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论文题目：To Hear or Not to Hear: An Evolutionary Question of the Moths' Binary Ear Against Diverse Bat Predators

To Hear or Not to Hear: An Evolutionary Question of the Moths' Binary Ear Against Diverse Bat Predators

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Abstract

To evade bat predation, moths have evolved a simple ear capable of detecting ultrasound. In contrast to the human ear, which performs detailed frequency discrimination, the moth's auditory system consists of only 1–4 receptor cells and cannot differentiate sound sources by frequency. Instead, it operates as a binary sensor that triggers an evasive maneuver whenever a detected ultrasound exceeds a threshold—regardless of whether the source is dangerous or not. Given this constraint, it is compelling to investigate how moths adapt their hearing strategy under different bat communities.

In this study, we develop a mathematical model to simulate moth auditory function and bat–moth interactions. The moth's hearing organ is represented by a gain function comprising two Gaussian modes, capturing its capacity to detect ultrasound signals. Embedded in a probabilistic predation framework, the model relates auditory characteristics to the moth's survival probability. We numerically determine optimal hearing thresholds by identifying parameter combinations that maximize survival.

Our findings indicate that increasing sensitivity in frequency bands used by threatening bats substantially enhances moth survival. Conversely, suppressing sensitivity to non-threatening signals minimizes distractions and conserves sensory resources. Thus, by selectively "deactivating" hearing in specific frequency ranges, moths gain an evolutionary advantage. This study illustrates that in complex auditory environments, "hearing less" can indeed increase survival—a counterintuitive yet highly efficient sensory adaptation.

Keywords: moth auditory system, predator-prey interaction, evolutionary adaptation, optimal hearing, mathematical biology

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1. Introduction

When darkness falls, bats use ultrasound to hunt. As the main prey for bats, some moths have evolved "ears" capable of detecting these ultrasonic waves [1, 2]. These ears help them monitor the presence of bats in their surroundings, allowing them to take evasive action, such as erratic flight or diving to the ground [3, 4].

This perpetual cycle of search (by the bat) and escape (by the moth) represents a classic example of an evolutionary "arms race" between bats and moths. The moth's ear functions as a passive radar system against bat echolocation. A key constraint that moths must adapt to is their inability to support a complex auditory system like that of humans. The human ear contains approximately 25,000 nerve endings, enabling it to perform detailed sound processing such as frequency discrimination [5]. In contrast, the moth's ear is structurally far simpler. Depending on the family, moths have only one to four receptor cells in their ears, making these ears some of the simplest sensory structures in nature [6]. With such a basic auditory device, moths cannot distinguish between high and low frequencies; they merely detect the presence or absence of ultrasound [7]. An intriguing question arises: how does this binary acoustic detection system influence the decision-making process in moths under predation pressure?

The natural environment in which the moth lives is complex. As mentioned in [8], different species of bats use ultrasound of different frequencies to hunt. Moreover, the foraging (觅食) behavior and prey selection are also different among different types of bats. For example, some bats prefer to hunt above the forest canopy (树冠) or in clearings, while others may forage near trees and brush. Some bats prefer to eat moths, and some bats prefer to eat nectar (蜂鸟). This diversity in bat hunting strategies leads to varying predation pressures on different types of moths.

One might think that for a moth's ear, the more sensitive it is, the better it is for its survival. However, this is not necessarily the case. As we mentioned earlier, the moth's ear cannot discriminate frequency. As a result, a moth cannot identify which kind of bat is based on their characteristic ultrasound frequency. To a moth's ear, any detected ultrasound signal triggers a pre-programmed neural response — regardless of whether the source poses a true threat. Consequently, there is a risk that the moth gets over-reactor in the presence of an ultrasound of a bat that is only passing by. This may induce unnecessary stress that is harmful to the well-being of the moth. It was reported that the mere sound of a predator's call can significantly reduce the egg-laying output of certain bird species [9]. Similarly, when a moth perceives bat calls, it may enter a state of panic, wasting precious energy on futile evasive maneuvers. Therefore, a more efficient and sustainable strategy is to selectively tune into the specific frequencies used by their most dangerous predators while ignoring those from other bats or harmless sound sources. This selective hearing helps them to anticipate danger while also conserving energy. This suggests that the evolutionary success of a moth is not just about having the most precise ears, but about having the right ears—ears that are finely tuned to the specific acoustic threats within their unique ecosystem. This exemplifies a fundamental principle of natural selection: "it is not the strongest, nor the most sensitive, but the best-adapted that survives."

In this paper, we employ mathematical modeling to investigate the design principles of the moth ear and its adaptability to different environments. **The central question we aim to answer is: what is the optimal hearing strategy for a moth under different predation scenarios?** To address this, we derived a model for ultrasound propagation and formulated an expression for the survival probability of a moth based on the model assumptions. We then used a grid-search approach to identify the optimal hearing sensitivity pattern and compared the results with experimental data. This study provides insight into the functional rationale behind the moth's auditory system and highlights the intricate co-evolutionary interaction between moths and bats.

The remainder of the paper is organized as follows. Section 2 describes the anatomical structure of the moth ear and its basic ultrasound detection mechanism. In Section 3, a mathematical model is developed to formalize the survival probability of a moth under bat predation, incorporating ultrasound propagation and moth auditory gain. Section 4 presents the numerical optimization results, revealing optimal moth hearing strategies under different predation regimes, along with comparisons to biological data. Finally, Section 5 discusses the ecological and evolutionary implications of the findings and suggests directions for future research.

2. The anatomical structure of moth ears and their ability to pick up ultrasound

2.1. Moth ear structure

As shown in Fig. 1A, the moth studied in this work is Noctuidae. These moths are primarily active at night [10]. They are a major food source for bats [11]. The moth's two ears, which serve as ultrasound detection organs, are located on either side of the body (indicated by black arrows).

After dissecting the moth, one ear was exposed under the microscope for examination. As shown in Fig. 1B, the tympanic membrane consists of two distinct anatomical zones, a very thin, transparent zone (TZ) and a thicker, opaque region known as the conjunctivum (Cj). The attachment site of the auditory receptor organ, which is an elastic shaft, is located at the centre of the transparent zone (OZ, indicated by an arrow). While the overall structure of the tympanic membrane is similar across moth species, the specific shape and size of the TZ and Cj exhibit considerable variation among different types of moths [12].

Similar to the tympanic membrane in the human ear, the moth's tympanic membrane is responsible for converting acoustic signals into mechanical motion of the auditory receptor organ. It responds to ultrasound within the frequency range of 10 kHz to 100 kHz. However, the vibration patterns of the tympanic membrane differ significantly depending on the frequency of the sound stimulus. In an experiment conducted by [4], high-resolution three-dimensional laser Doppler vibrometry was used to reconstruct the motion patterns of the noctuid tympanal system. For the moth species N. pronuba, the results revealed a conjunctivum (Cj)-dominated vibration pattern at lower frequencies at 20 kHz, whereas at higher frequencies like 45 kHz, vibration amplitude decreased in the Cj and became dominated by the transparent zone (TZ). This finding clearly demonstrates that the moth's tympanic membrane possesses complementary vibrational regions specialized for detecting ultrasound across different frequencies.

2.2. The response of the moth ear to ultrasound

The human ear is frequency discriminative, i. e, it can tell whether the sound is low or high. The human ear does so by having a very complicated device called the inner ear. Within it, frequency discrimination is achieved through the precise arrangement of tens of thousands of nerve endings. This process is explained by the travelling wave theory, a foundational concept for which Georg von Békésy was awarded the Nobel Prize in Physiology or Medicine in 1961 [13].

The moth ear, however, lacks this capability. In fact, the moth's auditory system is remarkably simple. Vibrations of the tympanum caused by ultrasound—whether originating from the Cj or the TZ—are transmitted to a pipe-like auditory receptor organ attached to the OZ. As a result, the auditory response of the moth is essentially binary: it either detects ultrasound and initiates an evasive maneuver, or it does not respond at all [14]. By adapting mechanical properties of the tympanum such as its shape, size, and stiffness, the moth's ear can be tuned to enhance sensitivity to high-risk frequency ranges while reducing sensitivity to low-risk ones [4]. Through natural selection, the moth's auditory system has evolved toward an optimal hearing strategy that best fits its specific ecological environment.

