:

$$\lambda(t) \leq \lambda_{\max}(T_a(t), k_r) \tag{8}$$

where $\lambda_{\max}$ is determined by the echo delay $T_a(t)$ and the responsivity parameter k_r.

It is important to note that bats are not limited to executing full 2π angular excursions with each wingbeat. Instead, they may increase wingbeat frequency not only by accelerating flapping rate, but also by reducing angular excursion—allowing for finer control of $\lambda(t)$ and the temporal spacing of echo updates, without a proportional increase in energetic cost or aerodynamic thrust. This motoric flexibility enables bats to maintain temporally precise sampling even under rapidly changing sensory demands.

2.2.4 Decoupling Threshold

A central question in the wingbeat–call coordination problem is: *What is the minimum wingbeat frequency necessary to maintain strict synchrony with call emission, given the sensory–motor timing constraints of echolocation?* The answer emerges naturally from the temporal requirements of the call–echo–response loop.

I formalise this constraint by considering the sequence of events necessary for closed-loop control. Each call event must allow enough time for (i) the outgoing call to reach a target and return as an echo (T_a), (ii) neural processing (T_p), and (iii) the motor reaction necessary to adjust the next call or movement. The temporal budget for these operations, relative to the echo delay, when scaled by responsivity parameter k_r accounts for behavioural flexibility and reaction window.

For a bat to maintain perfect synchrony—i.e., one call per wingbeat—the interval between calls (T_c) must match the wingbeat period, so that $T_c = 1/f_w$. However, the bat must also respect the sensory–motor timing constraint:

$$T_c + T_p \leq k_r \cdot T_a(t) \tag{9}$$

which ensures that enough time is allotted for echo arrival and subsequent processing before the next call is emitted.

Rearranging this constraint, I derive the *minimum wingbeat frequency* necessary for synchrony as:

$$f^*_{w,\min}(t) = \frac{1}{k_r \cdot T_a(t) - T_p} \tag{10}$$

This value defines the lower bound: the wingbeat frequency must be *at least* as high as $f^*_{w,\min}(t)$ for the bat to emit each call in perfect alignment with a wingbeat cycle.

If the actual wingbeat frequency $f_w(t)$ falls below this threshold, the interval between wingbeats becomes too long to accommodate both the echo delay and the required processing time. As a result, strict synchrony cannot be maintained without violating the closed-loop sensory–motor requirement. Under these circumstances, the bat is forced to decouple call emission from the

wingbeat cycle—that is, it must emit calls asynchronously, inserting additional calls between wingbeats or at arbitrary phases within the wingbeat cycle (see Figure 1).

This decoupling threshold is not simply a theoretical artifact, but reflects a biologically meaningful boundary imposed by physics and neurobiology. As the bat accelerates towards a target (shortening T_a), or as behavioural demands for temporal precision increase (raising k_r), the minimum required wingbeat frequency for synchrony increases. Once this frequency surpasses the biomechanical or physiological capacity of the bat's flight system, the animal must switch to an asynchronous regime to preserve sensory precision.

Thus, the decoupling threshold formalised by $f^*_{w,\min}(t)$ marks the critical transition point between rhythmic coupling and the flexible emission strategy that characterises high-demand echolocation behaviour. This threshold predicts—both mathematically and biologically—when asynchrony is not just observed, but fundamentally necessary for biosonar performance.

2.2.5 Environmental Influence on Wingbeat Capacity

External factors such as wind speed $v_{\text{wind}}(t)$ alter the bat's effective airspeed:

$$v_{\text{air}}(t) = v_{\text{bat}}(t) - v_{\text{wind}}(t) \tag{11}$$

This modifies the aerodynamic load, which in turn constrains the bat's ability to achieve the necessary $f_w(t)$. The net acceleration becomes:

$$a(t) = \frac{F_{\text{thrust}}(t) - F_{\text{drag}}(v_{\text{air}}(t))}{m} \tag{12}$$

where drag force scales as:

$$F_{\text{drag}} \propto v_{\text{air}}(t)^2 \tag{13}$$

Increased aerodynamic load may reduce the bat's capacity to increase $f_w(t)$ via either flapping rate or amplitude modulation, thereby making synchrony unfeasible under certain conditions.

2.2.6 Decision Rule for Wing Modulation

Operationally, assuming the bat seeks to maintain synchrony by modulating its wingbeat frequency, amplitude, or posture in order to keep the distance per wingbeat, $\lambda(t)$, within permissible bounds, i.e. $\lambda(t) \leq \lambda_{\max}$. If, despite these adjustments, the overall timing constraint cannot be met, the system must prioritise call timing over rhythmic coordination. This decision can be formalised as:

$$\text{if } T_c(t) + T_p > T_b(t) \Rightarrow \text{decouple call from wingbeat} \tag{14}$$

where $T_c(t)$ is the inter-call interval and $T_b(t)$ is the remaining biological reaction window. This rule formalises the adaptive switch: when flight mechanics alone cannot preserve the temporal precision required for echo-guided behaviour, the animal breaks synchrony, allowing calls to be issued independently of the wingbeat cycle in order to maintain sensory integrity.

2.2.7 Mathematical Proof of Necessary Asynchrony

The previous sections establish that synchrony between wingbeat and call emission is only feasible when the wingbeat frequency meets or exceeds a task-specific minimum, determined by the

sensory–motor timing constraints. Here, I formalise this principle and prove that asynchrony must arise when these constraints cannot be met.

Assume, for the sake of argument, that the system operates in perfect synchrony—each call is emitted precisely once per wingbeat. In this scenario, the call interval is governed by the wingbeat period:

$$T_c(t) = \frac{1}{f_w(t)} \tag{15}$$

The critical timing constraint demands that the sum of this call interval and any neural processing delay T_p does not exceed the biologically permissible response window, which scales with echo delay as $k_r \cdot T_a(t)$:

$$T_c(t) + T_p \leq k_r \cdot T_a(t) \tag{16}$$

Rearranging this yields the minimum wingbeat frequency required for synchrony:

$$f_w(t) \geq \frac{1}{k_r \cdot T_a(t) - T_p} \tag{17}$$

If the actual physiological or biomechanical capacity of the bat restricts $f_w(t)$ below this minimum, the synchrony condition is violated. In that event, to ensure that each call is timed to allow for complete echo processing and sensory–motor integration, the bat must decouple call emission from wingbeat rhythm:

$$T_c(t) < \frac{1}{f_w(t)} \implies \text{Call emission and wingbeat are asynchronous.} \tag{18}$$

Thus, asynchrony is mathematically inevitable solution imposed by the constraints of sensory–motor processing and flight mechanics. This proof clarifies that the observed breakdown of synchrony in high-demand phases of echolocation is not simply adaptive, but a necessary feature dictated by first principles.

2.2.8 Phase Model of Call Emission

To further refine the model, I consider the phase $\phi(t) \in [0, 2\pi]$ of the wingbeat cycle at which a call is emitted. Assuming the angular excursion is modulated, not all wingbeats traverse the full 2π range. Define the normalised phase velocity as:

$$\omega(t) = \theta(t) \cdot f_w(t) \tag{19}$$

where $\theta(t)$ is the angular range of the current wingbeat.

I define the expected call phase as:

$$\phi^*(t) = \omega(t) \cdot (T_b(t) - T_p - T_d(t)) \tag{20}$$

where $T_d(t)$ is the call duration, which shortens as the bat approaches the target [7], freeing more of the timing budget for motor adjustments.

