Super Moth: Moths Hear and Talk Back to Incoming Bat Predators

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Imagine going through a day not being able to hear whatsoever. You may become startled more easily by your approaching friends, you would not be able to jot down any notes in lecture, and overall you may feel like you had lost an important dimension of your senses. Now, couple not being able to hear with also not being able to speak—life would surely take a turn for the worse. With no way to hear or communicate you would begin to feel completely isolated from the world around you. Through this quick scenario, the importance of being able to both hear and speak becomes clear. We may sometimes take our senses and abilities for granted, but for many organisms, changes in the ability to hear and produce sound can become a game of life or death.

The ability to hear sound from approaching predators lends a great survival advantage to prey. Thus, a great selection pressure is placed against organisms that cannot hear. While not all insects have the ability to hear, the sound arms race is one that many insects take part in—a plethora of insects, including crickets, locusts, mantises and beetles, use the ability to hear sound produced by predators to their advantage (Miller & Surlykke 2001). However, one particular insect not only hears approaching predators, but also utters a response back, the moth. Moths of the super family Noctuoidea, which contains Noctuidae and Arctiidae moths, have ears on the lateral surfaces of their metathorax (Miller & Surlykke 2001). The metathorax is the most posterior segment in the thorax, and it bears the third pair of legs. It is in this last segment that the ears are located. The moth ear is somewhat similar to a human ear, in that it is composed of a tympanic membrane. However, it differs from a human ear in that it consists of two types of sensory cells (Alcock 2009). These ears function to allow Arctiidae moths to hear approaching bats. However, Arctiidae moths, such as the tiger moth, can also produce ultrasonic clicks when they hear bat signals (Miller & Surlykke 2001). The ultrasonic clicks, which are produced by buckling of the tymbals (Miller & Surlykke 1985), are speculated to have many functions (Miller 1991). An active debate surrounds the meaning of these clicks, and as such, clicking sounds produced by moths have been hypothesized to have many functions against predators. Clicks can serve to startle bats, jam sonar, or warn of unpalatability due to the presence of toxins (Miller & Surlykke 2001). However, no one knows for certain the mechanism behind how the clicks affect bats. While many of these hypotheses are likely and can explain the use of clicks in moths, the evidence surrounding the production of clicks as an aposematic warning holds particular weight—especially in the face of newly discovered moths that mimic these warning clicks.

One of the hypotheses concerning why arctuiid moths produce sound revolves around the concept that ultrasonic clicks may serve to startle bats. Several insects have been suspected of using this predator startle mechanism. Ultrasonic clicks produced by peacock butterflies were shown to startle inexperienced bats, thus preventing capture (Mohl & Miller 1975). Thus, the clicks were assumed to have a function similar to eyespots—both eyespots and sound serve to surprise attacking predators. Further, in a study conducted by Surlykke and Miller (1985), tiger moth clicks did startle some of their bat subjects to varying degrees. Their most nervous bat completely flew away from the test platform when exposed to moth clicks. Additionally, another one of their subjects used a completely different hunting tactic when subjected to moth clicks. Eventually, all the bats habituated to the clicks and were not startled by them, unless they were used out of context (i.e. using clicks in the middle of a trial that previously had not used clicks) (Surlykke & Miller 1985). This habituation response was also seen in the bats exposed to clicking peacock butterflies (Mohl & Miller 1975). Due to the quick habituation of bats exposed to insect clicks, it is doubtful that the startle response is the sole reason for the production of clicks (Surlykke & Miller 1985). Thus, for clicks to have any real effect on predators, predators cannot be frequently exposed to clicks. Once a naïve bat encounters a few clicking moths, he will cease to be startled by them. As a result, it is not likely that the startle hypothesis is the best explanation behind why arctuiid moths produce clicks.

Another explanation for why arctuiid moths produce clicks centers on the sound interference or jamming hypothesis. Many researchers have speculated that moth clicks are used at precise times when the bat's sonar is most vulnerable to interference. Moth clicks are remarkably similar in frequency to echolocation calls produced by bats as they locate their prey (Foulard et al. 1979). Additionally, the clicks, which are similar in acoustic characteristic to bat calls, can be misinterpreted as echoes. This may interfere with information processing in the bat at a critical time when a mistake can result in a deadly collision (Foulard et al. 1979). The degradation in the accuracy of hunting bats caused by moth clicks was shown to have a critical window of 1.5 milliseconds (Miller 1991). During this 1.5 millisecond window, the bat's range accuracy was degraded by about 4000% in the presence of clicks. Bats exposed to clicks in the 1.5 millisecond window can mistake their own sonar echo for the echo of the moth's click. This startling finding suggests that moth clicks may disrupt neural timing, resulting in an overshot or undershot compensation for range (Miller 1991). Another explanation is that the similarity of moth click calls to moth echoes may create the illusion of phantom prey targets, thus contributing to a sort of acoustic camouflage (Corcoran et al. 2010). As such, it seems that moth clicks may function to jam or interfere with bat sonar, causing phantom targets and range degradation that cannot be immediately compensated for. This interference allows a quick escape by the moth.

While the interference/jamming hypothesis seems to hold water at first sight, several findings point to holes in the theory. For instance, it was found that perfect bat call replicas had only a slightly higher sonar degradation rate than background noise. That is, random noise caused almost as much sonar interference as a perfectly mimicked bat call. Thus, for moths to reap any benefit from the interference hypothesis, they would have to nearly perfectly mimic each bat call every time (Corcoran et al. 2010). Further, the fact that clicks must be made within a 1.5 millisecond window to have an interference effect is highly limiting. Some clicks may by chance fall within the window, but it is nearly impossible for moths to position every click in the small window needed to interfere with bat sonar (Foulard et al 1979). While the jamming/interference hypothesis is not the most improbable, it just does not seem completely realistic that moths can perfectly time their clicks in the window needed to really affect bat sonar and range.

