frontiers | Frontiers in Ecology and Evolution

TYPE Editorial
PUBLISHED 05 September 2022
DOI 10.3389/fevo.2022.989763

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OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Behavioral and Evolutionary Ecology, a section of the journal Frontiers in Ecology and Evolution

RECEIVED 08 July 2022
ACCEPTED 15 August 2022
PUBLISHED 05 September 2022

CITATION
Bernal XE and Page RA (2022) Editorial: How enemies shape communication systems: Sensory strategies of prey to avoid eavesdropping predators and parasites. *Front. Ecol. Evol.* 10:989763. doi: 10.3389/fevo.2022.989763

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Editorial: How enemies shape communication systems: Sensory strategies of prey to avoid eavesdropping predators and parasites

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KEYWORDS

predator-prey interaction, sensory ecology, animal communication, signal exploitation, parasitoids

Editorial on the Research Topic
How enemies shape communication systems: Sensory strategies of prey to avoid eavesdropping predators and parasites

Animal communication is an impressive phenomenon, with adaptations that dazzle the senses. But communication is a risky business. Signalers strive to produce signals that transmit well, grab attention, and stay in memory. But the very traits that function best for eliciting responses in target receivers open the door to exploitation by eavesdropping enemies, who use them to their advantage and ultimately cause damage to signalers. While traditionally considered a dyadic interaction between a single sender and a single receiver, we now understand that communication occurs in a network, often with multiple diverse receivers attending to a single signal. Eavesdropping natural enemies such as predators, parasitoids and parasites can impose strong selective pressure on communication systems. In response, signalers have evolved numerous anti-eavesdropper strategies to mitigate the tradeoff between eavesdropper detection and conspecific communication. Knowledge of anti-eavesdropper responses in the context of communication provides an opportunity to recognize patterns of strategies used to address this tradeoff and ultimately to understand the evolution of communication systems. Despite well-recognized concerns about the role of sexual ornaments increasing risks to enemies, historically attention has focused on how and why these traits attract females, with much less attention to how signalers confront the dangers of exposing themselves to eavesdroppers. Drawing on diverse research from a range of taxa and sensory modalities, this Research Topic combines the expertise of researchers with new perspectives in the field covering a wide range of research, drawing on both traditional and cutting-edge experimental approaches. The aim of this Research Topic is to bring together studies and perspectives that highlight the strategies used by signalers to communicate under the pressure imposed by eavesdropping enemies.

Eavesdropping across sensory modalities

It has long been recognized that eavesdropping enemies have the potential to exploit communication systems using different sensory modalities. A recent meta-analysis confirmed that eavesdropping predators, parasites, and parasitoids can impose strong selection pressure on sexual signalers (White et al., 2022). Most anecdotal cases and experimental work, however, involve eavesdroppers using acoustic and visual modalities. Until relatively recently, some sensory modalities were assumed to be safer than others, allowing covert communication. But current evidence shows that signals across sensory modalities are vulnerable to exploitation by eavesdroppers. Over the last few decades, for instance, advancement in technology has resulted in our improved ability to quantify and reproduce substrate-borne vibrations. Such developments in the tools available to researchers have opened up our understanding of how this particular type of acoustic signals are also vulnerable to exploitation by eavesdropping predators. Virant-Doberlet et al. highlight how exploitation of vibrational cues by enemies have been neglected, making a strong case for how this sensory modality provides fertile ground to examine and understand eavesdropping on these signals. Hamel and Cocroft elegantly use playback experiments to illustrate that a vibration-sensitive predator attends to vibrational signals produced by offspring in oak treehoppers. Together these studies reveal that, contrary to early predictions, eavesdropping predators increase the cost of social communication in species that signal with substrate-born vibrations.

Similar to signals using substrate-borne vibrations, there has been limited work on the vulnerability of electric signals to exploitation by predators. Stoddard et al. show how eavesdropping by electroreceptive predators such as catfishes and electric eels have imposed selection for traits that increase crypsis in the electric signals of weakly electric fishes. In contrast, chemical signals have attracted more attention given their potential role at luring pests for biological control (Zuk and Kolluru, 1998). Despite studies examining the use of pheromones for capturing predators and thus incidentally establishing signal exploitation is some systems, there has been limited attention to the ecological and evolutionary contexts of those interactions. Using ants as a case study, Adams et al. provide a valuable perspective on the intricate ways in which exploitation of chemical signals can shape behavior, and in particular, communication in social insects. Chemical communication used by social ants is critical to maintaining their cohesiveness and ultimately allows them to function as a superorganism, but it also increases their vulnerability to eavesdropping enemies. The review by Adams et al. highlights the impact that signal exploitation may have in previously unconsidered systems.