If $\phi^*(t) > \theta(t)$, then the call emission falls outside the biomechanical bounds of the current wingbeat, and thus requires asynchronous insertion:

$$\phi^*(t) > \theta(t) \Rightarrow \text{Call is emitted asynchronously} \tag{21}$$

The wingbeat phase corresponding to the call emission may thus be derived from:

$$\phi(t) = \theta(t) \cdot f_w(t) \cdot \left(k_r \cdot \frac{2d(t) - v(t) \cdot T_d(t)}{c} - T_p - T_d(t) \right) \tag{22}$$

This relationship enables computation of the exact wingbeat phase of call emission given the bat's relative position and velocity to the target, its kinematic parameters, and acoustic timing constraints. This relationship may serve as a tool for decoding wing–call coordination strategies from behavioural data in future studies.

2.2.9 Model Implications and Predictions

The theoretical framework developed here yields several important, testable predictions about the interplay between wingbeat dynamics and echolocation call timing in flying bats:

1. **Synchrony Breakdown with Decreasing Target Distance:** As the bat closes in on a target ($d(t) \to 0$), the echo delay $T_a(t)$ shortens rapidly. According to my model, the minimum feasible wingbeat frequency required to preserve synchrony rises sharply under these conditions, quickly outpacing the bat's physiological capacity. Consequently, strict coupling between call emission and wingbeat becomes impossible, and the bat must adopt an asynchronous regime. This predicts a universal pattern: as bats approach prey, or during the terminal phase of an attack, call emission increasingly decouples from the wingbeat cycle.

2. **Decoupling Under Challenging Flight Conditions:** The requirement for asynchrony is further exacerbated under demanding environmental or behavioural contexts. Situations such as flying in strong wind, at low altitude (where aerodynamic load is elevated), or while executing rapid or complex motor manoeuvres (e.g., sharp turns or sudden accelerations) can limit the achievable wingbeat frequency and/or amplitude. My model predicts that under such conditions, bats will more frequently exhibit call–wingbeat decoupling, as the sensory–motor timing demands can no longer be met within the constraints imposed by biomechanics and aerodynamics.

3. **Aerodynamic Efficiency Modulates the Synchrony Window:** Morphological adaptations that increase aerodynamic efficiency—such as higher aspect ratio wings, lower wing loading, or optimised tip shapes—permit bats to generate higher wingbeat frequencies and maintain effective lift at lower energetic cost. My model therefore predicts that species with such morphological traits can preserve synchrony across a wider range of call rates and behavioural states. Nonetheless, even these species will encounter a threshold where synchrony must be sacrificed in favour of temporal precision, as the sensory–motor system approaches its operational limits.

Taken together, these predictions establish a mechanistic link between temporal precision in echolocation, biomechanical flight constraints, and the emergence of call–wingbeat asynchrony. They provide a conceptual roadmap for future empirical studies: high-speed audio–video recording, 3D kinematic tracking, and onboard telemetry can be used to test these predictions by quantifying the phase relationship between call emission and wingbeat, the temporal evolution

of synchrony during different flight tasks, and interspecific differences linked to wing morphology and flight style. Ultimately, my framework not only unifies previously disparate findings in the literature, but also generates specific, falsifiable hypotheses for experimental investigation in both laboratory and field settings.

2.3 Wingbeat–Call Synchrony Simulation

To systematically explore the capacity and constraints for maintaining synchrony between wingbeats and call emission, I implemented three distinct simulation regimes:

1. *Constant wingbeat frequency (f_w)*: The bat's wingbeat frequency was held constant throughout the simulated approach, set to a nomical cruising frequency. Call emission timing was determined solely by the echo-processing constraint, independent of the wingbeat cycle. Synchrony was deemed possible only when the calculated call insertion phase ($\phi^*(t)$) fell within the biomechanical limits of the fixed wingbeat excursion (θ), and when no more than one call was required per wingbeat cycle.

2. *Dynamic wingbeat frequency*: Here, the bat's wingbeat frequency was allowed to increase in step with the required call rate, up to a physiologically defined maximum ($f_{w,\max}$). Synchrony was maintained by locking call emission to the wingbeat cycle as long as $f_w \leq f_{w,\max}$ and the phase constraint ($\phi^*(t) \leq \theta$) was met. Once the required call rate exceeded this maximum, synchrony necessarily broke down and calls were emitted asynchronously relative to the wingbeat.

3. *Dynamic frequency with adaptive wing excursion (θ)*: Recognising that bats can also modulate the angular excursion of each wingbeat to further increase beat frequency, I implemented a third regime where, upon reaching $f_{w,\max}$, the model allowed the wing excursion angle (θ) to decrease dynamically in proportion to the required increase in frequency, down to a set physiological minimum ($\theta_{\min}$), implying an aerodynamic threshold. This adjustment enabled the simulated bat to maintain synchrony further into the high call rate regime. Synchrony, in this context, was defined as the condition in which (i) a single call could be accommodated per wingbeat, and (ii) the predicted call insertion phase fell within the instantaneous wing excursion limit.

Across all regimes, *synchrony* is thus operationally defined as the temporal and biomechanical alignment of call emission with the wingbeat cycle: a call is synchronous if it occurs within a new wingbeat, at a phase within the instantaneous excursion angle (θ), and at no more than one call per wingbeat. This framework allows explicit identification of when synchrony is lost—either due to echo-processing constraints, biomechanical limitations, or both—and thus enables predictive testing of the hypothesis that asynchrony becomes inevitable as sensory demands intensify.

2.3.1 Simulation Parameters

Each simulation was fully specified by a MATLAB parameter structure, `params`, whose key fields are as follows:

- `bandwidth` [Hz]: Two-element vector $[f_{\min}, f_{\max}]$, the frequency range of simulated FM calls.

- `kr` [dimensionless]: The biological reaction constant (or responsivity coefficient), relating echo delay to the required call emission interval. (See [7])
- `target_distance` [m]: Initial range to the target at the start of the simulation.
- `initial_velocity` [m/s]: The initial approach velocity of the bat relative to the target.
- `initial_call_duration` [s]: Duration of calls at the beginning of the approach.
- `max_call_rate` [Hz]: Maximum call rate, empirical buzz call rate.
- `motile` [logical]: Boolean indicating whether the target is stationary or includes randomised motion (simulating unpredictable prey).
- `makeAudio` [logical]: Option to generate synthetic audio signals (calls and echoes) in the output.
- `f_wing` [Hz]: Baseline wingbeat frequency (used when frequency is fixed).
- `theta` [rad]: Maximum wing excursion angle.
- `min_theta` [rad]: Minimum physiological wing excursion (used in dynamic theta regime).
- `max_wingbeat_freq` [Hz]: Maximum physiological wingbeat frequency.
- `wing_sync_mode` [string]: Simulation regime; either `'fixed'` (constant frequency), or `'dynamic'` (frequency adapts).
- `theta_mode` [string]: Mode for wing excursion; either `'fixed'` (constant excursion) or `'dynamic'` (amplitude adapts to allow higher frequency).

A typical call to the simulation function is as follows:

```
params = struct();
params.bandwidth = [45000, 90000];
params.kr = 5;
params.target_distance = 9; % m
params.max_call_rate = 200;
params.initial_velocity = 2;
params.initial_call_duration = 0.005;
params.f_wing = 5;
params.theta = pi/4;
params.min_theta = 0.3 * params.theta; % lowest wing excursion angle
params.max_wingbeat_freq = 3*params.f_wing;
params.wing_sync_mode = 'dynamic'; % or 'fixed'
params.theta_mode = 'dynamic'; % or 'fixed'
params.motile = true;
params.makeAudio = false;
result = simulateEcholocationWings(params);
```

All simulation outputs described above (including synchrony flags, wingbeat frequency, call phase, and so on) are returned as fields of the output structure `result`.

