A Battle of Intelligence: Review of Organismal Eavesdropping and Predation

Tate Rosenhagen
Lake Forest College
Lake Forest, Illinois 60045

ABSTRACT

In the complex natural world, organisms constantly seek to gain an advantage in any way possible to survive, including eavesdropping on signals from other organisms. Eavesdropping is the interception and reading of signals that are not intended for the recipient. Those signals can be both interspecific communication between similar trophic level organisms and predator-prey relationships. Both the predator and the prey can eavesdrop on each other's signals, whether they be auditory, vibrational, or pheromonal. In this review paper, I examine the different forms of eavesdropping that exist, beginning with intraspecific eavesdropping and interspecific eavesdropping of the same trophic level to examine the mutualistic and commensality of such eavesdropping and the multiple ways they exist. This will be followed by an examination of predator and prey eavesdropping and the multiple sensory modalities in which they eavesdrop, auditory, vibrational, and chemical, as well as a specific dive on the eavesdropping involving sexual pheromones. I also examine the unique relationship of a three-way parasitoid eavesdropping relationship, and a plant trapping prey pheromonal eavesdropping relationship. This paper aims to summarize multiple forms of eavesdropping and the need for further study on eavesdropping of sexual pheromones.

INTRODUCTION

Since the beginning of life, organisms have been in a constant search for nutrients in order to survive. As time progressed, some organisms became predators and others became prey. Both predators and prey have evolved ways to communicate in order to signal food availability, warn of threats, and find mates, such as winter moths releasing pheromones to find a mate and bees stingers releasing pheromones to encourage other bees to sting its target, which are all driven by survival.

Naturally, each organism, both predator and prey, evolved methods to locate and either hunt or avoid each other, respectively. This act, known as eavesdropping, is where an organism intercepts and responds to a signal not meant for the receiver, and locates the signaler or recipient via said signal. Eavesdropping can occur across a variety of modalities such as sounds, pheromones, and vibrations and can be intraspecific, prey eavesdropping predators, and predators eavesdropping prey.

This article aims to review the multiple forms in which eavesdropping occurs in nature. While this review paper is not exhaustive of all possibilities and relationships in which eavesdropping occurs, it serves to create a baseline of knowledge and inform the readers of the ways eavesdropping exists in nature, beginning with predators eavesdropping on their prey. Within this section, I review literature showing eavesdropping through vibrational stimuli and pheromone eavesdropping, two different media in which predators locate their prey, and where multiple signals are intended for mating but observed by predators. I also discuss the reverse relationship, prey eavesdropping on their predators to avoid predation, again through the media of vibrational stimuli and pheromone eavesdropping, with a further emphasis on the duality of this relationship between predators and prey. Finally, I move into intraspecific competition, within both predator species and prey species, discussing vocal stimuli and varying response to warning cries in prey animals. I then end by briefly discussing some of the complex real-world examples of eavesdropping, such as a fungus eavesdropping on its prey and an example of a vector placing hormones on a plant for the plants parasite to locate, then consuming the parasite from the plant, also known as an eavesdropping web.

This paper is designed to educate readers on the topic out of an abundance of interest from the writer. Understanding of the complex ways in which organisms eavesdrop on each other helps create a better understanding of the ecosystem, niches, and how organisms coexist with each other in such complex ecosystems. It is also vital to understand how invasive species may have an edge in eavesdropping in their new environment. Invasive species create mayhem throughout an ecosystem or even towards one organism, such as what happened to the Kiwi, a small, flightless bird in New Zealand that has no native predators but has since become endangered after the introduction of dogs and rodents to the island.

Predator eavesdropping prey

Organisms communicate across a variety of media when trying to signal for danger, food, mates, among others. One such media over which they communicate is through vibrations, something commonly only thought of after auditory and pheromonal signaling but is an efficient way to communicate and one way in which predators can eavesdrop on prey. For instance, the sand scorpion, a nocturnal, burrowing predator that can locate its prey by eavesdropping on vibrational stimuli conducted by the sand (Brownell & Van Leo Hemmen 2001). This serves as a huge benefit to the scorpion as, given the time and way in which it hunts, tapping into the vibrational network in the sand will aid a scorpion in knowing when prey is nearby. The desert scorpion, *Paruroctonus mesaensis*, evolved specialized receptors on the tips of its arms in order to eavesdrop on this vibrational network, known as the slit sensilla. With this receptor, *Paruroctonus mesaensis* are able to sense vibrations through the sand approximately 20 centimeters away from their receptor, as calculated by vibration source localization model designed by Brownell and Van Leo Hemmen (Brownell & Van Leo Hemmen 2001). This study attempted to mathematically model the sensory field of the scorpion, calculating the degrees at which the slit sensilla are angled when the scorpion in the hunting stance, and then making an 'informed guess' to account for the neuronal mechanism through which the stimulation reached and activated the scorpion's brain (Brownell & Van Leo Hemmen 2001). Their theory involves an educated guess along with their mathematical model and lined up very well with their anticipated results to the stimuli presented in their experiment. Thus, suggesting a slight similarity to the auditory pathway (Brownell & Van Leo Hemmen 2001).