Experimentally, the auditory sensitivity of the moth ear can be measured across different ultrasound frequencies. Fig. 2 shows the hearing threshold curves as a function of frequency, where the sound level threshold indicates the minimum intensity required to trigger a neural response. Both curves

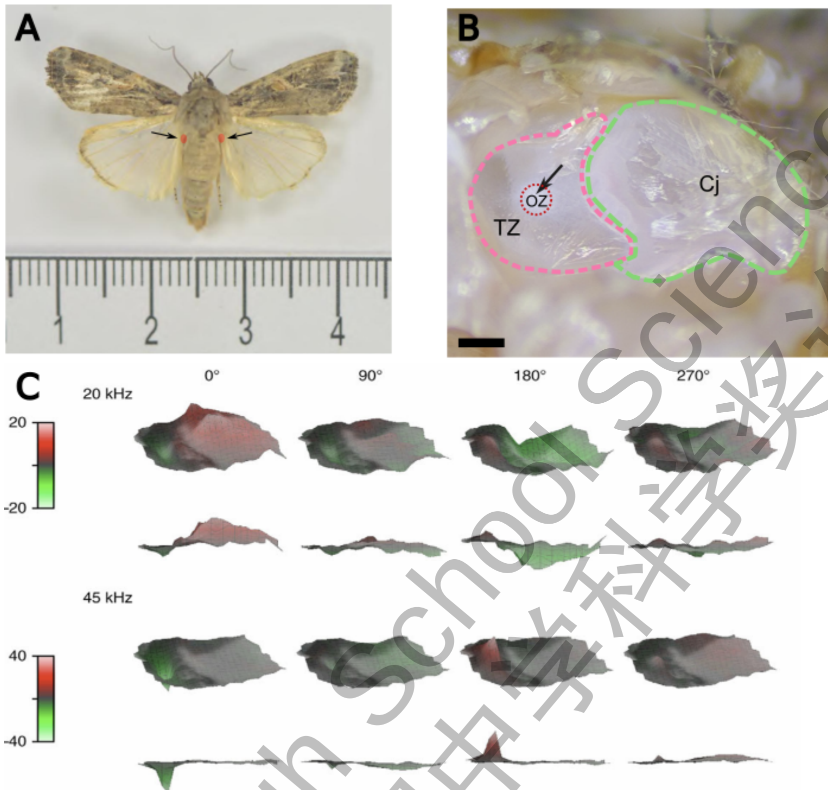

Figure 1: Morphology and functional zones of the moth tympanic ear. (A) Spodoptera frugiperda, a species of the Noctuidae family, with black arrows indicating the bilateral location of its ultrasound-sensitive ears. (Source: [11]) (B) Detailed view of the tympanic membrane, showing the thin, transparent zone (TZ) and the thicker, opaque conjunctivum (Cj). The arrow marks the attachment point of the auditory receptor organ (OZ). (Source: author) (C) High-resolution three-dimensional reconstruction of the laser Doppler vibrometry at 20kHz and 45kHz, respectively. The deflections are shown for four different phases along the oscillation cycle: 0°, 90°, 180°, 270°. (Source: [4]).

correspond to ears of Noctuidae moths from two different habitats. The red dashed curve represents a species found in France [15], while the blue solid curve corresponds to a species from Denmark [3]. The French Noctuidae exhibit the highest sensitivity around 20kHz, with reduced sensitivity at higher frequencies. In contrast, the Danish population displays a bimodal threshold profile, with one sensitivity peak near 30kHz and another around 70kHz.

So why do the threshold curves of the same moth living in different en-

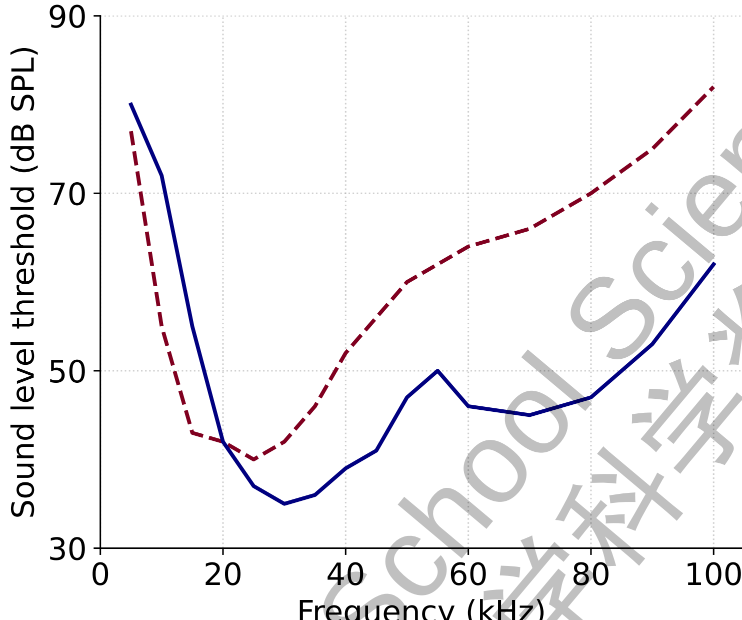

Figure 2: Experimentally measured sound level threshold of Noctuidae moths from two different locations. The dashed red curve represents a species from France (data from [12]), exhibiting the highest sensitivity around 20 kHz. The solid blue curve corresponds to a species from Denmark (data from [13]), showing a bimodal sensitivity profile with peaks near 30 kHz and 70 kHz. The sound level threshold indicates the minimum sound intensity (in dB SPL) required to trigger the neural response of the moth.

vironments look so different? This question is not fully understood yet. We hypothesize that the difference in the hearing threshold curves arises from the predator pressure coming from the environment. The moth exhibiting a single sensitivity peak may inhabit an environment dominated by a single bat species that hunts primarily around 20 kHz. In contrast, the moth with a bimodal auditory profile likely inhabits an environment with a more diverse bat community, where predators employ both low- and high-frequency echolocation calls, thereby driving the evolution of broader auditory sensitivity. Due to the complexity of natural ecosystems, this hypothesis is challenging to validate experimentally. **We therefore use mathematical modeling to test whether environmental predator pressure shapes the frequency sensitivity of the moth's auditory system.**

3. Mathematical modeling

In this section, we propose a mathematical model that relates a moth's hearing ability to its survival probability within different bat communities. This community comprises bat species that employ distinct ultrasound frequencies for hunting and exhibit varied foraging preferences. The model integrates the following three key components:

- Q1: How does the moth's ear pick up the ultrasound signal?
- Q2: How does the ultrasound emitted by bats propagate through the air?
- Q3: What determines the survival probability of a moth during a bat predation event?

3.1. Q1: Ultrasound detection in the moth ear

We propose a simplified model for the moth's auditory system. As illustrated in Fig. 1, we assume that the moth's tympanal membrane can selectively respond to two distinct ultrasound hearing modes: a low-frequency mode peaking at μ_1 and a high-frequency mode peaking at μ_2. Each mode is associated with a gain coefficient $0 \leq g_i \leq 1$ and exhibits a bell-shaped response around its central frequency, with the width of each peak controlled by a parameter β_i. The overall frequency-dependent gain of the tympanal organ is thus given by:

$$G(\nu) = g_1 e^{-\beta_1(\nu-\mu_1)^2} + g_2 e^{-\beta_2(\nu-\mu_2)^2}. \tag{1}$$

The shape of $G(\nu)$ is shown in Fig. 3 for the parameter values $g_1 = g_2 = 1$, $\mu_1 = 20$ kHz, $\mu_2 = 40$ kHz, and $\beta_1 = \beta_2 = 0.1$.

