

A review of the Use of Acoustic Organs in Insects in Terms of Predatory Behaviors

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Abstract. Acoustic organs, generally involved in sound generation and hearing, play a crucial role in insects, particularly in communication and mating behaviors. However, although rare, they also contribute to predatory behaviors. Some well-known examples include parasitism in various parasitic flies like *Emblemasoma* sp., aggressive mimicry in bush crickets (*Chlorobalius leucoviridis*), which imitate the female cicada's response song, and the use of stridulation by myrmecophilous social parasites like butterflies (*Maculinea* sp.) and beetles (*Paussus* sp.) to infiltrate ant nests. Despite the significance of these behaviors, research in this area is limited due to barriers such as lack of facilities and difficulties in collecting samples. Consequently, few studies have been conducted on acoustic behaviors in predatory contexts compared to other major uses like mating. This article will review several general studies on these three aspects, summarizing the methods and findings. The studies indicate that playback experiments and observations play a crucial role, that these behaviors are highly specialized for survival, and that challenges such as limited sample collections remain.

Keywords: aggressive mimicry, parasitism, myrmecophilous, predation, stridulation.

1. Introduction

Hearing and sound production play a very crucial role in the lives of insects. In the summertime, we often hear the songs of crickets, cicada, and many other insects. These behaviors are commonly used for social interactions, such as mating calls, and are also employed by some insects to avoid predators like bats. Insects may have been the first animals to develop sound-perceiving organs, and many species possess [1]. These calls are typically essential in speciation and serve as a form of behavioral isolation [2].

While it is rare, some insects use this specific behavior for predatory purposes. These sounds are often species-specific, as seen in many myrmecophilous social parasites [3]. Insects' auditory organs have evolved to perform slightly different functions and are uncommon even within the same family of insects. For example, parasitic flies use these hearing organs for sound localization to locate their host insects, which is also crucial for their life cycle as they need to deposit larvae in the host, where they develop.

Due to scarce resources and difficulties in this field of study, there have been relatively few studies, and lots of aspects remain unknown. This paper will review some of the existing research, summarizing the results and conclusions. The aim is to provide a more comprehensive understanding of these studies and offer inspirations for further research.

2. Introduction to acoustic behaviors of insects

Sound production varies greatly among insects. For example, some cicadas and moths use tymbals, through the bending and releasing of cuticular springs in their exoskeleton, while some grasshoppers produce sound through stridulation or wing clapping. Hearing, on the other hand, is involved in pattern recognition and sexual signaling, such as the response songs of female bladder grasshoppers (*Bullacris* sp.) [4]. Despite the diversity of hearing organs in insects, they generally consist of three parts: a tympanal membrane, a tracheal air space, and scolopidial sensory units [5]. According to Insect Hearing and Acoustic Communication by Hedwig [1], seven insect orders possess acoustic organs: butterflies and moths (Lepidoptera), locusts, crickets, and bush crickets or katydids (Orthoptera), flies (Diptera), cicadas and water striders (Hemiptera), beetles (Coleoptera), mantids (Mantodea) and lacewings (Neuroptera). Sounds can be received both externally and internally. For example, in bush katydids, the ears are often located on the two forelegs, and each ear consists of two tympanal membranes. In addition to external sound input, there is also an air-filled tube known as the acoustic trachea [6]. Beyond hearing, sound generation and stridulation play crucial roles in acoustic behaviors. It is known that interneuron structures are quite similar despite differences in the patterns generated [7]. For instance, stridulation organs are found in 30 beetle families and typically consist of elevated pars stridens with fine parallel ribs and a plectrum [8]. These sounds are generated through intracellular stridulations [9]. The various patterns produced by these acoustic structures serve different functions, including mating, courtship, aggression, defense, and aggregation [8].

3. Acoustic behaviors related to predation

As mentioned earlier, the use of hearing organs varies significantly among insects. While most insects use these organs during mating and reproduction, predatory behaviors also represent a notable application of hearing organs. In the following part, we will explore several representative examples of how hearing organs are used in predatory behaviors. These behaviors demonstrate a high level of specialization towards specific hosts and provide evidence that, from an evolutionary perspective, hearing plays a crucial role in the life cycle of these insects. Specifically, I will discuss acoustic parasitism in various parasitic flies, aggressive mimicry in bush crickets, and stridulation in social parasites like butterflies and beetles within ant nests.