Furthermore, one of the most common ways in which predators can eavesdrop on prey is through pheromones, which are hormones that are given off and sensed by another member of the same species, typically for mating purposes. However, pheromones are also used in social insects to communicate colony identity and coordinate group behavior. Predators are believed to cue into these pheromones to locate prey easier, such as the case of the great tit and blue tit picking up pheromones from the winter moth. The winter moth, *Operophtera brumata*, emits a pheromone to attract mates when landing on trees. To further examine its behavior, an experiment was set up involving placing artificial larvae on trees (Saavedra & Amo 2018). Half of the trees were sprayed with the winter moth's reproductive pheromone, and half were not, and it was found that more trees sprayed with the pheromones were attacked by their predators. In addition, regarding the trees sprayed with pheromones, a greater percentage of larvae were attacked on those trees than the trees without the pheromone (Saavedra & Amo 2018). This is similar to the eavesdropping performed by *Odontoponera transversa*, a termite raiding ant that uses pheromones to track its prey. In this example, *O. transversa* was able to perceive two different pheromones, DDE and DEO, given off by the various termites during their foraging activities (Wen et al. 2017). Between the two pheromones, the termites first studied the secretion of DOE on their initial foraging trail while they initially searched for food. At this stage, there are few termites on the trail or around the foraging termite. However, once food was found, DDE was released along the trail, which acts as a recruiting pheromone to other termites, leading to a larger number of termites moving along the newly marked trail. *O. transversa* were found to distinguish between these two hormones. Moreover, when both hormones were present, they hunt along the DDE trail as it leads to more abundant prey (Wen et al. 2017). By being able to perceive their prey, both *O. transversa* and pheromones, the blue and great tit, were able to successfully locate prey, giving them an advantage for finding food in their environment.

Furthermore, the ability of predators, such as O. transversa, to distinguish between pheromones and act upon the pheromone that gives them the largest amount of prey is clearly incredibly important to their predation habits.

Finally, it should be noted that predator-prey eavesdropping is not limited to insects and animals. An interesting example of this is the nematode-trapping fungus, which is capable of eavesdropping on pheromones given off by its nematode prey. While most commonly known eavesdropping relationships between predator and prey are between animals and insects, carnivorous fungi have been found to eavesdrop on ascarides, which are a conserved family of molecules secreted by soft soil nematodes (Hsueh et al. 2013). These fungi developed a relatively small number of traps in their neutral state. However, when certain concentrations of ascarides are present, the fungi observed, *Arthrobotrys* oligospora, not only perceives the pheromone but rapidly develops more traps to catch their nematode prey (Hsueh et al. 2013). This serves as a reminder that eavesdropping is occurring on various scales and involving organisms we may not see or think about daily. Besides, it provides evidence of the complexity of the ecosystem as well as the intensity of the fight for survival between a multitude of creatures living in it.

Prey eavesdropping predators

While predators can eavesdrop on their prey to discern their location and hunt them down, prey are not defenseless in this struggle. Studies have shown that just as predators are able to perceive prey's signals across multiple media, prey are also able to do the same thing. In the previous section, I described how predatory ants are able to track pheromones given off by termites, but termites are able to eavesdrop on the ants as well. Furthermore, in the relationship between the termite, *Coptotermes acinaciformis*, and their predatory ant, *Iridomyrmex purpureus*, *C. acinaciformis* eavesdrops on the footsteps of the ant (Oberst et al. 2017). Originally, they were unsure whether the method of eavesdropping was chemical or vibrational in nature, since termites communicate amongst themselves in both manners. They tested this by playing recordings of ants walking while termites were in containers with no ants present. They found that termites responded in the manner matching how they responded to ants in the wild, with termite soldiers banging their heads into the substrate or shaking their bodies to sound the alarm (Oberst et al. 2017). This information helps to paint the larger picture of the relationship between predators and prey; neither of them exist in a vacuum, rather, they both eavesdrop and react to each other.