Parameter Sampling for Comparative Simulations

To further examine how synchrony and asynchrony emerge under different motor control scenarios, I performed a Monte Carlo simulation across a range of biologically plausible parameter combinations. For each of the three simulation conditions—(i) fixed wingbeat frequency and excursion, (ii) dynamic wingbeat frequency with fixed excursion, and (iii) dynamic wingbeat frequency and excursion—I generated 200 independent simulation runs with randomly sampled input parameters and a simulated motile prey that randomly shifted in position within ± 0.1 m. The initial target distance was drawn uniformly between 10 and 15 metres, initial flight velocity between 2 and 5 m/s, and responsivity coefficient k_r between 3 and 7. The initial wingbeat frequency was randomly selected between 3 and 7 Hz, and the maximum excursion angle θ was sampled between $\pi/6$ and $\pi/4$ radians. To account for biologically realistic modulation of wingbeat properties, the maximum wingbeat frequency was set as a multiple between 2 and 4 times the baseline frequency, and the minimal excursion amplitude was drawn between 10% and 50% of θ. In each run, all other physiological and acoustic parameters (e.g., sampling frequency, call bandwidth, and call duration) were held constant. This stochastic sampling approach allowed quantification of system behaviour across a wide but biologically relevant parameter space.

3 RESULTS

Analytical Approach and Methodological Rationale

I combined high-resolution field recordings, advanced signal processing, and first-principles mathematical modelling to rigorously evaluate the conditions governing wingbeat–call synchrony in echolocating bats. Using a synchronised four-microphone array, I recorded free-flying bats in the wild, then localised their 3D flight paths using TDOA (time-difference-of-arrival) methods. Custom MATLAB routines extracted call times, durations, intensities, and positions, enabling calculation of instantaneous velocity, interpulse interval (IPI), and distance travelled per call. Call source levels were estimated by correcting received signals for both geometric spreading and atmospheric attenuation using the Bass et al. (1995) [10] approach (see Eq. 1). This methodology allows me to link call timing, intensity, and flight kinematics under naturalistic conditions and to test the predictions of my temporal precision paradigm.

I then implemented a mathematical framework that formalises the constraints imposed by the call–echo–response loop (see Eqs. 2–22). Within this framework, the IPI is dictated by the need to allow each echo to return and be processed before the next call can be safely emitted—a principle encoded by the responsivity parameter k_r [7]. This real-time constraint is hypothesised to underpin all observed patterns in call timing, with synchrony with the wingbeat maintained only as a secondary outcome, not a primary control mechanism.

Field Data Reveal a Universal Temporal Structure

Figure 2 shows the fundamental relationship between call rate and IPI in the field data. Across all trajectories and contexts, the data fit a perfect hyperbolic curve:

$$\mathrm{IPI} = \frac{a}{C_r + b} \tag{23}$$

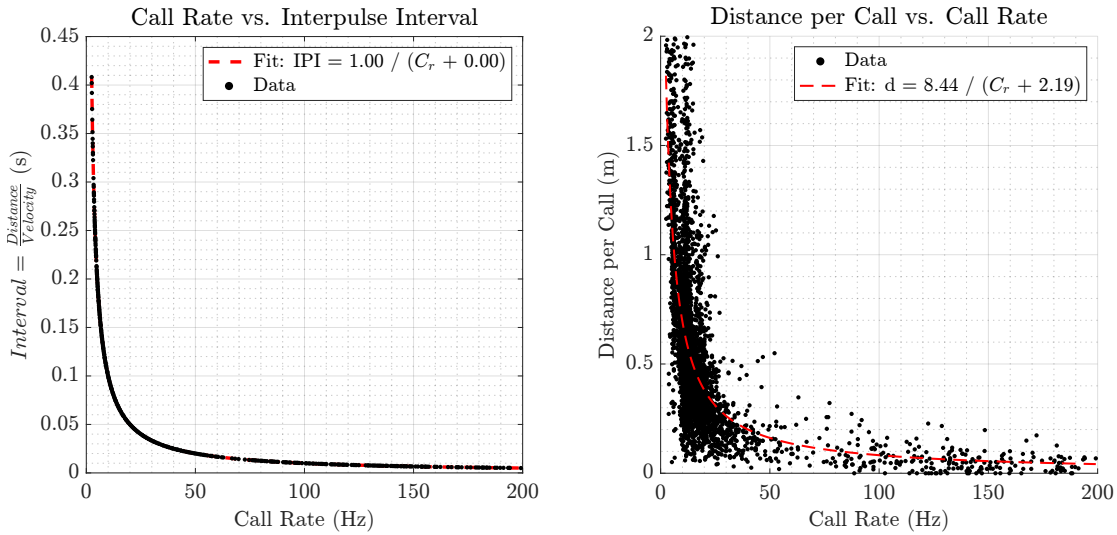


Figure 2: Temporal coordination in free-flying bats. **Left:** Interpulse interval (IPI) plotted against call rate (C_r) reveals a strong hyperbolic relationship, indicating that bats systematically adjust the timing of successive calls based on their acoustic sampling needs and relative motion. **Right:** Distance per call (DPC) also scales inversely with C_r, further supporting the view that bats modulate their flight velocity in coordination with call timing to preserve echo-processing integrity. Together, these plots demonstrate the maintenance of a precise temporal structure in biosonar behaviour, forming the basis for evaluating when and why wingbeat–call synchrony must be broken.

where a is a scaling constant and b a small offset (1 and 0, for the data fit, respectively). This quantitative fit is consistent with the predictions of Eq. 25, and directly reflects the temporal bottleneck imposed by echo delay and reaction time. The right panel of Figure 2 further shows that distance travelled per call also declines hyperbolically with increasing call rate, indicating that bats flexibly adjust their spatial resolution to meet changing sensory–motor demands, rather than maintaining a constant distance or spatial sampling window.

Call Level Analysis Refutes the Sonar Range Paradigm

Figure 3 presents a multi-panel analysis of the relationship between call rate, call level, call duration, and distance covered per call. Although a weak negative correlation exists between call rate and source level (reflecting the known drop in intensity during buzz phases), there is no systematic relationship between call level and distance per call, nor between level and call duration. These results decisively refute the "dual convergence" hypothesis of Jakobsen et al. (2025) [6], which proposes that bats maintain a fixed sonar range by modulating both call rate and intensity in proportion to velocity. Instead, my data demonstrate that temporal precision—not spatial constancy—is the governing principle: as echo delay and reaction time tighten, bats reduce the spatial window per call, while source level modulation remains largely decoupled from flight kinematics (cf. Eq. 1). This supports my central claim that bats flexibly modulate spatial resolution as needed, but preserve strict closed-loop timing at all stages.

