Weapons of Moths against Bats and Their Bionic Applications

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Abstract. The evolutionary arms race between moths and bats has spurred the development of intricate defense mechanisms in moths, which are not only crucial for their survival but also serve as a rich source of inspiration for biomimetic innovations. This study delves into the array of biological "weapons" that moths employ to evade bat predation, including behavioral adaptations, acoustic properties of wing scales, chemical defenses, and acoustic strategies. By presenting a comprehensive overview of these defense tactics, we lay the groundwork for understanding how these biological insights translate into groundbreaking applications in modern science and technology. The review begins with an exploration of passive defenses such as behavioral changes and the acoustic absorption capabilities of moth wing scales, which significantly reduce detection by bats. It then transitions into active defense strategies, such as the production of ultrasonic clicks for sonar interference and the execution of evasive flight maneuvers. These natural strategies are then extended into the realm of biomimetics, where we examine the development of innovative technologies like directional hearing aids and acoustic metamaterials, inspired by the auditory systems and wing structures of moths. By framing biomimetic applications as a direct extension of the moth's defense mechanisms, this study aims to provide a clear link between biological adaptations and their technological counterparts. The research underscores the potential of moth-inspired designs to enhance acoustic imaging, environmental monitoring, and medical diagnostics, ultimately highlighting the mutually beneficial relationship between the study of nature and the advancement of human technology.

1 Introduction

In the vast stage of the natural world, the survival struggle between moths and bats is an ancient and intricate evolutionary dance. Moths, nocturnal insects, have evolved a variety of defense strategies to evade predation by bats. From behavioral adaptations to chemical defenses, and from acoustic mimicry to active defense mechanisms, moths demonstrate innovative heights in biological survival strategies. This article explores how moths utilize these defense mechanisms, particularly acoustic warning signals and chemical defenses, to counteract predation by bats. Additionally, it analyzes how these natural phenomena inspire developments in modern scientific technologies, especially in the field of biomimetics.

To systematically analyze the social behaviors of birds and insects, we employed a multi-faceted approach that included quantitative and qualitative methodologies. Quantitatively, we used statistical analyses to compare social interaction data collected from various species. Qualitatively, we applied ethological frameworks to interpret behavioral patterns observed in the field and laboratory settings.

2 Passive defense

2.1 Behavioral adaptations

Moths employ behavioral adaptations to reduce the risk of predation. For instance, moths unable to hear sounds often evade bat predation by flying rapidly or erratically in direction. Certain moth species also choose hiding spots such as among leaves or branches to make themselves less detectable by bats.

2.2 Scale wing absorption of ultrasound

Moths possess scale wing structures that play several crucial roles in their survival (Fig. 1). For example, brightly colored scales can serve as warnings to predators, deterring predation. Scale wings also generate camouflage during bat ultrasound detection, thereby confusing bats. In instances where moths inadvertently land on sticky webs, selective shedding of scales allows them to escape. Scale wings absorb ultrasound, thereby reducing echo reflection and lowering the detectability of moths in bat echolocation [1-2]. This ultrasound absorption significantly decreases the risk of moth predation by bats. The detectable distance of moths by bats is closely related to the distribution of their scales, which can be classified into ground scales and covering scales. Research has shown that the removal of moth

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scales directly leads to a decrease in the distance at which bats can detect moths by 5% to 6%.

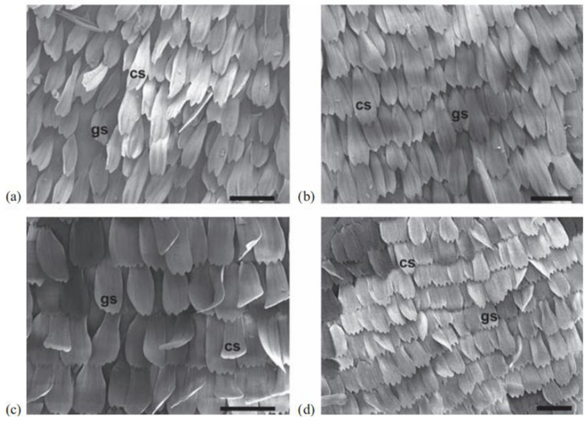

Fig. 1. Scanning electron micrographs of the hind wings of two moth species, illustrating the presence of ground scales (gs) and cover scales (cs), which effectively absorb ultrasound.