3.2. Q2: Bat ultrasound emission and propagation

We consider two bat species that employ distinct hunting frequency bands: one utilizes a relatively low frequency, while the other uses a higher frequency. The low-frequency bats emit ultrasound centered at approximately 20 kHz during predation, whereas the high-frequency bats emit ultrasound around 40 kHz. Let $w \in [0, 1]$ denote the proportion of the low-frequency bat species in the population, implying that the proportion of high-frequency bats is $1-w$. For simplicity, we assume that individual bats maintain a fixed emission frequency during a predation event, but that frequency may vary across individuals within the same species. Thus, the emitted ultrasound frequencies follow species-specific distributions, denoted $f_l(\nu)$ for low-frequency

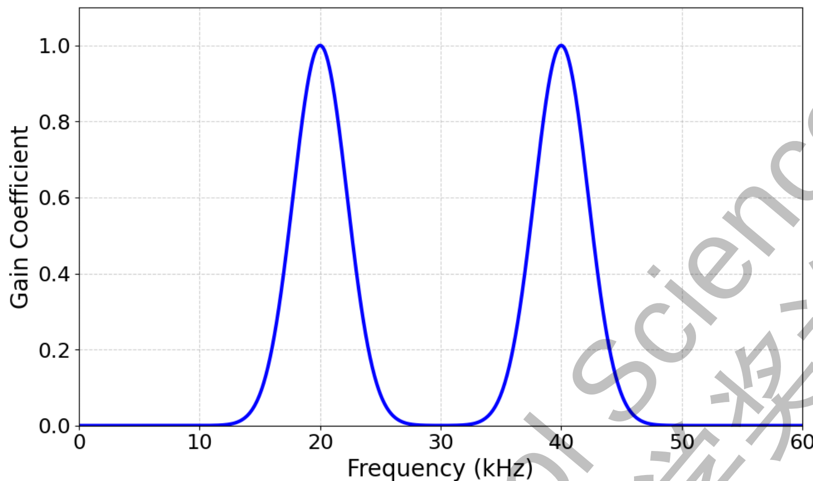

Figure 3: Moth auditory gain function. This graph illustrates the proposed two-mode gain function of a moth's ear as described in Eq. (1). The curve is a combination of two distinct bell-shaped curves, one peaking at 20kHz and the other at 40kHz.

bats and $f_h(\nu)$ for high-frequency bats. In what follows, we assume that both $f_l(\nu)$ and $f_h(\nu)$ are Gaussian distributions with means of 20 kHz and 40 kHz, respectively, and share a common variance σ^2, i.e.,

$$f_l(\nu) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{(\nu-20)^2}{2\sigma^2}\right),$$
$$f_h(\nu) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{(\nu-40)^2}{2\sigma^2}\right).$$

We assume that the intensity (in dB SPL) of the ultrasound emitted by each bat is $L_0 = 120$ dB, independent of the sound frequency. The sound wave attenuates as it propagates through the air, governed by the following equation:

$$L(d) = L_0 - 20\log_{10}\left(\frac{d}{d_0}\right) - \alpha_\nu(d-d_0). \tag{2}$$

Here, d denotes the distance the sound wave has traveled, and d_0 is a reference distance. The second term on the right-hand side accounts for the spreading of the sound wave as it propagates in the space, while the third term corresponds to the absorption by the air. The absorption coefficient α

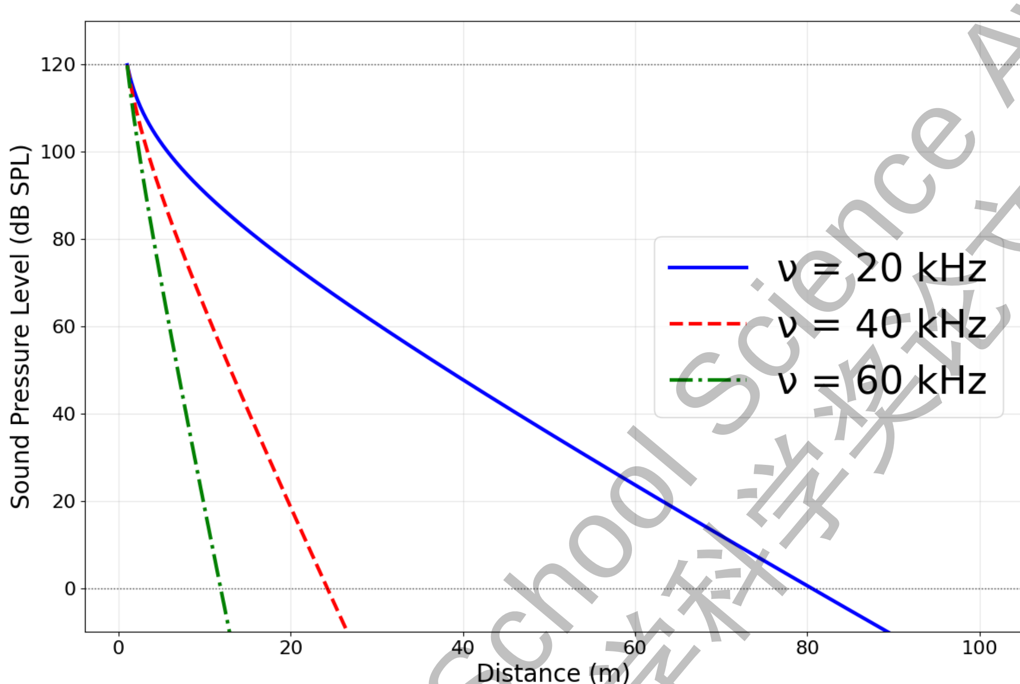

Figure 4: Ultrasound attenuation with distance. This graph shows how the intensity of bat ultrasound (in dB SPL) decreases with distance traveled according to Eq. (4). The different colored lines represent the received ultrasound intensity for frequencies $\nu = 20, 40, 60$ kHz.

depends on the humidity, temperature of the air, and the frequency of the sound wave. At $T = 20$ °C and relative humidity $H = 50\%$, an empirical approximation for α_ν is given by:

$$\alpha_\nu \approx 0.0027\nu^2 - 0.015\nu + 0.25 \tag{3}$$

Note that since sound intensity is expressed on a logarithmic (dB) scale, the contributions from spreading and absorption combine additively, rather than multiplicatively as in the linear case. The detailed mathematical derivation of Eq. (2) is provided in Appendix A.

Setting the reference distance $d_0 = 1$m we get

$$L_\nu(d) = L_0 - 20\log_{10} d - \alpha_\nu(d-1). \tag{4}$$

The value of L_ν as a function of d for different frequencies ν is shown in Fig. 4. From it, we can see that higher frequencies exhibit stronger attenuation due to increased atmospheric absorption.

3.3. Q3: Modeling the predation and evasion process

Consider a bat patrolling the air and emitting ultrasound at frequency ν to detect prey. The intensity of the ultrasound decreases with propagation distance as described by Eq. (4). As the bat approaches the moth, the received signal level at the moth's ear gradually increases. We assume that a minimum vibration intensity Q_0 (in dB SPL) is required to trigger a neural response in the moth; based on experimental data from [4], we set $Q_0 = 35$ dB. Once the received sound level exceeds this threshold, the moth detects the bat and executes its programmed response action. The maximum detection distance d_m at which the moth can sense the bat is thus determined by the equation:

$$Q_0 = L_\nu(d_m) + 10 \log_{10} G(\nu), \tag{5}$$

where $G(\nu)$ represents the moth's auditory gain at frequency ν (see Eq. (1)). See Appendix A for more details about the derivation of this equation. Substituting the expression for $L_\nu(d)$ from Eq. (4) yields the following equation for d_m:

$$L_0 - 20 \log_{10} d_m - \alpha_\nu(d_m - 1) + 10 \log_{10} G(\nu) = Q_0. \tag{6}$$

Eq. (6) is a nonlinear equation and can be solved numerically using methods such as the bisection method. Note that this equation always has exactly one solution (see Appendix B for a proof). However, we consider the solution biologically valid only if $d_m > d_0 = 1$m. This is because when a bat is too close, the aerodynamic disturbances generated by its flight are sufficient to alert the moth, making ultrasound detection an unreliable sensory mechanism. Hence, if the solution d_m obtained from Eq. (6) is less than 1m, we conclude that the moth cannot detect ultrasound at the given frequency. For convenience, we introduce a binary indicator variable ξ, where $\xi = 0$ indicates that the moth cannot detect the bat, and $\xi = 1$ indicates that it can. Further details regarding the existence of the solution to Eq. (6) are provided in Appendix B.