Model Captures Sonar Sound Group Formation as an Emergent Pattern

My simulation framework also captures the spontaneous emergence of Sonar Sound Groups (SSGs) as a visible pattern during erratic or unpredictable target motion (Figure 4). Whenever expected echoes fail to arrive within the predicted window—as occurs when prey motion is sudden or unpredictable—the feedback system compresses call timing, producing clusters of closely

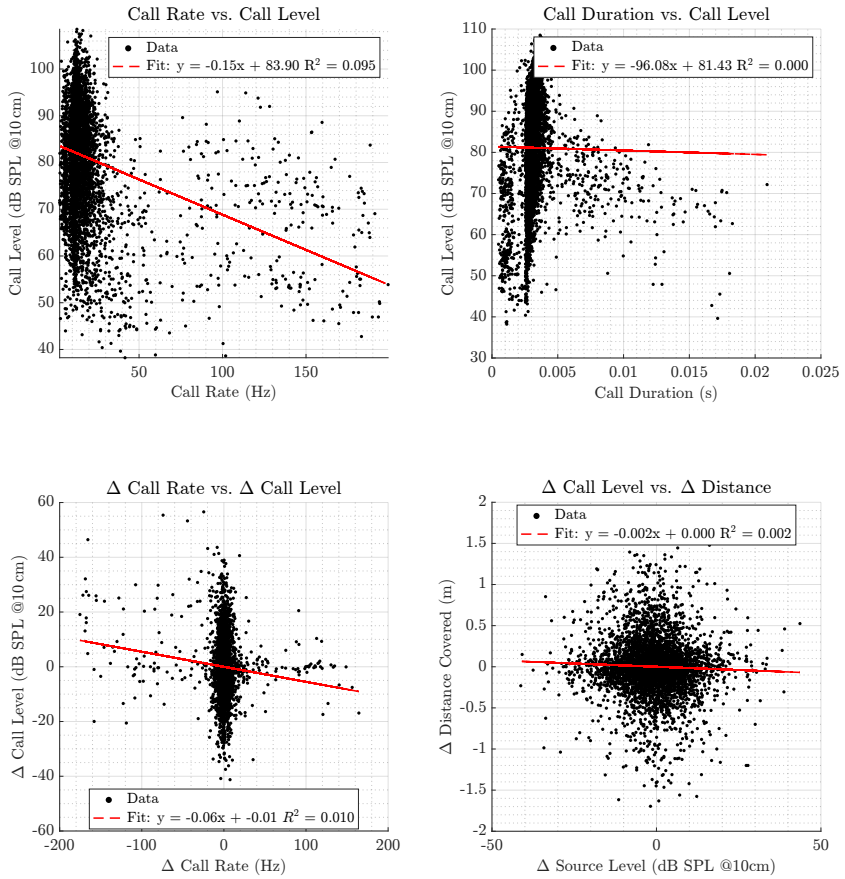


Figure 3: Relationships between echolocation call level, call rate, and call duration. **Top left:** Call level plotted against call rate, showing a weak but significant negative trend whereby higher call rates are associated with slightly reduced call levels. **Top right:** Call level as a function of call duration, showing no significant systematic relationship. **Bottom left:** Change in call level (Δ call level) relative to change in call rate (Δ call rate) across consecutive calls, again showing a weak negative trend. **Bottom right:** Change in distance covered between calls plotted against change in source level, indicating no significant systematic relationship. Together, these plots demonstrate that while bats modulate call rate and level with some degree of coupling, there is substantial variability and no rigid correlation between call level, call duration, and flight progression (also see Figure 2).

spaced calls (SSGs), separated by longer intervals. This context-dependent grouping is not a separate behavioural module, but a natural outcome of the temporal precision requirement, as predicted by the model–the echolocation system striving to maintain call timing at its hyperbolic, closed-loop structure. This resolves longstanding debates on the function and meaning of SSGs: I show they are observable signatures of feedback-driven adaptation, not discrete modules of behaviour.

Simulation Demonstrates Inevitable Asynchrony Under High Demand

To explore the boundaries of synchrony, I conducted simulation experiments under three regimes: (i) constant wingbeat frequency and amplitude, (ii) dynamic frequency with fixed amplitude, and (iii) dynamic frequency with amplitude modulation (see Section 2.3 and Eq. 10). Figures 5c and 6c depict the transition from perfect synchrony (green points) at low call rates, through progressive phase variability, to inevitable asynchrony (orange points) at high call rates. These transitions occur precisely at the critical points predicted by the decoupling threshold (Eq. 10). Allowing both wingbeat frequency and amplitude to adapt can prolong synchrony, but even the most flexible strategy eventually fails as the required call rate surpasses the biomechanical

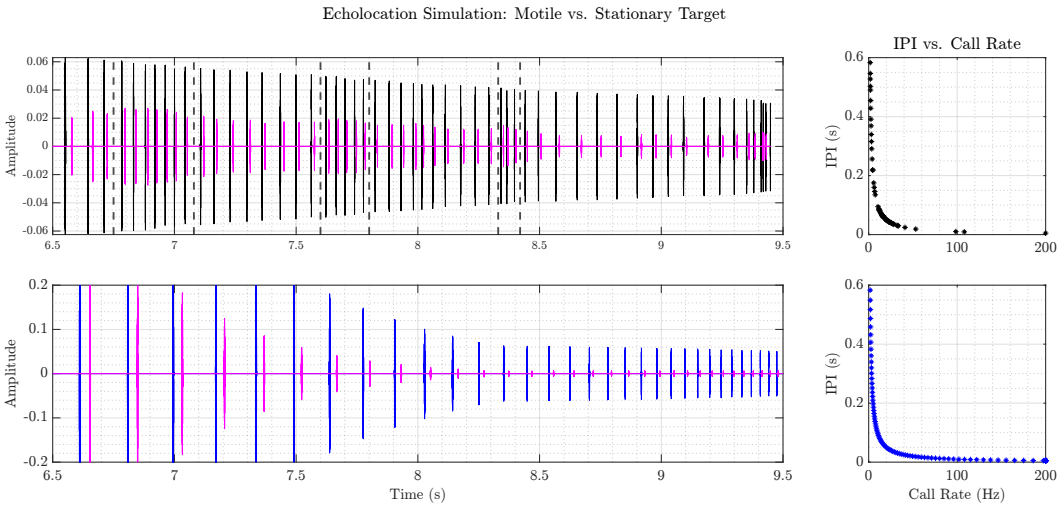


Figure 4: Temporal Spacing of Calls in Sequences Simulated Under Motile and Stationary Target Conditions. Left panels: Example segments of simulated echolocation call sequences as amplitude waveforms (*black and blue*) for a motile target (top) and a stationary target (bottom), respectively. Echoes (*magenta*) are overlaid, and dashed vertical lines indicate the visibly identifiable of Sonar Sound Groups (SSGs), where relevant, emerging in response to erratic target motion. **Right panels:** For each simulation, I plot the corresponding relationship between interpulse interval (IPI, y-axis) and call rate (x-axis). Each data point represents a call event, and the hyperbolic relationship (IPI $\propto 1/C_r$) is clearly preserved in both motile (*top right, black*) and stationary (*bottom right, blue*) target conditions. Despite major differences in target behaviour, the system always maintains the fundamental temporal structure predicted by the closed-loop call event model: every call emission is separated by a minimum interval necessary for echo reception and processing. This robust hyperbolic fit demonstrates that bats' call timing is governed by a strict echo-guided feedback loop, independent of the predictability of the target, and underscores the universality of the call–echo control mechanism across different ecological scenarios.

capacity of the system.

The simulated waveforms (Figure 5c) visualise how synchronous call emission becomes increasingly rare at high sensory–motor demand. The corresponding phase plots (Fig. 6c) reveal how the window for synchrony narrows inexorably, and the system switches from rhythmically coordinated to asynchrony-driven emission. These predictions are in close agreement with recent findings by Xia et al. (2025) [5] and Stidsholt et al. (2021) [4], both of whom report increased asynchrony and phase flexibility during high call rate and cluttered navigation scenarios.