2.3 Acoustic camouflage

Acoustic camouflage is a defense strategy employed by moths to reduce detection by predators using environmental acoustic properties. For instance, when moths perceive the presence of predators in their surroundings, they may selectively perch on rough surfaces to confuse bats. These rough surfaces typically scatter and absorb sound, thereby reducing the propagation distance and intensity of sound emitted from the moths' body surfaces. Therefore, perching on rough surfaces decreases the moths' acoustic detectability, making them less likely to be detected by predators. This acoustic camouflage strategy involves moths selectively utilizing environmental surfaces with specific acoustic properties to lower their own acoustic detectability, thereby enhancing their survival rate.

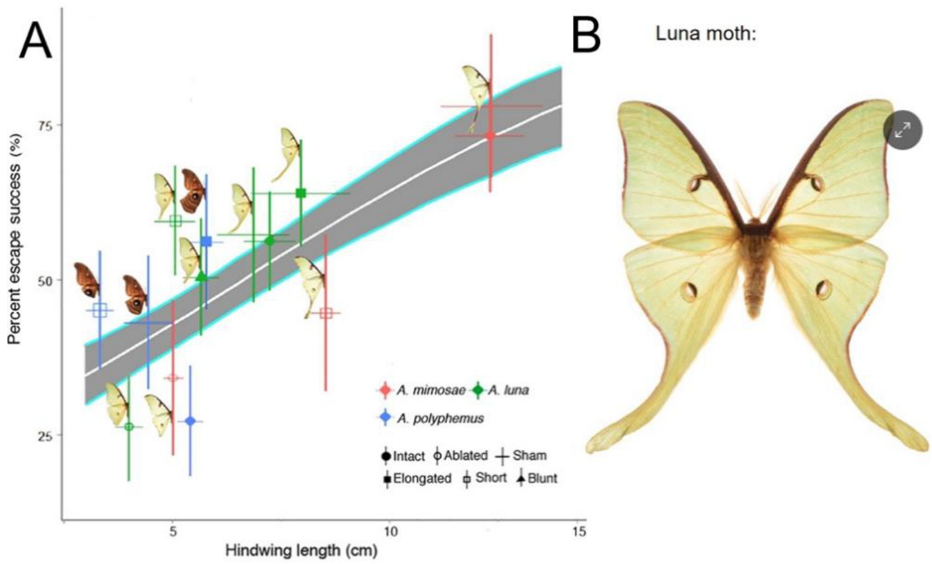

Fig. 2. Longer hind wings of moths can lead to misdirected bat attacks.
A, Moths with longer hind wings increase their escape rate from bat attacks by [number a].
B, Luna moth (Actias luna) with exaggerated hind wings, image from FLORIDA MUSEUM PHOTO BY GEENA HILL.

2.4 Acoustic batesian mimicry

Similar to the eyespots found on many butterflies and beetles that divert visual predators' attention, some moths exhibit characteristics of acoustic batesian mimicry. Acoustic batesian mimicry can attract the attention of bats and lead to erroneous attacks. A typical representative morphology includes elongated hindwings of moths, such as those observed in the Luna moth, which serve as alternative targets (Fig. 2). Moreover, studies indicate that Luna moths rotate their exaggerated hindwings during flight, confusing bats' sonar navigation used for imaging and locating prey and other objects [3-4]. This significantly increases their survival chances during hunting or protects vital body parts. Interestingly, in the evolutionary process of Saturniidae moths, their elongated hindwings have independently evolved elongation four times, highlighting the importance of hindwing acoustic batesian mimicry in the evolutionary arms race between moths and bats.