If we think of the moth ear as some type of passive radar system, then d_m is the detection distance of the radar. A larger value of d_m implies that the moth has more time to initiate evasive maneuvers, thereby increasing its chances of survival against a predator (but not for non-predators, see below). We model this monotonic relationship between the detection distance d_m and the moth's probability of successful escape E using a Hill-type function:

$$E(d_m) = \frac{k\sqrt{d_m}}{D + k\sqrt{d_m}}. \tag{7}$$

Here, the constant D represents the median evasion distance, at which the probability of successful evasion equals 0.5. The behavior of $E(d_m)$ as a function of d_m is illustrated in Fig. 5.

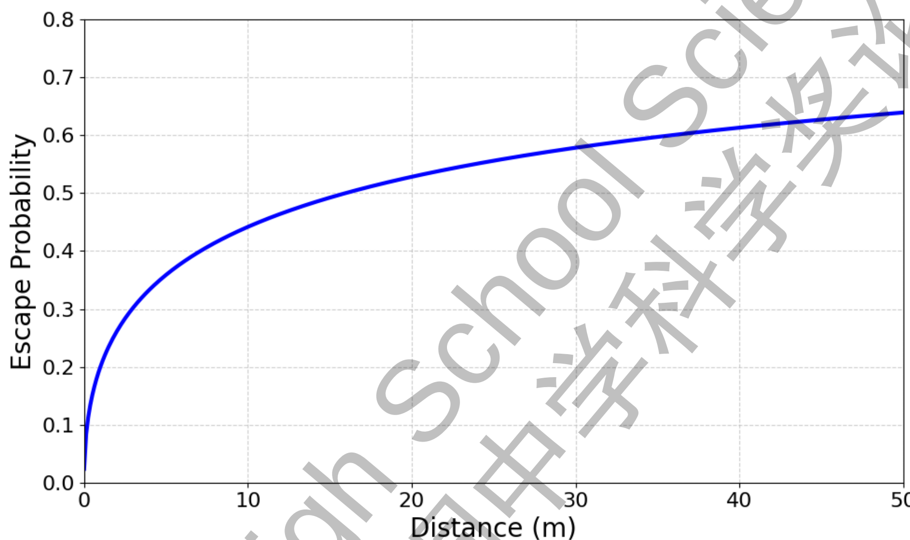

Figure 5: The escape probability $E(d_m)$ as a function of detection distance d_m as given by Eq. (7). This graph plots the probability of a moth successfully evading a bat. The function increases monotonically with d_m, illustrating how a larger detection range enhances the moth's likelihood of successful evasion.

In the following model, we assume that upon detecting an ultrasonic signal, the moth will try to escape. The outcome of this evasion attempt depends on both the bat's dietary preference and the moth's escape performance. If the moth is a prey species for the bat, the escape attempt succeeds with probability $E(d_m)$, and the moth survives. With probability $1 - E(d_m)$, the escape fails and the moth is captured. Conversely, if the moth is not a prey item for the bat, it will not be captured regardless of its behavior.

However, engaging an escape behavior is not without cost for the moth. An escaping attempt would lead to extra energy consumption and risk to other predators, and may also disrupt the moth from foraging or mating. For simplicity, we model this cost as a small but non-negligible risk of death associated with the escape attempt itself. We assume that any escape action carries a probability $r = 0.1$ resulting in the moth's death.

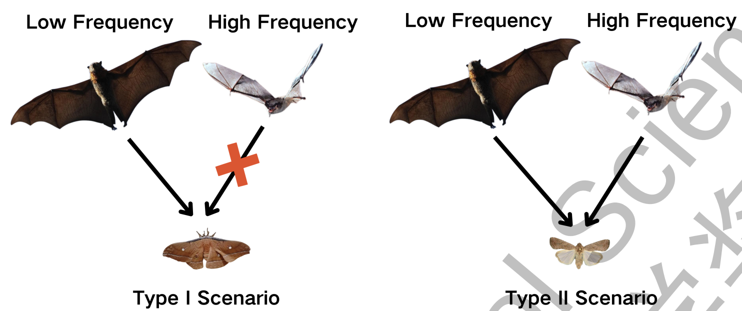

Figure 6: Predate-prey relationship between bats and moths. The environment contains two types of bats: one emitting low-frequency ultrasound and the other high-frequency ultrasound. In the Type-I scenario, the moth is preyed upon exclusively by low-frequency bats. In the Type-II scenario, the moth is vulnerable to both low-frequency and high-frequency bats.

We consider an environment containing two types of bats: one emitting low-frequency ultrasound and the other high-frequency ultrasound. Two distinct predator-prey scenarios are examined, reflecting different ecological contexts in which the moth may reside. In the Type-I scenario, the moth is preyed upon exclusively by low-frequency bats. In the Type-II scenario, the moth is vulnerable to both low-frequency and high-frequency bats. The respective hunting relationships are illustrated in Fig. 6. Note that this configuration represents a highly simplified ecosystem, designed to qualitatively investigate optimal moth hearing strategies under different environmental conditions.

3.4. Survival probability

By combining the various assumptions introduced in the previous sections, we are now able to compute the overall survival probability of a moth in a given environment. This probability reflects how likely the moth is to survive an encounter with bats, taking into account its hearing ability, the bat's foraging habit, and the risks associated with evasion.

Type I Scenario

In the Type I scenario, the moth is preyed upon only by the low-frequency bats. High-frequency bats do not target this moth. We therefore analyze the moth's survival in two cases: when a low-frequency bat is present, and when a high-frequency bat is present.

- **If a low-frequency bat appears:** The moth detects the bat at a distance d_m and initiates an escape maneuver. The escape succeeds with probability $E(d_m)$. However, the escape attempt itself carries a risk r of death (e.g., due to energy expenditure or increased exposure to other predators). We already introduced an indicator variable ξ, where $\xi = 1$ indicates that the moth has detected the bat and attempts to escape, while $\xi = 0$ means the moth fails to detect the threat and will be captured. Therefore, the overall survival probability of the moth in this encounter is given by:

$$p_I^l = (1 - r) \cdot \xi \cdot E(d_m). \tag{8}$$

  In this expression, $(1 - r)$ represents the probability that the moth survived from the escape attempt itself. After this, $E(d_m)$ is the probability that the escape is a successful one. Note that the moth only has a chance to survive when $\xi = 1$. If $\xi = 0$, the moth does not try to escape and is certain to be captured by this bat.

- **If a high-frequency bat appears:** Since this type of bat does not prey on the moth, the moth is not directly threatened. However, if the moth detects the bat (i.e., $\xi = 1$) and initiates an escape, it still has a risk r of death. If the moth does not detect the bat ($\xi = 0$), it remains safe. Therefore, the survival probability in this case is:

$$p_I^h = 1 - r \cdot \xi. \tag{9}$$

  This expresses that the moth survives with certainty if it does not attempt to escape ($\xi = 0$), but should an escape occur ($\xi = 1$), its survival probability is reduced by the risk factor r. **Note that this is the key assumption behind the main idea of the paper: hearing everything may not always be the best.**

To compute the *overall* survival probability P_I across all possible bat encounters, we take a weighted average over both bat types and all ultrasound frequencies they might emit. The survival probability is then:

$$\begin{aligned} P_I &= \omega \int_0^{+\infty} p_I^l(\nu) f_l(\nu) d\nu + (1-\omega) \int_0^{+\infty} p_I^h f_h(\nu) d\nu \\ &= \omega \int_0^{+\infty} (1-r)\xi E(d_m(\nu)) f_l(\nu) d\nu + (1-\omega) \int_0^{+\infty} (1-r\xi) f_h(\nu) d\nu. \end{aligned} \tag{10}$$

Here ω is the proportion of low-frequency bats in the environment. $d_m(\nu)$ can be solved from Eq. (6) for a given ν. The integrals account for the fact that bats emit ultrasound at different frequencies ν. The functions $f_l(\nu)$ and $f_h(\nu)$ represent the probability distributions of emitted frequencies for low- and high-frequency bats, respectively. Intuitively, this equation averages the survival probability over all possible frequencies, weighting each by how common that frequency is within each bat group.

This formulation allows us to quantitatively assess how the moth's hearing sensitivity (through $d_m(\nu)$) and the composition of the bat community (through ω, f_l, and f_h) jointly influence its survival odds.