The extended simulations (Figure 7a) further revealed that allowing flexibility in wingbeat frequency and excursion substantially improved synchronisation between call emission and wingbeat phase. When both parameters were held constant, synchronous call placement was limited, resulting in a high number of asynchronous calls per trial (median asynchronous calls: Condition 1). Allowing dynamic adjustment of wingbeat frequency alone (Condition 2) significantly increased the number of synchronous calls while reducing asynchronous emissions (Wilcoxon rank-sum, $p < 10^{-18}$ for all pairwise comparisons). When both frequency and excursion were allowed to adapt dynamically (Condition 3), synchronous call counts further increased with a concomitant reduction in asynchronous calls, indicating near-optimal coordination of call timing.

Additionally, the number of calls emitted per wingbeat also reflected the degree of flexibility permitted. Under fixed wingbeat conditions, the system often produced multiple calls per wingbeat cycle, whereas dynamic frequency and excursion adjustments yielded more consistent patterns of approximately 1.2–2 calls per wingbeat (Figure 7b). This demonstrates that motor control flexibility permits efficient temporal allocation of calls while minimising unnecessary redundancy. However, the simulation with Condition 3 requires high wingbeat frequencies combined with lower excursion angles—a restricting factor that is ultimately constrained by

biomechanical and aerodynamic limits. At such extremes, generating sufficiently high wingbeat frequencies demands increased muscle power output and imposes mechanical strain on the wing structures, while maintaining stable aerodynamic control becomes increasingly challenging. These combined constraints define the upper boundary for synchrony maintenance, beyond which the system must necessarily transition into asynchronous call emission to preserve temporal precision.

Theoretical Framework Unifies Constraints and Predicts Species Differences

By linking the empirical results above to a mathematical proof (Eqs. 17, 18, & 22), I demonstrate that asynchrony is not simply a flexible or "emergent" solution, but a mathematically inevitable one. Once the minimal wingbeat frequency required for synchrony exceeds the bat's biomechanical capacity, asynchrony must arise. The model further predicts that aerodynamic efficiency (e.g., higher aspect ratio wings, lower wing loading) can extend the range of synchrony, but that all species ultimately confront the same fundamental constraint: temporal precision cannot be sacrificed for rhythmic convenience.

Finally, by incorporating morphological and aerodynamic parameters (see Section 2.2.9 and Jones et al. 1994 [12] ; Norberg & Rayner, 1987 [13]), I explain interspecific variation in synchrony flexibility. Species with greater aerodynamic efficiency and flexible flight mechanics can prolong synchrony, but all are governed by the same temporal bottleneck. This predictive, unified framework sets the stage for future comparative studies that integrate kinematic, acoustic, and ecological data.

Taken together, my results reveal that temporal precision is the principal axis of adaptation in bat biosonar. Strict closed-loop echo processing—rather than rhythmic or energetically optimal synchrony—determines when and how bats emit their calls. The temporal paradigm unifies a range of empirical findings, resolves apparent contradictions, and provides specific, falsifiable predictions for future experimental and comparative work.

4 DISCUSSION

Interpretation of the Hyperbolic Relationship between IPI and Call Rate

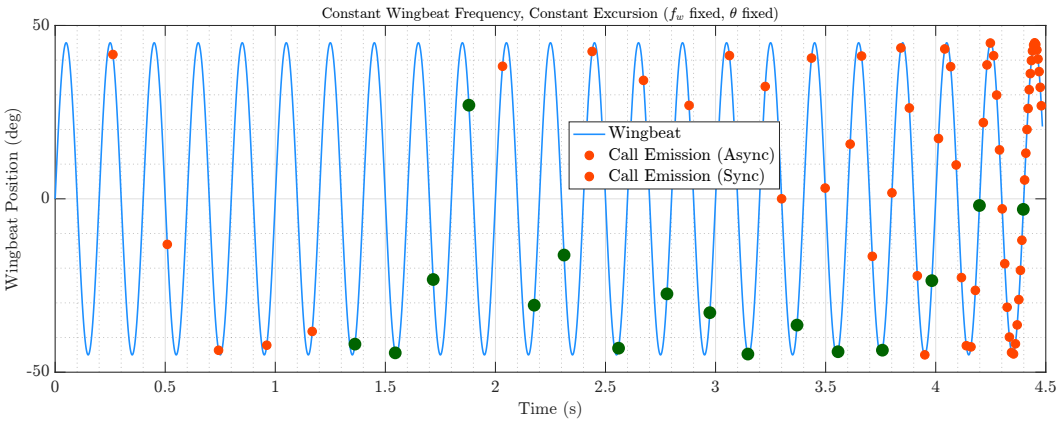
A central prediction of my responsivity and call event models is that the interval between successive echolocation calls—the interpulse interval (IPI)—should scale hyperbolically with call rate (C_r), particularly as bats approach a target or navigate variable environments. Mathematically, this relationship is expressed as:

$$\mathrm{IPI}_n = \frac{\Delta s_n}{v_n} \tag{24}$$

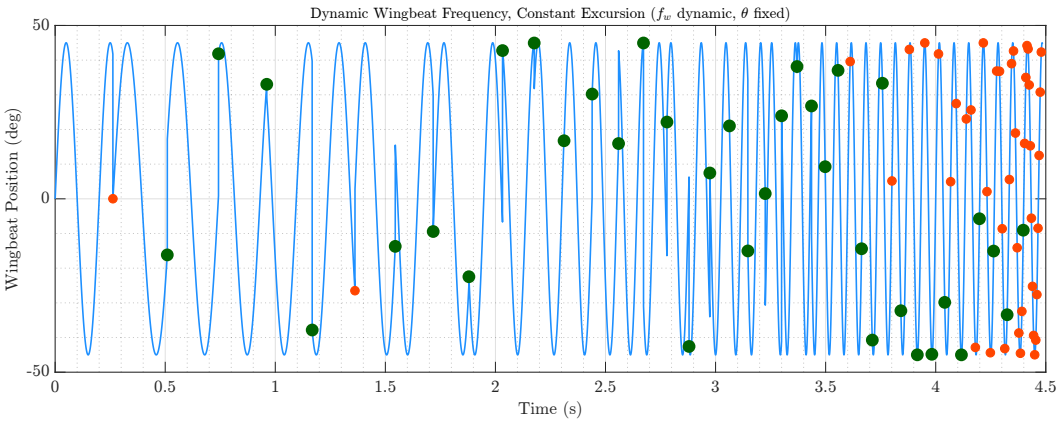
where Δs_n is the distance traversed and v_n is the velocity in the interval between calls n and $n+1$. Given that $C_r = 1/\mathrm{IPI}$, this yields

$$\mathrm{IPI} \propto \frac{1}{C_r} \tag{25}$$

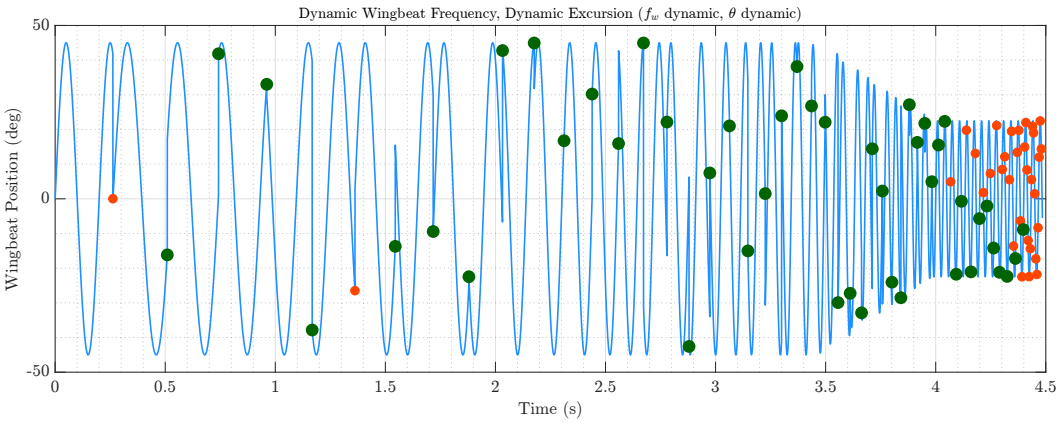
This hyperbolic relationship is not a trivial consequence of movement but emerges from the sensory–motor timing constraints intrinsic to biosonar.