2.5 Chemical defense

Chemical defense refers to moths utilizing toxins or other chemical compounds derived from their own secretions or decomposition of toxic plants [5-6], making themselves taste bitter or causing tissue damage to predators, thereby deterring predation within their species. Tiger moths (Arctiidae) can utilize pyrrolizidine alkaloids (PAs) to produce bitterness and toxicity, thus reducing predation by bats. From their larval stages, tiger moths feed on specific host plants rich in PAs, whereas adults absorb PAs directly from dried plant surfaces. Conversely, moths like Arctiidae can store cardiac glycosides (CGs) accumulated during their larval stage in their body tissues, which are then secreted from neck glands upon adulthood emergence, effectively deterring bat predation [7-8].

3 Active defense

3.1 Ultrasound production

Some moths can generate ultrasound by contracting and relaxing muscles to vibrate their tympanic membranes, producing ultrasound waves similar to those of bats. Certain species have evolved specialized microtympanic membranes to enhance the complexity of ultrasound production. Two hypotheses exist regarding the purpose of ultrasound produced by moths: the first suggests moths use these sounds for intraspecies communication, while the broader accepted view is that moths emit ultrasound to directly interfere with bat hunting. Sonar interference refers to the emission of highly disruptive acoustic signals by numerous moths, characterized by varying intervals, frequency modulation, and periodicity, potentially disrupting bat echolocation during attacks. These features indicate moths may have evolved mechanisms to interfere with bats' echolocation systems. Three widely accepted interference mechanisms explain moths' use of clicks to disrupt bat localization systems: the phantom echo hypothesis, range-finding hypothesis, and masking hypothesis.

3.2 Evasive flight

Evasive flight refers to moths detecting bat ultrasound emissions in advance and adjusting their flight trajectory subtly to avoid precise bat detection. Research shows bats continuously adjust their flight direction and speed in response to changes in bat calls. Typically, moths employ behaviors such as diving, looping, and zigzagging to evade bat pursuit. Some moths have evolved specialized tympanic membranes of specific shapes to counter-locate bats and adjust their evasive flight accordingly. Interestingly, studies indicate certain moths with tympanic membranes on both sides can use differences in arrival time or intensity between the two listeners to gather information about the direction of sound sources.

3.3 Acoustic warning

Moths use acoustic deception to evade bats, mimicking the ultrasound emitted by toxic moths as a warning signal to bats. Bats learn to identify these sounds and associate them with unpleasant feeding experiences. Consequently, they avoid moths emitting these sounds. Some non-toxic moths mimic these sounds to reduce predation risk, exploiting this widespread bat response as an effective self-defense mechanism.

4 Biomimetics insights

Biomimetics draws inspiration from biological structures, functions, and behaviors in nature to inspire innovative engineering designs. Through long-term evolution, organisms have developed efficient mechanisms to solve complex problems, such as the optical properties of butterfly wings, the extraordinary strength of spider silk, and the hydrodynamic capabilities of dolphin skin. These natural phenomena inspire scientists and engineers to develop more efficient and environmentally friendly technologies and products. In nature, the predator-prey relationship between moths and bats has driven moths to evolve a range of sophisticated adaptations to evade bat echolocation predation. These adaptive features include auditory systems capable of detecting ultrasound, wing scale structures capable of disrupting bat echolocation, and the ability of certain moth species to communicate and defend using ultrasound emissions. These features are crucial for the survival of moths and provide valuable insights for biomimetics. Contemporary biomimetic research has utilized these moth characteristics to design novel acoustic sensors, demonstrating immense potential in acoustic imaging, environmental monitoring, and medical diagnostics. Meanwhile, the scale structure of moth wings has been imitated to create new acoustic materials for sound absorption and noise reduction, enhancing acoustic stealth. These advancements foreshadow an increasingly important role for biomimetics in future developments.

4.1 Applications of directional listeners

Directional listeners are specialized auditory organs capable of precisely determining the direction of sound sources. This ability is crucial for many animals, relying on sound for evading predators, finding food, social interaction, or mating. In nature, larger animals typically utilize spatial differences between their two ears, such as differences in the time, intensity, and phase of sound arrival at each ear, to calculate the location of sound sources and achieve sound source localization. However, for smaller organisms such as certain insects, the distance between their two auditory organs is too small to determine sound source direction using traditional time and intensity differences.