Type II scenario

In the Type II scenario, the moth is vulnerable to both low-frequency and high-frequency bats. This means that regardless of which type of bat appears, the moth must attempt to escape if it detects the threat. The escape process is the same in both cases: the moth detects the bat at a distance d_m, initiates an escape with an inherent risk r, and succeeds with probability $E(d_m)$. Therefore, the survival probability when encountering either a low-frequency or high-frequency bat is given by the same expression:

$$p_{II}^l = (1-r) \cdot \xi \cdot E(d_m), \quad p_{II}^h = (1-r) \cdot \xi \cdot E(d_m)$$

Here, the indicator variable ξ signifies whether the moth has detected the bat ($\xi = 1$) or not ($\xi = 0$). The term $(1-r)$ accounts for the survival probability from the escape attempt itself, and $E(d_m)$ represents the success probability of evading the bat given that detection occurred.

To compute the overall survival probability P_{II} for the Type II moth across all possible bat encounters, we integrate over the frequency distributions of both bat types, weighted by their respective proportions in the environment:

$$
\begin{aligned}
P_{II} &= \omega \int_0^{+\infty} p_{II}^l \, f_l(\nu) \, \mathrm{d}\nu + (1-\omega) \int_0^{+\infty} p_{II}^h \, f_h(\nu) \, \mathrm{d}\nu \\
&= \omega \int_0^{+\infty} (1-r) \, \xi \, E(d_m) \, f_l(\nu) \, \mathrm{d}\nu + (1-\omega) \int_0^{+\infty} (1-r) \, \xi \, E(d_m) \, f_h(\nu) \, \mathrm{d}\nu
\end{aligned}
\tag{11}
$$

In this expression, ω denotes the proportion of low-frequency bats, while $f_l(\nu)$ and $f_h(\nu)$ are the frequency distributions of ultrasound emitted by low- and high-frequency bats, respectively. The integrals ensure that the survival probability is averaged over all possible ultrasound frequencies that the moth might encounter.

4. Numerical results

Equations (10) and (11) give the survival probability of a moth in two distinct bat communities. These probabilities depend critically on the parameters g_1, μ_1 and g_2, μ_2 of the auditory gain function $G(\nu)$, which are determined by the physiological properties of the moth's hearing system. Different values of these parameters alter the moth's sensitivity to ultrasound frequencies, thereby influencing its survival chances. It is through the evolutionary arms race between bats and moths that these parameters are subject to natural optimization. In this section, we numerically determine the parameter values that maximize the survival probability in each environment. Given the complexity of the integrals and the structure of the objective function, an analytical solution is infeasible. We therefore adopt a numerical approach, performing an exhaustive search over the relevant parameter space to address this optimization problem.

4.1. Selective enhancement of hearing modes

Our numerical results demonstrate that moths can evolutionarily adapt their auditory systems by selectively enhancing specific hearing modes—effectively tuning the gain coefficients g_1 and g_2 in their auditory gain function $G(\nu)$. This strategic adjustment allows moths to optimize their detection capability under different predation pressures.

Fig. 7 illustrates the optimal gain configurations obtained from numerically maximizing the survival probability P under both Type-I and Type-II ecological scenarios. The numerical optimization was performed over a 40×40 grid spanning the parameter space of g_1 and g_2 (both in the range [0,1]), with fixed auditory parameters $\mu_1 = 20$ kHz, $\mu_2 = 40$ kHz, and $\beta_1 = \beta_2 = 0.1$. The bat community composition was set to $\omega = 0.5$, representing equal proportions of low- and high-frequency bats. The left column of the figure shows heat maps in which the color at each point represents the survival probability P for the corresponding (g_1, g_2) pair; the horizontal and vertical axes correspond to g_1 and g_2, respectively. The global maximum in each scenario is marked with a green asterisk (panels A and C). The right column displays the corresponding auditory threshold curves (panels B and D) at the optimal gain values.

In an environment dominated by a single bat species (Type-I), the moth tends to amplify only the relevant hearing mode. For instance, when only low-frequency bats are present, the optimal strategy strongly favors high gain at the corresponding frequency (i.e., $g_1 \gg g_2$), while suppressing sensitivity to irrelevant high-frequency signals. Specifically, for Type-I, the optimal gains are $g_1 = 1$ and $g_2 = 0$. Conversely, in a more complex environment with multiple bat species (Type-II), the moth benefits from maintaining significant sensitivity in both frequency bands, resulting in a bimodal gain profile with both g_1 and g_2 substantially greater than zero. In this case, the optimal values are $g_1 = 1$ and $g_2 = 1$.

This adaptive tuning of gain coefficients reflects an efficient resource allocation strategy in the moth's auditory system. By enhancing only the necessary hearing modes, the moth not only improves its detection performance but also reduces potential energy costs and neural processing loads associated with unnecessary auditory activation. Such a mechanism underscores an evolutionary trade-off between sensory performance and physiological constraint.

4.2. Fine-Tuning of Auditory Peak Frequencies

After establishing the effect of the gain coefficients g_1 and g_2 for the survival probability of the moth, we now investigate a more nuanced aspect of auditory adaptation: the ability of moths to fine-tune their peak hearing frequencies μ_1 and μ_2. To isolate the effect of the gain coefficients, we fixed $g_1 = 1, g_2 = 1$, effectively allowing maximum sensitivity in both modes. We then performed a parameter sweep over μ_1 and μ_2 to identify the frequency combinations that maximize survival probability under different ecological

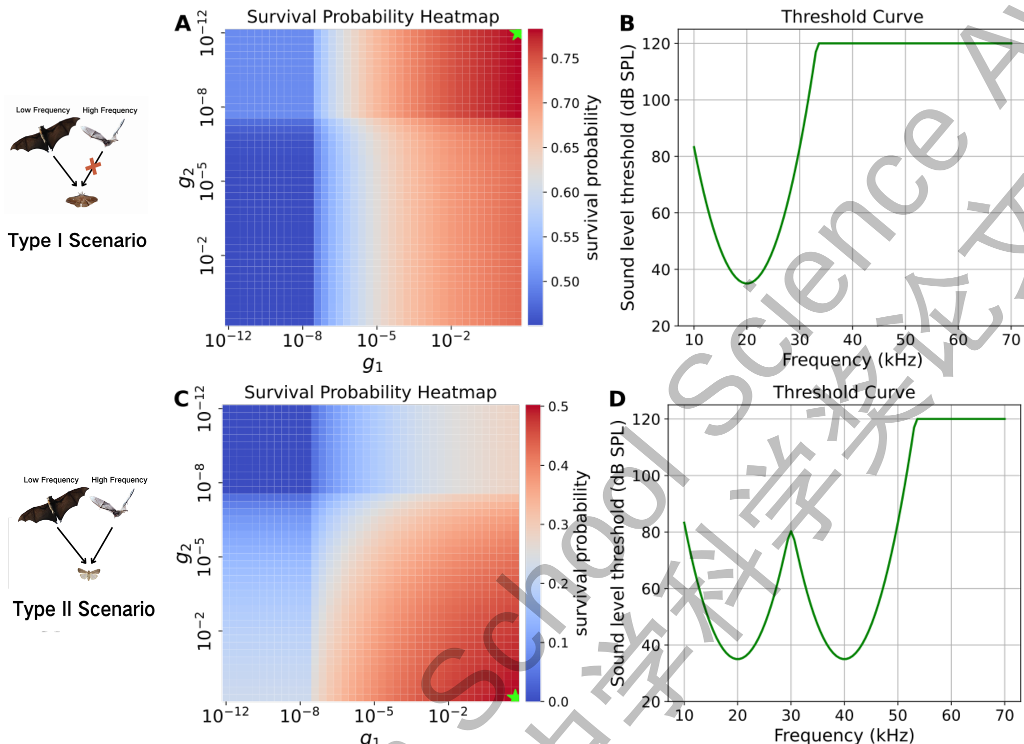

Figure 7: The optimal hearing strategy under Type-I and Type-II ecological scenarios. (A, C) Heat maps showing the survival probability P across the gain coefficient space (g_1, g_2), computed over a 40×40 grid with fixed auditory parameters $\mu_1 = 20$ kHz, $\mu_2 = 40$ kHz, $\beta = 0.1$, and bat proportion $\omega = 0.5$. The green asterisks mark the global optima. (B, D) Auditory threshold curves corresponding to the optimal gain values (in dB SPL). In Type-I environments (top row), moths enhance only one hearing mode relevant to the dominant bat species. In Type-II environments (bottom row), a bimodal sensitivity profile is favored, enabling detection of both low- and high-frequency bats.

conditions.