(a) Constant wingbeat frequency and constant excursion.

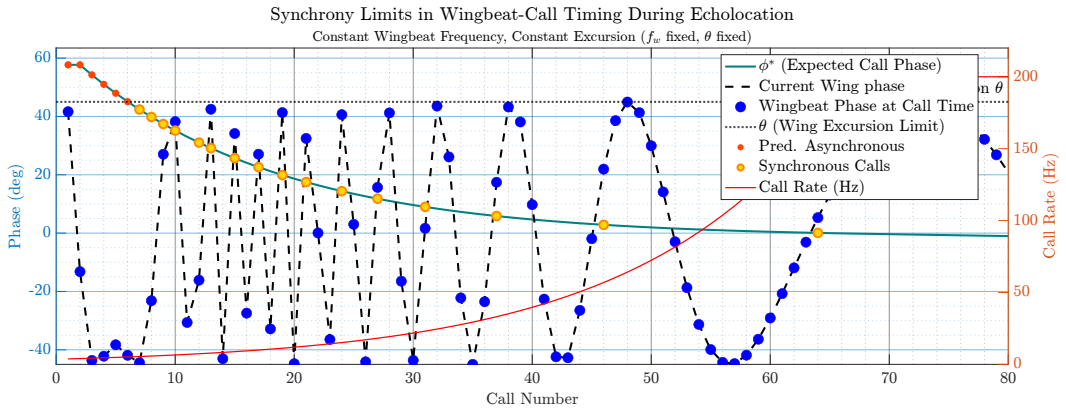


(b) Dynamic wingbeat frequency, constant excursion.

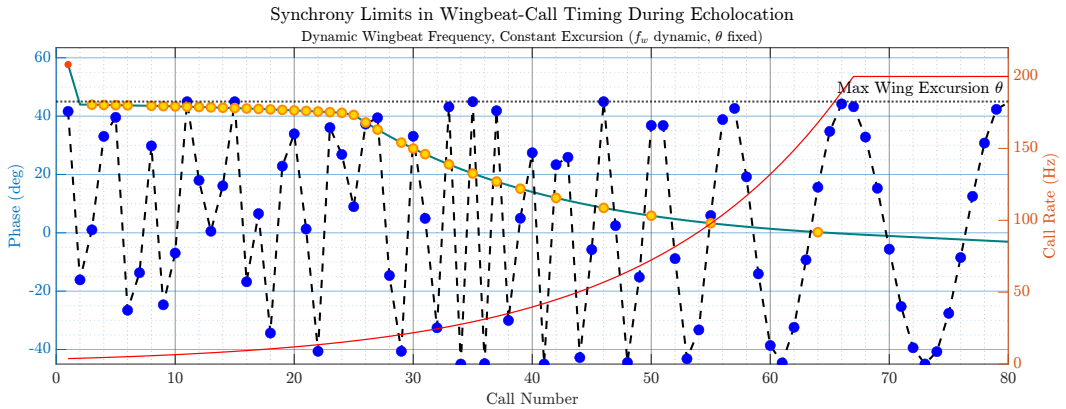


(c) Dynamic wingbeat frequency and dynamic excursion.

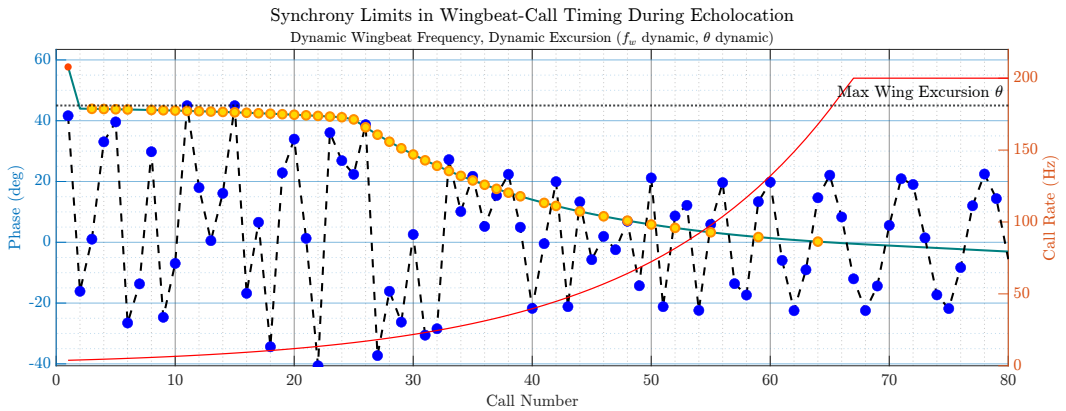
Figure 5: Waveform representations of wingbeat–call synchrony and asynchrony under different motoric strategies. Each panel shows the simulated wingbeat waveform as a function of time, with vertical markers indicating the timing of call emissions. **(A)** With a fixed wingbeat frequency, synchrony between call emission and specific wingbeat phases is maintained only at low call rates; as call rate increases, calls occur at increasingly variable phases. **(B)** When wingbeat frequency is allowed to increase dynamically (up to a maximum), synchrony persists for longer as the bat accelerates its wingbeats to match call timing, but ultimately breaks down as the maximum is reached. **(C)** When both wingbeat frequency and excursion are allowed to adjust, synchrony can be extended, but only within physiological bounds; as call rate surpasses the system's capacity, asynchrony becomes unavoidable and call emission is dissociated from wing movement. These results demonstrate that the maintenance of precise temporal coordination between vocal and flight motor systems is fundamentally constrained by the physical limits of the wingbeat, and that asynchrony is a necessary and predictable outcome under high sensory-motor demand.



(a) Constant wingbeat frequency and constant excursion.



(b) Dynamic wingbeat frequency, constant excursion.



(c) Dynamic wingbeat frequency and dynamic excursion.