3.1. Acoustic parasitism

Certain parasitic flies (Diptera) have developed hearing organs that help them locate their hosts, usually cicadas, by detecting their calling songs. Two specific families that exhibit this behavior are Sarcophagidae and Tachinidae, with *Ormia ochracea* and *Emblemasoma* sp. being particularly well-known examples. Although these flies have a preference for specific hosts, their larvae can successfully develop in several host species [10]. For example, *Ormia ochracea* is attracted to various *Gryllus crickets*. These flies are highly specialized in their behavior. The ears of female *Ormia ochracea* are most sensitive to the peak frequencies of cricket songs [11]. Their hearing organs are used for finding and selecting hosts, which involves habitat localization, host localization, host discrimination, and host acceptance [12]. This process relies heavily on interaural amplitude and interaural time differences [13], meaning the flies use the distance between their ears and the time difference of sound arrival to locate the source [11]. As sound arrives, the ear closer to the source experiences a significantly greater amplitude [14]. While many animals increase the distance between their ears to improve sound localization, this is less feasible in a tiny fly, where the acoustic sensors are only 520 μm apart, resulting in a time difference of just 1-2 μsec . According to Robert et al., 1996, a simple model has been constructed to explain the response of *Ormia ochracea* [14]. In this model, the fly's auditory system is divided into two components: one where the two tympana vibrate out of phase and another with a higher natural frequency, the tympana vibrate in phase. Both modes contribute to the fly's ability to detect a broad range of frequencies.

3.2. Aggressive mimicry

In the bush cricket subfamilies of Tettigoniidae, *Chlorobalius leucoviridis* performs an astonishing behavior of acoustic mimicry. This aggressive mimicry behavior generally occurs when a predator mimics the signal of its prey to lure them in for predation. A well-known example of this is the bolar spiders, *Mastophora* sp., which chemically mimic the sex pheromones of fall armyworms, *Spodoptera frugiperda* [15]. Very similarly, the Australian katydid *Chlorobalius leucoviridis* attracts male cicadas from the Tribe Cicadettini by imitating the acoustic reply signals of female cicadas [16]. This is possible as the male cicada will sing a species-specific song with specific elements that triggers a response in females. By mimicking the "wing flick sound," made by females, the katydid is able to attract male cicadas to fly toward them, only to become prey. Due to the fact that *Chlorobalius leucoviridis* is the only species in its genus and the only known katydid capable of this behavior, there has only been one study on it.

3.3. Myrmecophilous

Another possible use of acoustic organs in insects is by social parasites, which infiltrate ant nests. Social parasites, often referred to as myrmecophiles, are guests of ants. Since ant nests provide a well-protected, stable environment rich in resources [17], many other insects attempt to integrate into ant community for protection and food. Ants produce air-borne pressure waves through stridulation [3], and some myrmecophiles exploit these signals for nestmate recognition, essentially disguising themselves as ants. In addition to chemical signals like pheromones and physical adaptations, sound production plays a crucial role for certain myrmecophile insects, including beetles and butterflies. For instance, Paussini, known as "ant nest beetle", prey on adult ants and their broods. They possess 3 different stridulation organs, according to a study by Di Giulio et al. in 2014 [18]. Type I organs are located on the hind legs and basal abdominal ventrites, consisting of a stridulatory file and scraper. Type II organs, found only in the genus *Euplatyrhopalus*, are hypothesized to be involved in mating behaviors, while Type III organs are unique to *Platyrhopalopsis*. These findings suggest that these organs evolved independently 3 times, with mechanoreceptors that perceive vibratory sounds, which may contribute to speciation. Compared to these beetles, butterflies are more "mutualistic". Among the Lycaenidae family, 523 species across 63 genera have been observed as ant guests [19]. These butterflies possess nectar glands, which entice ants to drag them back to their nests.

4. Review of past studies

In this section, this paper will review seven studies that provide a comprehensive overview of the use of hearing organs in predatory and parasitic behaviors. These articles cover all the species previously discussed across the three different categories of usage. The review will address the relationship between the insect and its host, the key variables, procedures, major findings, and some of the controls and limitations in these studies. The goal is to identify commonalities in the research methods and assess how they contribute to our understanding of these insects. Ideally, this review would offer a broad perspective on these insects and inspire future studies.

4.1. Acoustic parasitism

The infection behavior of the parasitoid fly *Emblemasoma auditrix* and its host, the cicada *Okanagana rimosa*, was studied by Schniederkötter and Lakes-Harlan in 2004 [13]. The study involved observing cicadas that were captured and pinned to loudspeakers covered with cloth. The sound was stopped when flies arrive and resumed if a fly stayed for 2 minutes without any action. After each trial, nearby vegetation was disturbed by researchers, and the location was changed. If a fly was distant from the cicada, it would land either directly on or near it; if close, the fly would move sideways and search for the caudal end of the cicada, suggesting that visual organs are used for short-range host finding. After depositing a larva, the fly would immediately fly away. The results indicate that the fly spent significantly more time on female cicadas due to their defensive behaviors, with a lower attack rate compared to males. Also, no female cicadas were found injured or infected with larva. However, due to

limitations in collecting hosts, few defensive behaviors were observed, and a preference for the left side of cicadas was noted. A related species, *Okanagana canadensis*, exhibited more defensive behaviors, including protest songs, but the fly remained on the host and seemed unaffected by the song. In this case, escape appeared to be the only effective defense.