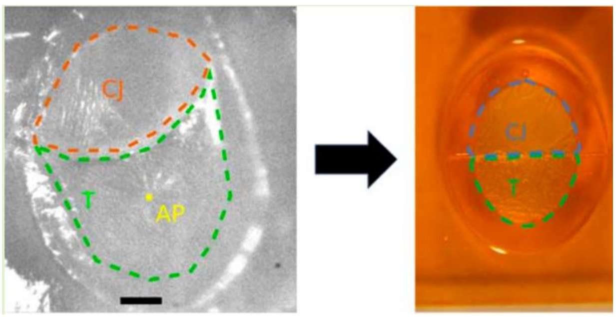

Fig. 3. Biomimetic Applications Based on the Tympanic Membrane Structure of the Wax Moth.
On the left is the tympanic membrane structure of the wax moth, and on the right is the 3D-printed model of a directional listener based on the wax moth tympanic membrane.

In such small-sized organisms, the design of directional listeners is particularly ingenious. The lesser wax moth (Achroia grisella) achieves single-ear directional hearing through the unique shape and structure of its eardrum, even though the distance between its two ears is much smaller than the wavelength of ultrasound.

Lara Díaz-García et al. modeled and simulated this listener, utilizing 3D printing technology [9-10], to create a small-scale directional listener based on moth biomimetics. By mimicking these biological auditory mechanisms, engineers can design smaller, lighter, and more efficient directional acoustic devices, greatly advancing related technologies (Fig. 3).

4.2 Acoustic metamaterials

Acoustic metamaterials are a class of artificial materials with unique acoustic properties controlled by their structure rather than their inherent material properties. Thomas R. Neil et al. discovered that the complex scale layers on moth wings act as acoustic metamaterials with extraordinary physical attributes. This structure can achieve up to 72% sound absorption in the ultrasonic range, particularly within the frequency range used for bat echolocation, despite being only 1/111th the thickness of the longest absorbing wavelength. These scales function as resonant unit cells [11], interconnected through the shared wing membrane, forming a metamaterial capable of broad-bandwidth, deep subwavelength absorption. This collective absorption effect surpasses the sum of individual scale absorptions, providing moths with acoustic camouflage against bat echolocation.

The acoustic metamaterial of moth wings holds significance not only biologically but also offers new design inspirations in engineering and materials science. By mimicking this structure, scientists and engineers can design higher-performance noise reduction devices that absorb wide-bandwidth sounds while being lightweight and ultra-thin, meeting aerodynamic constraints on wing weight and thickness. Furthermore, the design principles of these nature-inspired acoustic metamaterials could find applications in other fields such as architectural acoustics, noise control technologies, and potentially in medical imaging and acoustic sensors.

5 Conclusion

Through a comprehensive analysis of moth defense strategies, including passive mechanisms like behavioral adaptations, scale wing structures, acoustic camouflage, and active defenses such as sonar interference, flight evasion, and acoustic warning signals, a complex defense system is revealed. These mechanisms not only hold biological significance but also provide novel design inspirations in engineering and materials science. In the application of biomimetics, we witness how moth characteristics stimulate the development of innovative technologies. For instance, the application of directional listeners demonstrates how mimicking the moth's monaural directional auditory capability can lead to the design of compact acoustic devices. The development of acoustic metamaterials utilizes the acoustic properties of moth wing structures, offering new avenues for the design of high-performance noise reduction devices. These advancements illustrate that biological traits from nature can be translated into efficient solutions for real-world problems. Ultimately, the ongoing battle between moths and bats presents numerous new approaches and methods for technological innovation, bringing countless opportunities for scientific and technological development. Overall, this study provides a comprehensive analysis of the defensive strategies employed by moths, revealing the intricate ways in which these nocturnal insects have adapted to survive in a world filled with predators. By examining the unique social behaviors exhibited by moths in response to bat predation, our research not only contributes to the understanding of animal social behavior diversity but also highlights the innovative ways in which evolutionary pressures have shaped the complex social interactions within the animal kingdom. The findings of this study offer novel insights into the field of ethology and have significant implications for future research in animal communication and defense mechanisms

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