Another example of prey eavesdropping on predators is seen through the Giant Asian honey bee, which detects pheromones from predatory ants to avoid predation during foraging. Often, as previously discussed, predators use pheromones, specifically sexual pheromones, to locate their prey. However, in such instances, the opposite occurs. In this relationship, line weaver ants, *Oceophylla smaragdina*, ambush the Giant Asian honey bee, *Apis dorsata*, by hiding underneath a flower and waiting for the bee to land before leaping up and attacking them. While this is a somewhat rare event for the honeybee, it still poses a threat. *A. dorsata* has developed olfactory senses to sense the ants and avoid them (Li et al. 2014). They tested this by placing wire near an ant colony and waiting until about thirty ants, the average number of ants which ambush the bees, have crawled along the wire (leaving their pheromones on the wire). Then, they extracted the pheromone from the wire and administered it to flowers in the nearby area. Other flowers were baited naturally with live ants. The researchers found that bees avoided both the live ants and the pheromone, which pointed to the eavesdropping on the pheromone (Li et al. 2014). Moreover, the fact that the bees avoided both the live ants and the pheromones, which will be circled back to later in the paper as an example of intraspecific eavesdropping, is the fact that *A. dorsata* releases alarm pheromones when harmed on a flower to alert other honeybees not to land on the same flower. To remove this error from their data, researchers removed the bees as soon as they landed on the flower, so no attacks could happen and no pheromone was released, which was important as honeybees avoided flowers with this alarm pheromone present (Li et al. 2014). This prey-predator eavesdropping assists in helping the Giant Asian honey bee avoid predation by both picking up on their predator's trail pheromones and being able to leave a warning pheromone to others in the event of an attack, highlighting the multiple warning signs and complexity of the eavesdropping relationship.

Further exemplifying the complex relationship is the fact that both predators and prey are able to eavesdrop on each other, which has already been briefly discussed. This complex scenario is highlighted in the relationship between brown rats and house mice, both of which can perceive the other's pheromones and hunt or avoid the other, respectively. In this study, the 'counterespionage' hypothesis was tested, which, as previously stated, claims that both predator and prey perceive the opponents' pheromones and react accordingly, to locate and hunt prey or locate and avoid predation (Varner et al. 2020). In this experiment, an experimental plot was set up containing food and testosterone on either side of the plot. One side contained the pheromone of the other species pheromone as well as testosterone, which was present to make sure the organisms were not simply avoiding any pheromone present. While their data did show that each organism was aware of the others presence, their results were rather confusing at first glance as both mice avoided the rat pheromones, as expected, but also the rats avoided the mice, which was the opposite of what should happen according to their hypothesis (Varner et al. 2020). Even though this data seems surprising, it makes sense when you put into context the set-up of the experiment, where the rats had an abundant and constant supply of food. The authors believe that the rats weighed the benefits of hunting the mice versus the risk of injury and, with a constant supply of food there, found no reason to take that risk. Furthermore, the brown rats are opportunistic predators of mice, not specifically mice hunters, which may have further weighed into them avoiding the mice. However, even with this data, the scientists were able to show that both the rats and mice can sense each other's pheromones and respond to them, setting the table for further tests on the specifics of the organisms' responses (Varner et al. 2020). With a better experimental set up, such as making the rats hungry before the test and with a different breed of rat or another test organism all together, like feral cats, the authors may find data that aligns more with their hypothesis and depicts an accurate reflection of predator-prey dynamics (Varner et al. 2020).

It should be noted that this method of prey-predator eavesdropping, or eavesdropping in general, is not limited to animals: plants perform this as well. While plants cannot move to avoid their predators, they are able to increase defenses to protect themselves from further predation. This eavesdropping can be explored through a variety of medias once again, but one astonishing way in which the plant *Arabidopsis thaliana* eavesdrops on its predators is by picking up on vibrations of their predatory caterpillars, *Pieris rapae* (Appel & Cocroft 2014). When exposed to vibrations simulating caterpillar feeding mechanisms, the authors found that chemical defenses, particularly glucosinolate and anthocyanin, give these plants a higher chemical defense to their predators than unstimulated plants. This is fascinating to see as it means the plants are able to distinguish between vibrations caused by caterpillar predation and those caused by wind, bumps, insect songs, and raindrops, only eliciting a response in the presence of predation (Appel & Cocroft 2014).