Farris et al. studied the auditory sensitivity of an acoustic parasitoid (*Emblemasoma* sp., Sarcophagidae, Diptera) and the calling behavior of its potential hosts in 2008 [20]. The research focused on host preferences by using playback and observation methods. Sound traps mimicking cicada calls, specifically those of *Tibicen pruinosus* or *T. chloromera*, were used to attract the parasitic flies. Dissection of the flies revealed a fused thoracic ganglion. In this study, only female flies were trapped (as only females need to lay eggs), so the specific species could not be identified. The study suggests that fly attraction increases with sound intensity, with the most flies responding to songs between 3 dB and 6 dB. Unlike katydids, which will be discussed later, the flies were attracted throughout the day, overlapping with the chorus time of *T. chloromera* and preceding the start of *T. pruinosus* chorus. However, more data is needed for further conclusions.

Another genus of parasitic flies, *Ormia* sp., also shows a range of potential hosts with different preferences. In a 2006 study by Gray et al. titled “Behavioral specialization among populations of the acoustically orienting parasitoid fly *Ormia ochracea* utilizing different cricket species as hosts” [11] b, behavioral specialization was tested on different hosts through field experiments using traps with playback recording of cricket songs [11]. This experiment was conducted with the knowledge that the fly had been introduced to Hawaii, and the study itself was a replication of a study by Walker in 1993 [21]. The study primarily focused on the song preferences of crickets by the flies. Field phonotaxis experiments were conducted using synthetic cricket songs, as these synthetic songs accurately replicate species-specific stimuli. The experiment method was similar to the previous study: involving field playbacks of cricket songs to track the numbers of flies attracted to each song. Two synthetic songs are created for each cricket species, and the recordings were made under controlled temperature conditions. 4-night replicates were conducted in multiple locations: Florida, Texas, Los Angeles, and Hawaii. A total of 768 flies were caught over 28 nights of playbacks, and the data was analyzed using ANOVA. The results suggest strong behavioral specialization among different populations of flies, with local host songs typically being the most preferred. This findings indicates an adaptive behavioral phenotype, which likely drives the evolution of genetic adaptation. These results are consistent with the Walker’s earlier study.

4.2. Aggressive Mimicry

As there is only one study on this topic, there isn’t much to compare. The study “Versatile Aggressive Mimicry of Cicadas by an Australian Predatory Katydid” by Marshal & Hill in 2009 [16] explored how katydids respond to specific elements of male cicada calls. When the katydid produces the correct respond song, it attracts male cicadas, who mistake the katydid for a female cicada. The study primarily used two methods: playback experiments of cicada songs to caged katydids and direct observations. The katydid were released into a tent with cicadas and left undisturbed for a few minutes before observation began. The results showed that the katydids responded correctly in 22 out of 26 trails, with a 90% accuracy. Generally, the calls of the cicada can be separated to 3 types: simple songs with 1 echeme, non-cueing songs, and complex songs with multiple cueing sections. It was observed that katydids were less likely to respond to complex songs, but they usually produced correct response songs. Interestingly, the katydids occasionally switched between song types during their responses. A sonagram was also graphed, showing the responses cues of the katydid alongside the cicada species. Observations also suggest that these katydids did not respond to cicada songs in darkness but instead generated their own calling songspossibly indicating that the clicking sound is primarily a method used for preying on cicadas.

4.3. *Myrmecophilous*

Di Giulio et al. conducted this study in 2015: The Pied Piper: A Parasitic Beetle's Melodies Modulate Ant Behaviors [22]. The main finding of this study is the ability of the beetle to mimic the sound of the queen. Other than chemical mimicry, this study investigates the acoustic behavior of *Paussus favieri* and its host ant, *Pheidole pallidula*. The samples were collected and kept under artificial conditions. 276 sound sequence measurements of ants and 482 pulses of beetles are examined. Specimens are placed on microphones, and playback experiments are used. The sound of the beetle, ants' queen, worker, soldier, and two controls were recorded. Observations were made and behaviors like walking, guarding, antennating, digging and staying were recorded. Sound sources were randomly assigned to perform a blind experiment in order to eliminate any researcher bias. All equipment is deeply cleaned after each trail. Findings suggest that sounds of ants are produced by abdominal stridulatory organs, queen and soldier sounds were not distinguishable on the basis of pulse length and frequency. The beetles are able to generate 3 kinds of sounds. The Mann-Whitney test was used to analyze pulse parameters and showed no difference between the sexes of the beetle. To compare variation between 3 sounds, Pa, Pb, and Pc, Univariate analysis and Generalised Linear Models (GLM) were used. A principal components analysis (PCA) was also used. There is a significant separation between the sounds of Pc and Pa, Pb; the sounds slightly overlap with queens and soldiers. The control group also suggests that the beetle is able to distinguish and mimic the sound of its host. A nested analysis of similarity (ANOSIM) of the Euclidean distance matrix demonstrated a separation between signals produced by queens, soldiers, workers, *Paussus favieri* Pa, Pb, Pc. Pulse Pa has the same pulse length as those of workers and soldiers, Pb is more similar to sound of workers and Pc is more similar to the queen.