Figure 6: Simulation of wingbeat–call synchrony under increasing sensory-motor demand. Each panel shows the evolution of predicted and actual wingbeat–call phase relationships as a simulated bat approaches a stationary target, with call rate and wing kinematics computed from the theoretical framework (see text). **Teal line**: Predicted call insertion phase (ϕ^*) in degrees, representing the optimal phase within the wingbeat cycle for emitting each call, given the current echo delay and response window. **Blue dots on black dashed line**: Actual phase of the wingbeat at the time of each call emission. **Red dots**: Calls that are asynchronous by the phase-only criterion (predicted phase exceeds the current excursion). **Yellow dots**: Calls that are truly synchronous, i.e., occur within a new wingbeat, at a phase within the current excursion, and at no more than one call per wingbeat. **Red line (right axis)**: Call rate profile (Hz), increasing as the bat nears the target. **Horizontal dashed line**: Maximum (or current) wing excursion (θ), serving as the phase limit for synchronous call insertion. (**a**) With fixed wingbeat frequency and fixed excursion, synchrony (green) is possible only at low call rates. As call rate rises, synchrony rapidly breaks down, as wingbeat cannot keep pace with the sensory-motor demand. (**b**) With dynamic wingbeat frequency (but fixed excursion), synchrony persists further into the approach, but is ultimately lost when the physiological limit of wingbeat frequency is reached. (**c**) When both wingbeat frequency and excursion are allowed to adapt (i.e., θ decreases as f_w is capped), synchrony can be maintained the longest. Only when both the frequency and amplitude limits are reached does synchrony become impossible, resulting in a rapid onset of asynchrony. These results illustrate the progressive trade-offs bats may employ to maintain temporal coordination of call emission and wingbeat, and reveal when and why asynchrony becomes inevitable in high call-rate regimes.

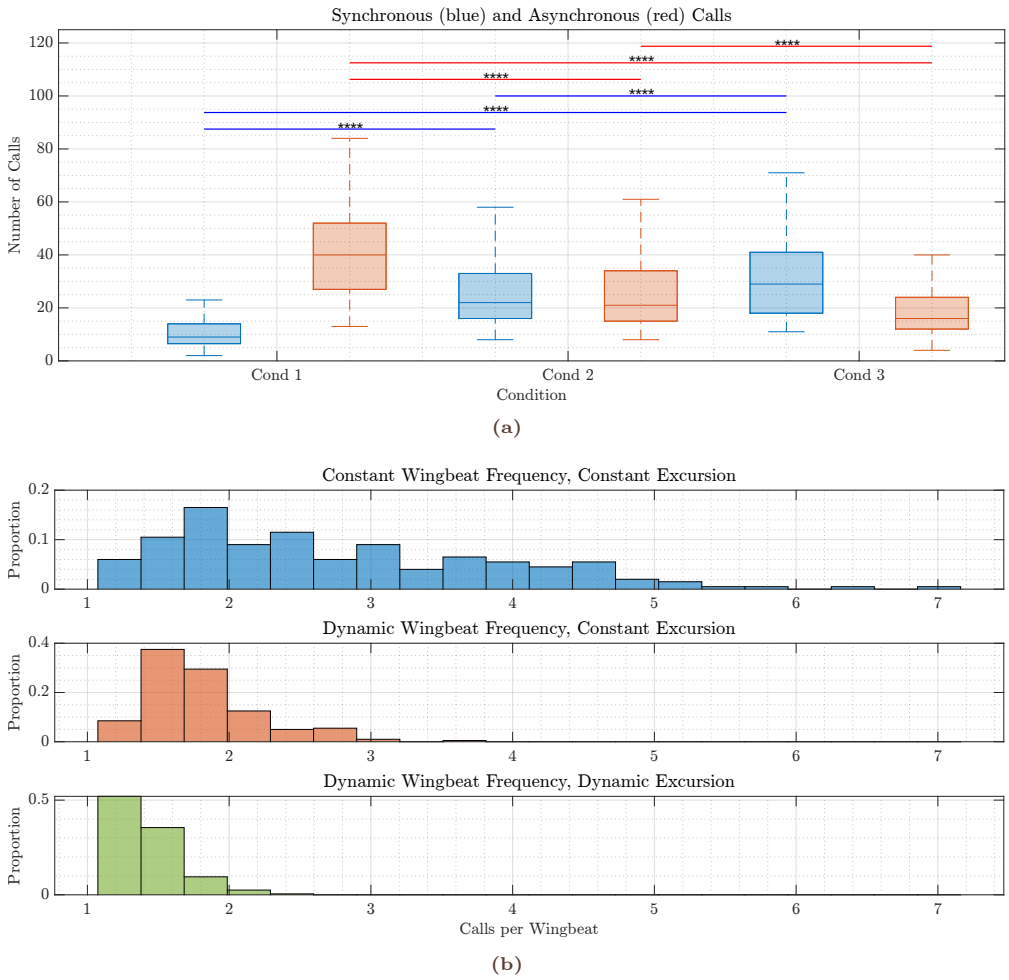


Figure 7: Simulation results (Monte Carlo sampling over parameter space, $n = 200$) demonstrating the effect of motor control flexibility on call timing during echolocation. **(a).** Number of synchronous (blue) and asynchronous (red) calls per simulation run across the three conditions: (Cond 1) fixed wingbeat frequency and excursion, (Cond 2) dynamic wingbeat frequency with fixed excursion, and (Cond 3) dynamic frequency and excursion. Statistical comparisons are indicated (Wilcoxon rank-sum tests). **(b).** Normalised distribution of calls emitted per wingbeat cycle across conditions. With increasing motor control flexibility, call placement stabilises around approximately one call per wingbeat, reflecting improved temporal coordination between call emission and wingbeat phase. The ability to achieve perfect synchrony across all calls is highly contingent on specific combinations of target distance, flight speed, and echo delay; in practice, attaining such synchrony would require near-perfect compensation in both wingbeat timing and excursion amplitude, reflecting a level of motor control that may not always be biologically feasible.

Closed-Loop Behaviour and the Call Event Model My call event model formalises the behavioural imperative that each call must complete a full loop of echo return, neural processing, and motor response before the next emission as described in the call event model, and equation 2

A key insight here is that call emission is dynamically regulated in real time, not periodic or pre-programmed, or random. As the bat nears a target and T_a shortens, the minimum IPI also shrinks, allowing higher call rates; at greater distances, longer echo delays enforce a longer minimum IPI.

Implications of the Hyperbolic Fit The robust hyperbolic fit between IPI and call rate in my field and simulation data is a quantitative hallmark of closed-loop control in echolocation. Each call is triggered only once sufficient time has passed for echo reception and processing—a behaviour at odds with open-loop or strictly rhythmic emission strategies, which would yield constant or linearly changing IPIs. This evidence strongly supports the echo-driven regulation

of call timing predicted by my responsivity framework [7].

Limitations of the Hyperbolic Relationship While the hyperbolic curve robustly signals closed-loop control, it does not, by itself, reveal which echo is used for behavioural guidance in complex environments. In open or controlled lab conditions, the nearest echo typically dominates, but in cluttered or social contexts, bats may flexibly attend to different echoes.

In sum, the hyperbolic IPI–call rate relationship is a robust quantitative signature of closed-loop, echo-guided call timing. It validates the premise that each call emission is governed by echo returns and subsequent sensory–motor integration, while allowing for adaptive flexibility under diverse behavioural demands.

Emergence and Role of Sonar Sound Groups (SSGs) A natural outgrowth of this feedback-driven loop is the appearance of temporally clustered call patterns—Sonar Sound Groups (SSGs) [5, 14, 15]. Rather than being imposed arbitrarily, SSGs emerge from the necessity to rapidly update spatial information in complex, unpredictable environments.

My simulations show that erratic or unpredictable target motion can yield clusters of calls, visible as SSGs in Fig. 4—as a direct consequence of maintaining temporal precision for each call–echo cycle. When the expected echo does not arrive in the anticipated window, the model compensates by increasing call rate, creating bursts (or groups) of calls separated by longer intervals, a pattern matching SSGs reported in field and lab studies [15].