Type I Scenario

For the Type-I moth, which is only preyed upon by low-frequency bats, the heatmap of survival probability is shown in Fig. 8A. The global maximum occurs at $\mu_1 = 17.7$ kHz and $\mu_2 = 20.3$ kHz. Apparently, both modes (peaked at μ_1 and μ_2, respectively) are now located near the peak frequency of the low-frequency bat (20 kHz). However, μ_1 and μ_2 are not equal to 20 kHz exactly. In fact, placing both modes exactly at 20 kHz would lead to saturated gain around that frequency. Instead, the moth spreads its sensitivity around the central frequency, forming a broader effective detection band (see the blue line in Fig. 8B, which is wider than the green line).

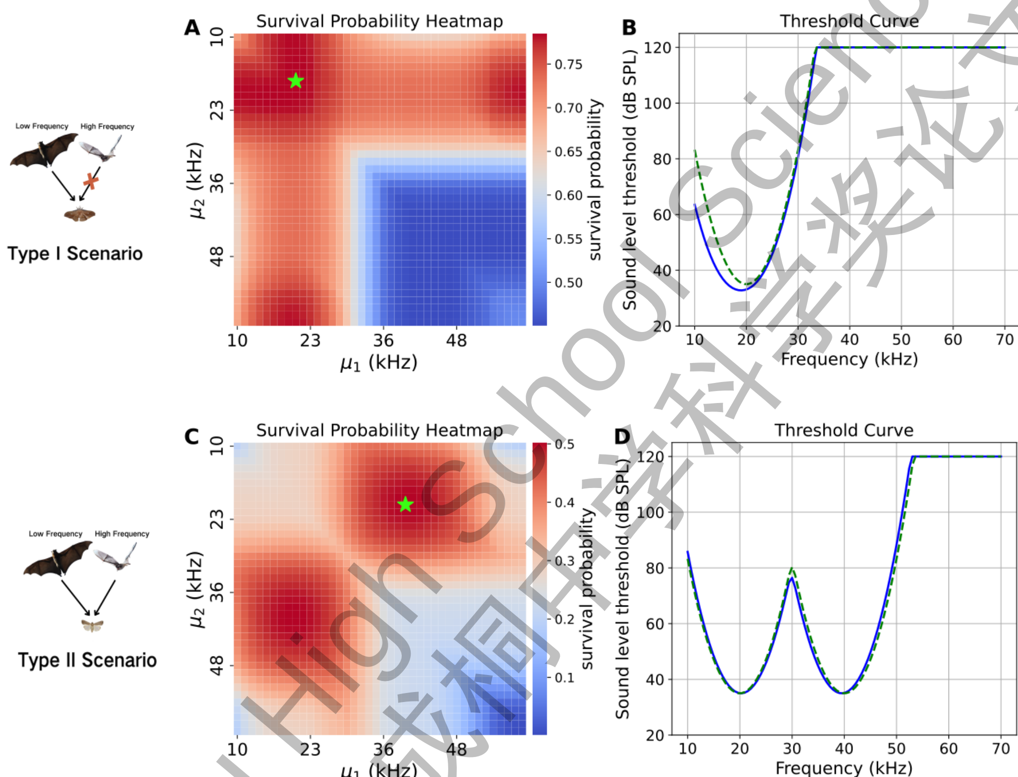

Figure 8: Optimal frequency tuning under Type-I and Type-II ecological scenarios. (A, C) Heat maps showing the survival probability across the frequency parameter space (μ_1, μ_2), computed over a 40×40 grid with fixed gain coefficients $g_1 = 1, g_2 = 1$, $\beta = 0.1$, and bat proportion $\omega = 0.5$. The green asterisks mark the global optima. (B, D) Auditory threshold curves corresponding to the optimal frequency values (in dB SPL). In Type-I environments (top row), moths concentrate both hearing modes near the dominant threat frequency. In Type-II environments (bottom row), distinct frequency peaks emerge, enabling effective detection of both low- and high-frequency bats.

Type II Scenario

For the Type-II moth, which is vulnerable to both bat species, the survival probability heatmap is shown in Fig. 8C). The optimal peak frequencies are identified at $\mu_1 = 20.3$ kHz and $\mu_2 = 39.5$ kHz. This distinct separation between the two auditory modes allows the moth to broaden its effective detection bandwidth, thereby enhancing its ability to perceive both low-frequency and high-frequency bat echolocation calls. Such frequency divergence represents a clear adaptive response to a mixed predator environment, in which the moth must dynamically allocate limited auditory resources to simultaneously monitor multiple threats across a wider frequency range. These findings indicate that moths can indeed fine-tune their peak auditory frequencies to gain an evolutionary advantage.

5. Discussions and Conclusions

In this work, we used a mathematical model to investigate how moths optimize their hearing ability in different bat environments. The model describes the moth's hearing sensitivity using a gain function made up of two Gaussian curves, representing the two hearing modes of their eardrum. By analyzing the hunting process through a probability-based approach, we linked the moth's hearing setup and the bat community to the moth's chance of survival. The results show that moths can "tune" their ears to focus on the frequencies used by threatening bats, while ignoring those from bats that do not prey on them. This study offers a new way to understand the evolutionary "arms race" between bats and moths.

The main idea this work aims to convey is: "Equipped with a simple binary ear, hearing everything is not always the best for a moth living in a complex environment. Sometimes, it's actually beneficial to 'turn a deaf ear' to certain frequency ranges." This serves as a vivid example of the famous saying in evolution: "it is not the strongest, nor the most sensitive, but the best-adapted that survives."

However, our model has some limitations. First, it assumes that the relationship between bats and moths is fixed, meaning that which bats hunt which moths doesn't change. In reality, bats can be very flexible in how they hunt. They might change the frequency of their calls or their strategy depending on what prey is around—something our model does not fully capture. Second, the model simplifies how a moth's ear really works. While we use a basic gain function to represent its hearing sensitivity, a real moth ear is far more complex. Its actual biological and neural mechanisms are much more intricate than a simple on/off response. In the future, adding more biological detail—like how neurons actually respond to sound—could help make the model more realistic.

Despite these limitations, our study contributes meaningfully in two key areas.

First, it offers valuable insights for bionics. The moth's ear—a simple yet highly efficient sound filtering system—serves as an inspiring model for designing compact and energy-efficient acoustic sensors. Unlike complex human-made devices that attempt to process all signals, the moth's auditory mechanism demonstrates the advantage of selective perception. This idea could be applied in anti-drone systems or specialized acoustic detectors, where focusing on specific signals while ignoring background noise is essential.

Second, our findings may help improve pest control strategies. By better understanding how insects respond to the sounds of their predators, we can develop new, non-invasive methods to protect crops. For example, studies have shown that playing predator sounds can reduce egg-laying in certain birds [9]. Similarly, if we learn how pest moths react to specific ultrasound signals, we might use sound to deter them as well. This offers a promising eco-friendly alternative to traditional pest management.

Appendix A. Derivation of the ultrasonic propagation model

A.1 The definition of sound pressure

Sound waves are mechanical waves that propagate through a medium, such as air, by creating regions of compression and rarefaction. An experimental device can measure the sound pressure p, which is defined as the deviation from the ambient atmospheric pressure caused by the sound wave. It is typically measured in Pascals (Pa).

Physically, it is more convenient to work on the *sound intensity*. The intensity I of a sound wave, which represents the power per unit area (W/m^2), is related to the sound pressure p for a plane wave by:

$$I = \frac{p^2}{\rho c}$$

where ρ is the density of the medium and c is the speed of sound.

A.2 The propagation equation of the sound intensity I

As sound propagates through air, its intensity decreases due to two main factors: *geometric spreading* and *absorption*.