Prey-Prey and Predator-Predator eavesdropping

As I have already established, predator-prey eavesdropping results in an interesting dynamic between the two organisms, with each organism using the information provided by eavesdropping to locate and either hunt or avoid the other. However, eavesdropping is not purely limited to the predator-prey relationship and can happen both intra- and inter-specifically by both predator and prey organisms. For example, in the case of the Brazilian free-tailed bats, *Tadarida brasiliensis*, intraspecific eavesdropping is used often to help them locate prey. As is very well documented, bats use echolocation to help them locate and hunt prey at night. These echolocation calls emit a strange buzzing sound that can be audible if one is near bats while they are hunting. As *T. brasiliensis* approaches a prey target, it emits a specific 'feeding buzz' right when it attacks its prey, which other bats are able to recognize as a signal of nearby prey (Gillam 2007). F urthermore, the author tested if it was the sound alone that made the bats swarm to an area as a signal prey was nearby; he found that when he played the feeding buzz, the feeding buzz backwards, and a silence control, the feeding buzz created the largest response by the bats (Gillam 2007). The sensitivity of *T. brasiliensis* to the call shown by recognizing the forward playing feed buzz best shows how specific this eavesdropping mechanism is and the advantages the bats gained in intraspecific competition by eavesdropping on their fellow bats. This ensured the individual eavesdropping was aware of any prey found by the rest of the swarm and allowed them to quickly move to and consume prey before it was gone.

While predators compete interspecifically by eavesdropping as we just discussed, prey can eavesdrop on other prey species signals to find food or avoid predators. In the case of the African plains, numerous predators are present and able to attack at any moment, including lions, leopards, and cheetahs, making it both important and challenging for prey animals to keep an eye out for their predators. In an interesting paper written by Palmer and Gross, alarm calls by Impalas, Wildebeests, and Zebras were examined and played to each species to examine their response to said calls. Not only did they respond to the alarm calls of other species, but they also reacted differently to each call based on the predators of the species giving the call (Palmer & Gross 2018). The authors found that Zebra calls elicited the largest response by all of the study species as the Zebra's predator is the Lion, a common predator for all of prey mammals, while the Impala's warning cries elicited the smallest response, as Impalas are much smaller than the other prey and thus had a larger variety of predators that did not prey on the Zebra and Wildebeest (Palmer & Gross 2018). The responses were sorted into vigilance, grouping, alarming, and fleeing, though every animal with every response exhibited signs of vigilance. The Impala can be seen to flee at any call, including the control, further showing their understanding that any predator in the area is likely to play upon them, while the Wildebeests and Zebras were more likely to only be alarmed. On the other hand, Zebra calls were responded to by every species, although the response of fleeing, grouping, or alarming varied in response to common predators (Palmer & Gross 2018). This interpretation of each call serves to benefit each animal by allowing them to be more aware of their surroundings and potential predators while tailoring their response based on the organism the alarm came from.

Eavesdropping Webs

In the context of the three different eavesdropping relationships we have already discussed, there are a few unique eavesdropping examples that I believe warrant their own section. One such example is a nematode-trapping fungus, which is capable of eavesdropping on pheromones given off by its nematode prey. While most commonly known eavesdropping relationships between predator and prey are between animals and insects, carnivorous fungi have been found to eavesdrop on ascarides, a conserved family of molecules secreted by soft soil nematodes (Hsueh et al. 2013). These fungi developed relatively small number of traps in their neutral state, but when concentrations of ascarides are present, the fungi observed, *Arthrobotrys* oligospora, not only perceives the pheromone but rapidly developed more traps to catch their nematode prey (Hsueh et al. 2013). This serves as a reminder that eavesdropping is occurring on scales and involving organisms we may not see or think about daily, and that the ecosystem is an incredibly complex fight for survival between a multitude of creatures living in it.