Comparison of acoustical signals in *Maculinea* butterfly caterpillars and their obligate host *Myrmica* ants by DeVries and Cocroft in 1993 focused on the butterflies [23]. In this study, pulse rate, dominant frequency, pulse length and bandwidth is measured for the 5 butterfly species in genus of *Maculinea* and 4 ant species of *Myrmica*, two separate butterflies and an ant species were also recorded and measured as the control group. The Mann-Whitney U-test was used for all variables. PCA is used to compare which butterfly is the closest to its host. It also determined how often the call was more similar to that of an incorrect host ant. The different recordings of each species were listed, a tabular comparison of single variables was done. Results suggest that ant calls have a significantly higher pulse rate but similar pulse length and dominant frequencies; there was no fine-level convergence between pairs of ant and caterpillar, the sound is broadly similar in these variables measured: some of them are more similar to wrong kinds of ants. This also suggests that chemical signals could be one of the essential communication channels.

Variation in Butterfly Larval Acoustics as a Strategy to Infiltrate and Exploit Host Ant Colony Resources by Sala et al. in 2014 separated caterpillars into cuckoo species and predator parasites, and pre- and post-adoption phases of ants were distinguished [24]. Compared to the previous study, only 2 butterflies, *Maculinea alcon* and *M. teleius* and 1 ant species *Myrmica scabrinodis* are investigated. This is a study largely based on observations. Specimens were placed on microphones in artificial cages. Spearman-Rank-Correlation was used to measure the sound parameters. ANOVA and PCA were used to test the difference between the group of sounds. For behavioral studies, the speaker was placed under soil at the bottom of the cage, adjusted to natural loudness; selected ant behaviors were observed, including antennating, guarding, alerting, and digging. The results suggest that ant queens produce sounds a lot higher in frequency. The pre- and post-adoption stages of caterpillar change the sound. *M. alcon* larvae in the post-adoption phase are much more similar to the sound of queens while *M. teleius* is more similar to workers. PCA is graphed peak Frequency, IQRBW, Pulse Length, Peak Power, ANOVA F-ratio and ANOVA p. Based on a t-test and Normalised Euclidean distances, The signals emitted by butterfly larvae in pre- and post-adoption were significantly closer to the stridulations of queens than to those of workers. In post adoption stage, stridulations are distinguishable among two butterfly species but are equally similar to the queen, and playback experiments suggest the sound produced by the cuckoo species tend to promote high amounts of worker response. The cuckoo species emitted sounds that exceeded the intensity by 4 dB, while predator parasites were 8 dB lower than those of the queens. This

also supports the previous study's finding that the sounds weren't perfectly matched. pre-adoption *Maculinea* species are equally similar to ant queens, while *M. teleius* is more similar to the queen in the post-adoption stage. This suggests the dynamic nature of the use of stridulation and that though both butterfly species can mimic the sound of the queen the number of responses triggered is very different.

5. Conclusion

As previous studies suggest, observation and playback experiments are two key methods for investigating the hearing and sound-producing organs of insects. These studies carefully control variables to ensure accurate results and minimize bias. They highlight the specific behavioral adaptations of the species being studied and demonstrate high dependence of these insects on their hosts. While the structural aspects of hearing organs have not thoroughly investigated, behavioral studies serve as an important basis for working on structures of these hearing organs. However, as many studies state, there is limited study in the three fields discussed previously, and unavoidable limitations exist. This is mainly due to the difficulty of locating and collecting these insects, as they are scarce, hard to capture, and present technical challenges. For examples, all the parasitic flies attracted in these studies are females, as only females need to lay eggs on hosts, and males do not even require hearing organs. These physical constraints make studies quite difficult to conduct.

Although these topics are not widely covered in the articles and don't contribute significantly to the development of technology, we can still observe various constructions of models, especially related to parasitic flies, such as those developed by Robert, Hoy, and other pioneering investigators [25] [26]. Moreover, a study by Michael L. Kuntzman and Neal A. Hall created a silicon-micromachined prototype that mimics the structures of *Ormia ochracea* and showed capabilities like sound localization [27]. Although these studies are still rare and their practical applications are not yet apparent, they have the potential to be useful in many fields in the future. Therefore, despite seeming irrelevant, studying these small and seemingly insignificant creatures is still very important.

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