(1) Geometric Spreading

For a spherical wave propagating outward from a point source, the intensity decreases with the square of the distance d from the source:

$$I_{\text{spread}}(d) \propto \frac{1}{d^2}$$

Thus, compared to a reference distance d_0, the intensity reduction due to spreading is:

$$\frac{I(d)}{I_0} = \left(\frac{d_0}{d}\right)^2 \tag{A.1}$$

(2) Absorption Loss

Additionally, the medium (air) absorbs acoustic energy, converting it into heat. This absorption is frequency-dependent and can be modeled with an exponential decay. The differential change in intensity over a small distance ds is:

$$dI = -\alpha I\, ds$$

where α is the frequency-dependent absorption coefficient (in Np/m). Solving this differential equation:

$$\int_{I_0}^{I} \frac{dI}{I} = -\alpha \int_{s_0}^{s} ds$$

$$\ln \frac{I}{I_0} = -\alpha(s - s_0)$$

$$I(s) = I_0 e^{-\alpha(s-s_0)}$$

In the following, we will replace the symbol s by d to denote the distance the sound traveled. So we obtain

$$I(d) = I_0 e^{-\alpha(d-d_0)} \tag{A.2}$$

Combined Effect

The total intensity at distance d is the product of the losses from spreading and absorption:

$$I(d) = I_0 \left(\frac{d_0}{d}\right)^2 e^{-\alpha(d-d_0)} \tag{A.3}$$

where I_0 is the intensity at the reference distance d_0.

A.3 Conversion to Decibel Scale

The decibel (dB) scale is a logarithmic unit used to express the ratio of a value to a reference value. For sound pressure level (SPL, Sound Pressure Level), it is defined as:

$$L = 20 \log_{10}\left(\frac{p}{p_0}\right) \quad \text{(dB SPL)}$$

Where p is the root-mean-square (RMS) sound pressure of the measured sound (in Pa), and p_0 is the reference sound pressure.

The standard reference sound pressure in air is:

$$p_0 = 20\ \mu\text{Pa} \quad (0.00002\ \text{Pa})$$

This value represents the threshold of human hearing at 1 kHz. Therefore, 0 dB SPL does not mean the absence of sound, but rather a sound pressure equal to p_0, which is the quietest sound a typical human ear can detect.

A negative dB SPL value is possible and indicates a sound pressure lower than the reference p_0. Such sounds are too quiet for the human ear to perceive.

Since intensity I is proportional to p^2, the sound intensity level can also be expressed in decibels as:

$$L = 10 \log_{10}\left(\frac{I}{I_0}\right)$$

where $I_0 = 10^{-12}\ \text{W/m}^2$ is the standard reference intensity, corresponding approximately to $p_0 = 20\ \mu\text{Pa}$ in air.

Applying this to the derived intensity function $I(d)$, the sound level at distance d becomes:

$$L(d) = 10 \log_{10}\left(\frac{I(d)}{I_0}\right) = 10 \log_{10}\left(\frac{I_0}{I_0}\left(\frac{d_0}{d}\right)^2 e^{-\alpha(d-d_0)}\right)$$

Simplifying and using properties of logarithms yields:

$$L(d) = L_0 - 20\log_{10}\left(\frac{d}{d_0}\right) - \alpha(d - d_0) \cdot 10\log_{10} e$$

Where L_0 is the sound level at the reference distance d_0. The term $10\log_{10} e \approx 4.34$. For simplicity, the absorption term is often combined into a single coefficient, leading to the final form used in the main text:

$$L(d) = L_0 - 20\log_{10}\left(\frac{d}{d_0}\right) - \alpha(d - d0).$$

A.4 Receiver Model: Moth Ear Detection

The moth's ear is modeled as a receiver with a frequency-dependent gain $G(\nu)$. The effective sound level arriving at the moth's auditory system is therefore the incident sound level $L(d)$ plus the gain (in dB):

$$L_{\text{eff}}(\nu, d) = L(d) + 10\log_{10}(G(\nu))$$

A neural response is triggered only if this effective sound level exceeds a fixed detection threshold Q_0 (in dB SPL). Thus, the condition for detection is:

$$L_{\text{eff}}(\nu, d) \geq Q_0$$

Substituting the expression for $L(d)$, the detection criterion becomes:

$$L_0 - 20\log_{10} d - \alpha(d - 1) + 10\log_{10}(G(\nu)) \geq Q_0$$

This inequality is used to calculate the maximum detection distance d_m for a given frequency ν, by solving for the distance d where equality holds. This is how Eq. (6) comes from.

Appendix B. Efficiently solving non-linear equations

In modeling the moth's detection of bat ultrasound, we need to solve the following nonlinear equation for the detection distance d_m:

$$L_0 - 20\log_{10} d_m - \alpha_\nu(d_m - 1) + 10\log_{10} G(\nu) = Q_0, \tag{B.1}$$

where:

- L_0: intensity of the ultrasound emitted by the bat (dB SPL),
- d_m: minimum distance at which the moth can detect the bat (m),
- α_ν: frequency-dependent attenuation coefficient of sound (dB/m),
- $G(\nu)$: auditory gain of the moth at frequency ν,
- Q_0: auditory threshold of the moth (dB SPL).

This equation describes the maximum detection distance d_m of a moth at frequency ν.

B.1 Transformation and Standardization

For numerical solution, Eq. (B.1) is rewritten as

$$f(d_m) = L_0 - 20\log_{10} d_m - \alpha_\nu(d_m - 1) + 10\log_{10} G(\nu) - Q_0 = 0. \tag{B.2}$$

The goal is to find $d_m > 0$ such that $f(d_m) = 0$.

B.2 Existence and Uniqueness of the Solution

We analyze the properties of $f(d_m)$ for $d_m > 0$:

1. Continuity:
   - $\log_{10} d_m$ is continuous for $d_m > 0$,
   - $\alpha_\nu d_m$ is linear and continuous,
   - Therefore, $f(d_m)$ is continuous on $d_m > 0$.
2. Monotonicity:
   $$f'(d_m) = -\frac{20}{d_m \ln 10} - \alpha_\nu. \tag{B.3}$$
   Since $d_m > 0$ and $\alpha_\nu > 0$, it follows that $f'(d_m) < 0$. Thus, $f(d_m)$ is strictly decreasing on $d_m > 0$.
3. Limits:
   $$\lim_{d_m \to 0^+} f(d_m) = +\infty, \tag{B.4}$$
   $$\lim_{d_m \to +\infty} f(d_m) = -\infty. \tag{B.5}$$
4. Conclusion: Since $f(d_m)$ is continuous, strictly decreasing, and ranges from $+\infty$ to $-\infty$, the Intermediate Value Theorem guarantees the existence of a unique root $d_m^* > 0$ such that $f(d_m^*) = 0$.

B.3 Numerical Methods

Because $f(d_m)$ is monotonic and continuous, it can be efficiently solved using the Bisection Method or Brent's Method, both well-suited for single-variable root-finding.

(1) Bisection Method

- Advantages: simple, stable, and always convergent.
- Procedure:
  1. Choose an interval $[a, b]$ with $f(a) > 0$ and $f(b) < 0$,
  2. Compute the midpoint $c = (a + b)/2$,
  3. Update the interval according to the sign of $f(c)$,
  4. Repeat until the interval length is below the tolerance tol.

(2) Brent's Method

- Advantages: combines bisection, secant, and inverse quadratic interpolation, achieving faster convergence,
- Well-suited for high-precision requirements.

(3) Implementation

An implementation in Python using `scipy.optimize.brentq` is given below:

```
from scipy.optimize import brentq
import numpy as np

def solve_d_bisection(g, alpha, L0, d_min=1e-6, d_max=1e3,
                      tol=1e-6, max_iter=100):
    def func(d):
        return L0 - alpha * (d-1) - 20 * np.log10(d) - g
    return brentq(func, d_min, d_max, xtol=tol, maxiter=max_iter)
```

Here:

- $g = Q_0 - 10 \log_{10} G(\nu)$,
- $\alpha = \alpha(\nu)$ is the frequency-dependent attenuation coefficient,
- $[d_{\min}, d_{\max}]$ is the initial interval, typically set to $[10^{-6}, 10^3]$ meters.