The final unique example I plan to discuss in this section involves a unique, three-wayrelationship between an insect, plant, and parasitoid. In this relationship, *D. citri* is a specialist parasitoid that harms its host plant, citrus trees. *D. citri* is able to eavesdrop on a bacterial vector known as Las, *Candidatus Liberibacter asiaticus*, to find its host plant (Martini et al. 2014). In this relationship, Las is also incredibly harmful to the citrus trees and can cause huanglongbing, a deadly disease in the citrus plant and the release of MeSA, which is a plant-defense-hormone that attracts the parasitoid's predator, *Taxarixia radiata*, to act as a 'bodyguard' of the plant. This bodyguard then consumes the parasitoids after a slight amount of damage has been done to the citrus tree, and the combination of the damage by the parasitoids and the infection by Las makes the citrus plant no longer attractive to parasitoids; this allows the tree to continue to grow with the Las infection inside of it (Martini et al. 2014). The parasitoids not preyed upon will also leave the plant after consuming some of the citrus tree leaves due to the increased chemical defenses, which can spread the Las infection to nearby trees, wreaking havoc upon a tree farm. This serves as a fascinating example of an incredibly complex eavesdropping relationship between a bacteria, plant, parasitoid, and predatory wasp to continue to spread the infection to nearby plants while preserving the initial plants health.

Eavesdropping webs like this add a further layer of complexity to the ecosystem that cannot be noticed when looking closely at an individual organism but can be observed when looking at the bigger picture. If we look throughout other ecosystems, there may be other examples of complex eavesdropping webs that may give us a greater understanding of the ecosystem where the relationship resides.

Conclusion

In review, these findings of eavesdropping interactions through different medias, in different relationships and ecosystems, and between animals, plants, bacteria, and insects across a range of complexity is of great importance to the scientific world. To truly understand the complexity of an ecosystem, eavesdropping relationships must be considered throughout the various organisms present in this ecosystem. While the authors all found eavesdropping relationships in the organisms they studied, the common thread amongst all the papers is the need for further study, further relationships to be explored, and further research into the mechanism behind the eavesdropping relationships.

Furthermore, the possibilities of future studies are endless. In the case of the citrus trees I discussed earlier, study on the bacterial vectors can be done to help farmers recognize infected plants early to prevent spreading and save crops. On the other hand, the complexity of eavesdropping relationships needs to be considered when introducing species that may become invasive to non-native ecosystems. It would be an interesting study to observe invasive species relationships in their native environment versus their invasive environments to observe any eavesdropping relationships that give them an advantage in their new environment.

In short, eavesdropping is a simple idea with incredibly complex mechanisms, relationships, and implications for the natural world. Further understanding of these relationships may aid in our understanding of the natural world, habitat reconstruction, and identification of possible invasive species to prevent them from ever being introduced.

References

Appel, H. M., & Cocroft, R. B. (2014). Plants respond to leaf vibrations caused by insect herbivore chewing. Oecologia, 175(4), 1257–1266.
Brownell, P. H., & Van Leo Hemmen, J. (2001). Vibration sensitivity and a computational theory for prey-localizing behavior in sand scorpions'. American Zoologist, 41(5), 1229–1240.
Gillam, E. H. (2007). Eavesdropping by bats on the feeding buzzes of conspecifics. Canadian Journal of Zoology, 85(7), 795–801.
Hsueh, Y. P., Mahanti, P., Schroeder, F. C., & Sternberg, P. W. (2013). Nematode-trapping fungi eavesdrop on nematode pheromones. Current Biology, 23(1), 83–86.
Li, J., Wang, Z., Tan, K., Qu, Y., & Nieh, J. C. (2014). Giant Asian honeybees use olfactory eavesdropping to detect and avoid ant predators. Animal Behaviour, 97, 69–76.
Martini, X., Pelz-Stelinski, K. S., & Stelinski, L. L. (2014). Plant pathogen-induced volatiles attract parasitoids to increase parasitism of an insect vector. Frontiers in Ecology and Evolution, 2(MAY), 1–8.
Oberst, S., Bann, G., Lai, J. C. S., & Evans, T. A. (2017). Cryptic termites avoid predatory ants by eavesdropping on vibrational cues from their footsteps. Ecology Letters, 20(2), 212–221.
Palmer, M. S., & Gross, A. (2018). Eavesdropping in an African large mammal community: antipredator responses vary according to signaller reliability. Animal Behaviour, 137, 1–9.
Saavedra, I., & Amo, L. (2018). Insectivorous birds eavesdrop on the pheromones of their prey. PLoS ONE, 13(2), 1–12.
Varner, E., Jackson, H., Mahal, M., Takács, S., Gries, R., & Gries, G. (2020). Brown rats and house mice eavesdrop on each other's volatile sex pheromone components. Scientific Reports, 10(1), 1–9.
Wen, X. L., Wen, P., Dahlsjö, C. A. L., Sillam-Dussès, D., & Šobotník, J. (2017). Breaking the cipher: Ant eavesdropping on the variational trail pheromone of its termite prey. Proceedings of the Royal Society B: Biological Sciences, 284(1853).