Kothari et al. (2014) [15] documented that *Eptesicus fuscus* increases SSG production in tasks requiring high spatial resolution, such as clutter navigation or tracking erratic prey. The "island" and "stability" SSG criteria—groups of calls with relatively constant intervals flanked by longer pauses—are directly predicted by my model as the animal compresses call timing to maintain feedback. This is evident in simulation runs with erratic target motion (Figure 4), where clusters of closely spaced calls appear as a direct results of temporal adaptations.

Recent findings by Xia et al. (2025) [5] further reinforce this model, showing that SSG formation is a flexible, species-specific behaviour, not a by-product of motor or respiratory limitations. Both *Hipposideros pratti* and *Myotis pilosus* produced a variety of call groupings in cluttered conditions, and the composition and frequency of SSGs reflected both environmental demands and ecological strategy. Critically, the phase coupling between calls and wingbeats is also plastic, adapting to behavioural context—a phenomenon paralleled in my simulations.

Taken together, empirical data and my simulations reveal that SSGs are not discrete modules, but visible patterns that emerge from the underlying demand for temporal precision. In my framework, SSGs are not biologically meaningful categories; rather, they are context-dependent, transient manifestations of ongoing sensorimotor regulation—observable but not essential to classify discretely.

4.1 Call Level, Wingbeat Synchrony, and the Sonar Range Paradigm

In biosonar research, it has been widely hypothesised that producing high-intensity calls is energetically costly and thus tightly coupled to the wingbeat cycle, with the expectation that calls are synchronised to the upstroke when muscular power peaks [1, 2, 4]. Indeed, some studies find higher call levels during the upstroke at low call rates [2]. Yet, evidence from both field and laboratory work indicates this coupling is transient: at high call rates, especially during approach

and buzz phases, bats emit calls at diverse wingbeat phases, and the link between source level and wingbeat phase is lost [1, 4]. Moreover, recent analyses demonstrate that echolocation call production is not as energetically costly as once believed [16, 17].

My field data directly test these theories. Figure 3 shows source level (corrected to 10 cm) as a function of call rate and distance between calls. There is a weak but significant negative trend between call rate and call level—levels decrease as call rate rises, consistent with bats lowering intensity during high-rate buzzes. However, I find no significant correlation between call intensity and distance covered between calls ($R^2 = 0.002$), nor between call level and call duration. These results strongly challenge the hypothesis that bats adjust call level to maintain a fixed sonar range as velocity or call rate changes. Instead, source level modulation is largely decoupled from spatial sampling, being only loosely coordinated with energetic or kinematic demands.

This decoupling is especially relevant to recent claims by Jakobsen et al. (2025) [6], who propose that bats modulate call rate in direct proportion to flight speed, thereby keeping both the distance travelled per call and the time to traverse the sonar range constant—a dual convergence [6]. Their argument, based mainly on laboratory data, is that bats share convergent spatio-temporal sampling strategies.

For Jakobsen et al.'s claim of dual convergence to hold in a natural context, specific interdependencies must exist. If distance per call is to remain constant, then velocity must scale linearly with call rate ($v \propto r$). Meanwhile, if time to traverse the sonar range (R/v) is also to remain constant, then sonar range must scale with velocity. Since sonar range depends on acoustic parameters (source level, directionality, atmospheric attenuation, target strength), this would require bats to increase call intensity or beam focus with increasing flight speed. Moreoever, under identical experimental conditions, trained bats are most likely to converge in the sonar behaviour, and a generalisation can not be drawn in the absence of directly comparable results from experiments in a natural environment. The behavioual flexibility of echolocation could, in fact, be a confounding factor in constrained environment [18]. My field data show that source level does not co-vary with distance per call, and that bats do not appear to compensate acoustically for speed-related changes in spatial sampling. Rather, I find strong evidence for temporal convergence: bats adjust call rate in line with closed-loop theory, with the IPI following a strict hyperbolic decay as call rate rises. This preserves the reaction window necessary for tracking and planning, and supports the primacy of temporal regularity over spatial uniformity. Conversely, the distance travelled per call decreases hyperbolically with call rate (see Figure 2), indicating that bats flexibly modulate spatial resolution in response to behavioural context and velocity. The absence of a relationship between source level and distance per call further undermines the dual convergence proposition.

4.2 Simulation Results: Motor Constraints, Synchrony Limits, and Emergent Asynchrony

To further examine the boundaries of synchrony, we simulated call–wingbeat coordination under varying motoric constraints. As shown in Figures 5c, 6c and the outcomes of the extended Monte Carlo simulation runs in Figure 7, synchrony between call emission and wingbeat is only possible when call rate remains within the biomechanical envelope defined by maximum achievable wingbeat frequency and amplitude. With constant wingbeat frequency and excursion, synchrony is

quickly lost as call rate increases; permitting adaptive changes in wingbeat frequency and excursion extends synchrony but cannot prevent its eventual breakdown as demand intensifies. Even the most flexible motor strategies cannot indefinitely maintain synchrony. Once the limits of the wingbeat are reached, asynchrony becomes inevitable—a predictable adaptation for preserving temporal precision in high-demand situations.

These results generalise and mechanistically underpin empirical findings:

- Synchrony is a convenient by-product of loose coupling under minimal constraint, not a behavioural imperative.
- Adaptive motor strategies can delay but not eliminate the onset of asynchrony at high call rates.
- The breakdown of synchrony is predictable at the intersection of biomechanical and sensory–motor demand.
- The framework unifies observations of synchrony at low rates, SSG emergence at high demand, and context-dependent flexibility across species and tasks.

My simulations and analyses show that bats operate within a temporally precise, closed-loop regime, modulating motor output flexibly. Synchrony is maintained only when compatible with sensory–motor demands, and asynchrony is not a breakdown but an optimisation, prioritising temporal precision when synchrony becomes unattainable.

Finally, while Xia et al. (2025) [5] highlight species-specific flexibility in wingbeat–call synchrony, I interpret this through the lens of morphometric and allometric diversity among bats. Wing structure—proportions, mass, and aerodynamic properties—sets biomechanical constraints that determine the achievable range of synchrony for a given species. Jones et al. (1994) [12] provide evidence that wingbeat frequency and amplitude, as well as the relationship to call emission, are governed by body size and wing morphology, with neither parameter scaling simply with mass or forearm length. The classic ecological morphology synthesis of Norberg & Rayner (1987) [13] further shows that wing shape, loading, and area ratios define aerodynamic performance, flight speed, manoeuvrability, and ecological niche. Species with wings adapted for agility and rapid flight may maintain tighter wingbeat–call coupling, while more generalist species show greater decoupling and flexibility. Thus, the diversity of synchronisation patterns arises from each species' evolutionary solution to the mechanical and ecological trade-offs of their foraging strategy and habitat, and can only be fully understood through an integrated morphometric, biomechanical, and ecological approach.

5 CONCLUSIONS

In summary, the results of my simulation and comparative analysis show that wingbeat–call synchrony is maintained only when it does not compromise temporal integrity of sensory acquisition. When demands on the bat's sensory–motor system rise, as during target approach or obstacle avoidance, the system transitions to a regime where call emission and wing motion are flexibly and independently controlled. This shift is a necessary outcome of the physical and biological constraints inherent in biosonar-guided flight, and must form a general principle applicable across species and ecological contexts.

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COMPTETING INTERESTS

The author declares no competing interests.

DATA AND RESOURCE

The simulation code, experimental data, and analysis scripts will be made available upon publication as required. Requests for access to data and code during the review process may be directed to the author via email.

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