B.4 Vectorized Implementation for Efficiency

In practical applications, solving for d_m across multiple frequencies ν simultaneously is often required. A vectorized implementation significantly improves computational efficiency compared to iterating over individual frequencies.

Vectorization Strategy

1. Precompute all frequency-dependent parameters as arrays:
   - $\boldsymbol{\alpha} = [\alpha_{\nu_1}, \alpha_{\nu_2}, \ldots, \alpha_{\nu_n}]$
   - $\mathbf{G} = [G(\nu_1), G(\nu_2), \ldots, G(\nu_n)]$
   - $\mathbf{g} = Q_0 - 10\log_{10}(\mathbf{G})$
2. Utilize NumPy's vectorized operations and broadcasting capabilities to compute function values efficiently.

This approach avoids Python loops and substantially accelerates computation time.

B.5 Biological constraint

Although Equation (B.1) guarantees a unique solution for $d_m > 0$, biological considerations impose an additional constraint for meaningful detection. Specifically, we regard a solution as biologically valid only if $d_m > d_0 = 1\text{m}$. This threshold is motivated by the fact that when a bat is too close (i.e., at distances less than 1 meter), the aerodynamic disturbances generated by its flight are sufficient to alert the moth, making ultrasound detection an unreliable mechanism. If the solution does not satisfy $d_m > 1\text{m}$, we conclude that the moth cannot effectively detect ultrasound at that frequency.

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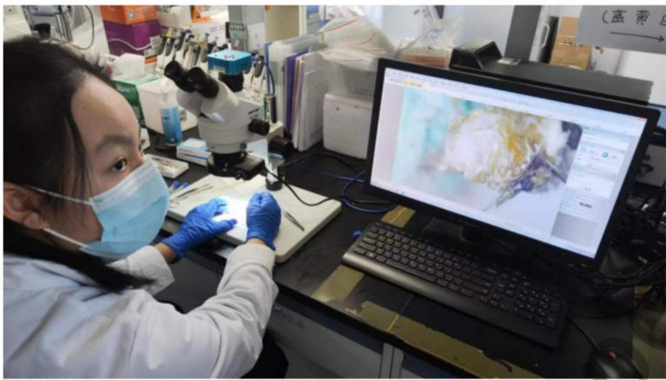
Acknowledgement

During middle school, I developed a strong interest in biology, fascinated by the theory of evolution and inspired by reading many books on the subject as well as by joining my school's biology club. Later, through a friend's introduction and my mentor's guidance, I was introduced to the field of mathematical biology. With their support, I participated in laboratory discussions as a student researcher and benefitted from inspiring and constructive advice.

In the summer of my third year of middle school, my teacher gave me The Blind Watchmaker. I was particularly fascinated by the section on bats and ultrasound. Coincidentally, my teacher was collaborating with Professor Aibing Zhang's team at Capital Normal University on the ecological relationship between moths and bats. This gave me the opportunity to participate in related discussions and explore a puzzling biological question: moths can detect ultrasound, but their auditory system is binary ("hearing" or "not hearing") without the ability to distinguish frequency or direction as mammals do. Their hearing sensitivity curves also vary widely across species, with some showing bimodal peaks. This inspired me to consider how mathematics might shed light on the phenomenon.

At that time, I was taking AP courses, where I learned the basics of calculus, differentiation, and probability. I also enjoyed programming, which allowed me to grasp numerical methods quickly. These skills prepared me to engage with the project. Beginning in December 2024, I joined lab activities: dissecting moths, discussing anatomy, conducting literature reviews, using Google Scholar for research, and exchanging ideas with ChatGPT about project design, feasibility, and methodology.



Through this process, I gained several insights. First, I realized that ultrasound propagation, which initially seemed complex, can be explained using high-school physics and mathematics: sound intensity decreases with the square of distance. Second, I learned that ultrasound, measured in decibels, involves logarithms and exponents, deepening my appreciation for mathematical precision. Third, I saw how attenuation in air can be modeled with differential equations, linking directly to exponential functions. Fourth, I tackled a nonlinear equation, analyzing existence and uniqueness of solutions, and implemented numerical methods. Though my initial program ran slowly, I refined the algorithm to make it efficient. Finally, I learned the importance of visualization, using Desmos and Inkscape to create figures, and with my teacher's guidance, I came to understand how standardized graphics communicate scientific ideas clearly.

This entire experience trained me not only in biology and mathematics but also in the process of research itself: identifying questions, building models, and presenting results. I was inspired by the power of mathematics to reveal hidden structures in biology, and I grew in critical thinking, problem-solving, and collaboration. Above all, I learned that research is not about instant answers, but about curiosity, persistence, and the joy of discovery.

The experimental facilities and equipment were provided by the School of Life Sciences at Capital Normal University. I am deeply grateful to Ms. Caiqing Yang and Dr. Yaning Zhang for their patient guidance during experimental procedures, and to my mentor for his generous support throughout the project. I also owe thanks to Ms. Fan and Mr. Wang from Beijing National Day School. They helped me a lot in my mock oral defense. I would also like to thank the senior students in the lab for sharing their valuable experience in literature research, model design, and experiment conduction, as well as my peers for their inspiration and companionship during discussions.

```
        r = PARAMS['r']
        if is_predator:
            return (1 - r) * xi * E
        else:
            return 1 - r * xi

    # 计算增益
    def calculate_gain(v, g1, g2, mu1, mu2, sigma1, sigma2):
        return g1*np.exp( -((v - mu1)**2) / (sigma1**2)) + g2*np.exp( -((v - mu2)**2) / (sigma2**2))

    # 逃生概率
    def escape_rate(d, E0=0.1, s=0.25):
        # result = np.zeros_like(d, dtype=float)
        # mask = d > 1
        # result[mask] = np.log10(d[mask]) / (5.0 + np.log10(d[mask]))
        # return result
        k = PARAMS['k']
        D = PARAMS['D']

        ds = k*np.sqrt(d)
        #ds = k*d
        return ds / (D + ds)
        #return 1 / (1 + ((1-E0)/E0) * np.exp(-s*ds))

    # 数值积分计算总逃生概率
    def integrate_probability(mu_bat, sigma_bat, is_predator=True):
        v = np.linspace(0, 100, 100)
        prob = calculate_probability(v, is_predator=is_predator)
        density = norm.pdf(v, mu_bat, sigma_bat)
        return np.trapezoid(prob * density, v)
[4]  ✓ 0.0s
```

In addition, we made heavy use of artificial intelligence tools to enhance both efficiency and accuracy. For example, when studying the conversion between decibels and sound intensity levels, we consulted relevant resources using DeepSeek, which helped us quickly locate authoritative references and clarify key physical concepts. For programming, we employed tools such as Cursor and DeepSeek to optimize our code, refine syntax, and improve readability and performance. These AI-assisted approaches were used responsibly and in accordance with academic integrity, serving as supportive tools rather than replacing independent thinking or original analysis. They not only saved time but also provided us with valuable feedback that supported iterative improvement, enabling us to focus more on the scientific questions at hand rather than being hindered by technical bottlenecks.

关于许可学生使用实验室资源开展科研项目的证明

单位： 首都师范大学 张爱兵教授课题组 / 生命科学学院

致相关赛事组委会：

兹证明 **方曼琳** 同学，自 **2024** 年 **7** 月 **1** 日 至 **2025** 年 **7** 月 **1** 日，于我校（我课题组）参与了一项名为 **“飞蛾鼓膜听器结构及功能研究”** 的科研项目。

在该项目研究期间，方曼琳同学在课题组指导老师的带领下，学习了相关的实验技术与研究方法。方曼琳采集的 **“飞蛾听器解剖显微成像图”** 等研究数据和成果，系在本课题组（实验室）的指导和资源支持下完成。

经本单位审核，许可方曼琳同学将上述研究过程及成果（包括但不限于飞蛾听器解剖显微成像图等）用于其个人 **论文撰写与展示**，并作为其参加丘成桐中学科学奖的参赛材料。

我们对方曼琳同学在项目期间的表现和所取得的成果表示认可，并支持其参与此次竞赛。

项目指导人员：

- **张爱兵** （教授）
- **杨采青** （讲师）
- **张亚宁** （博士）

负责人签名：

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