The most likely reason for moth clicks seems to be the warning or aposematic hypothesis. Many insects are brightly colored to advertise to predators that they are distasteful or noxious. While aposematic defense usually refers to the presence of warning colors, it can also describe the warning clicks produced by arctiid moths. Moths of the family Arctiidae are highly unpalatable due to the presence of toxins harbored in their bodies (Miller & Surlykke 2001). Additionally, arctiids are one of the only species of noctuoid that produce ultrasonic clicks. Thus, evidence supports the notion that clicks may have a warning function.

In a study carried out over several days, researchers found that bats quickly learned to avoid the noxious clicking arctiids (Hirstov & Conner 2005). Further, the bats only avoided the clicking moths that were associated with bad taste. Moths that clicked but did not have chemical defense were readily eaten, while muted arctiids that were caught were always spit out and rejected, presumably due to bad taste from chemical defense (Hirstov & Conner 2005). Additionally, researchers discovered that tiger moths with a low duty cycle, meaning the moths produced a few clicks per modulation cycle, supported the acoustic aposematism hypothesis (Corcoran et al. 2010). Moths that use low duty cycles, where clicks are few and spread out, support the aposematic hypothesis because the function seems to be to produce enough clicks to simply warn a predator, as opposed to producing many clicks—which is more closely associated with the jamming hypothesis (Corcoran et al. 2010). Another study conducted by Barber et al. (2009) showed that naïve bats discriminated between arctiids, that is, they could tell the difference between two tiger moths, but they generalized the aposematic meaning of the clicks. In accordance with the results found by Hirstov and Miller, Barber et al. also found that clicking moths without chemical defense were readily eaten, while bats failed to learn to avoid chemically protected moths that did not produce clicks. This finding supports the warning hypothesis and also shows that chemical defense and click production are necessary if the bats are to associate moth produced ultrasonic clicks with unpalatability (Barber et al. 2009). Additionally, the research shows that bats have finely scaled ability to discriminate between prey, even though they generalize aposematic meaning across multiple species (Barber et al. 2009). These findings, combined with an additional new discovery, support the reasoning that arctiid moth clicks have an acoustic aposematic function.

There are many mimics in the insect world. Usually, mimics are seen in the visual realm. Common examples of visual aposematism are the monarch and viceroy butterflies. Monarchs feed on milkweed, a toxic plant that makes them unpalatable. As such, their bright color warns predators of their toxicity. Viceroy butterflies are palatable, but use marking and coloration similar to the monarch (Alcock 2009). While at first the data presented may seem to deter the evolution of acoustic moth mimics, research has shown that like visual mimics, sound-producing moth mimics do indeed exist. Decades of research have pointed to acoustic mimics in snakes, owls, honeybees and droneflies (Barber & Conner 2007), so why not the moth?

Although bats can learn over time not to avoid sound producing moths with no chemical backup, bats have also been shown to avoid moths producing clicks even when they are palatable (Barber & Conner 2007). Over time, some bats do indeed learn the palatability of the sound-producing mimics, but this development does not happen rapidly. For instance, in Barber's study, only three of the ten bats learned the palatability of the moth mimics. The other seven never learned that the mimics were palatable, and they continued avoiding sound producing moths altogether. Thus, acoustic mimics can reap some benefits (Barber & Conner 2007). Regardless of their palatability, sound producing tiger moth mimics can enjoy survival advantages from both bat populations that specialize on moths, and bats that are infrequent moth predators (Barber & Conner 2007). Bats that are frequent moth hunters may at first generalize the sound meaning (Barber et al. 2009), while bats not familiar with hunting moths may be startled by the presence of the clicks (Surlykke & Miller 1985). In both cases, sound producing mimics may be able to get away unharmed, even though they do not possess a chemical defense.

Even though some predators may discover the true nature of mimics, many bats will continue to avoid sound-producing moths altogether. As a result, the benefit of producing sound, and potentially having a higher chance of escaping a predator, vastly outweigh the costs of remaining silent. Although, mimics can reap survival benefits, it is worth noting that mimics are under strong selection to adhere to the constraints of the noxious tiger moth model (Barber et al. 2009). However, in general, the tendency for bats to avoid sound producing moths outweighs the cost of testing out their palatability and possibly making a fatal mistake. The stand-off between moth mimics and bats results in a scenario that can favor the development of acoustic mimics. Further, the presence of mimics who reap survival benefits by producing acoustically similar sounds supports the notion that the acoustic aposematic hypothesis is likely the driving force behind the production of ultrasonic clicks in arctiid moths.

Hearing and sound have many important functions in our daily lives. Our ability to hear and speak links us with the world outside and is very important to our sense of connectedness and well-being. However, hearing and sound production are not only important to humans, as represented by the use of ultrasonic clicks in arctiid tiger moths as an important defense mechanism that increases survival chances in the face of bat predators. Ultrasonic clicks have been hypothesized to have many functions; clicks can be used to startle predators, jam or interfere with bat sonar or act as an acoustic aposematic warning signal. It is most likely that clicks are used to warn predators of unpalatability, as bats must be naïve to be startled or frightened by the clicks, and clicks must be precisely timed and strategically employed to have a significant effect on bat sonar. Additionally, the emergence of sound producing moth mimics further supports the hypothesis that clicks are used to warn predators. However, any way the problem is viewed, the ultimate reason for the use of clicks is clear—clicks give arctiid moths a survival advantage that allows them to escape bat predation.

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