Eavesdroppers as curtailers and promoters of sexual ornamentation

In general, we see a common pattern across taxa and sensory modalities: eavesdroppers dampen ornamentation of sexual signals of their hosts or prey. Eavesdroppers impose selective pressures favoring low risk signals, as we see in acoustically signaling moths that adjust the amplitude or the duration of their calls to avoid potentially eavesdropping bats. Nakano and Nagamine found that moths either produce "soft-and-long" or "loud-and-short" calls, likely reflecting low risk strategies to avoid eavesdropping enemies such as insectivorous bats, which are assumed to be a main predator. Similarly, Neotropical katydids, that are a favorite food for gleaning bats, avoid detection by these eavesdropping predators by using very low signal repetition rates. Symes et al. examined katydid signaling behavior in response to bat approaches in the tropical rainforest. While approaches by predatory bats are rare, katydids from some species show characteristic anti-eavesdropper responses to bat echolocation calls by ceasing to call. It is unclear, however, why not all katydid species respond to bat echolocation calls. This study highlights the complexity of interactions between eavesdroppers and their prey given that tradeoffs and their evolutionary solutions can result in diverse strategies in a community.

In the most extreme scenario, selection pressure from eavesdropping enemies can result in a sexual signal being lost completely. Heinen-Kay and Zuk discuss how male Pacific field crickets in Hawaii rapidly lost the ability to sing in response to intense natural selection pressure from an acoustically oriented parasitoid fly. This now classic system of the *Ormia* parasitoid fly and field cricket anchors a discussion of the factors that facilitate signal loss and the role eavesdropping enemies can play at driving this evolutionary outcome. Diverse contexts, and their concomitant costs, could explain outcomes as disparate as those seen across a community of katydids and bats vs. those seen in the Hawaiian crickets.

Eavesdropping enemies do not always curtail the sexual ornamentation of their hosts or prey. Lehmann and Lakes-Harlan found that in aggregations of sexually signaling bush-crickets and cicadas, the opposite may in fact be true. Under the pressure of acoustic parasitoids, males may benefit from singing fast and loud, as calling in a chorus imposes selection to successfully compete against other males. By ramping up signal conspicuousness, males secure a mate, allowing them to drop out of the signaling pool, ultimately reducing the risk of enemy detection.

Eavesdropping on non-sexual communication signals

While work investigating eavesdropping enemies has focused on sexual signals, enemies exploit a wide array of communication signals produced by their prey and host. Hamel and Cocroft examine the risks due to eavesdroppers of parent-offspring vibrational communication in treehoppers. In weakly electric fish, Stoddard et al. show that producing navigational signals can make individuals vulnerable to eavesdropping predators. The dangers of signaling, however, can extend beyond a single species affecting the community. Goodale et al. review the evidence and mechanisms by which eavesdropping enemies may affect communication in mixed species aggregations. Further discussing the effect of heterospecific signaling neighbors at modulating eavesdropper attacks in mixed species aggregations, Trillo et al. present a mathematical model to examine how eavesdropper attractiveness to particular signal features and composition of the aggregation shape the selective landscape for signalers.

The effect of eavesdropping enemies in signaling has been nested in investigations of animal communication. Despite the widespread recognition of the role of signaling in non-animal systems, exploitation by enemies has received little attention. Rebolleda-Gómez and Wood review evidence for eavesdropping in microbial and plant systems, translating our knowledge from animal-based studies to recreate a framework applicable in this novel context. This study presents a robust case for plant-microbial systems as a rich and tractable system to understand how signal exploitation is shaped by species interactions. Rebolleda-Gómez and Wood review highlights the need for a broader approach to our study of eavesdropping systems.

Directions for the future

A common denominator of the contributions compiled in this Research Topic is that, in addition to synthetizing knowledge and information on particular systems, the authors identify fruitful venues for future research. One contribution directly proposes a methodological approach to improve measurements of phonotaxis on eavesdropping insects. Lee et al. use an information-theoretic approach to develop and validate a sensitive phonotaxis performance index to identify eavesdropper preferences for particular signal features. Other contributions extend signal exploitation by enemies to previously unconsidered systems (e.g., social insects: Adams et al.; microbial-plant interactions: Rebolleda-Gómez and Wood), or beyond interactions between a single enemy and its prey or host to community interactions (Goodale et al.; Symes et al.; Trillo et al.). Together these studies highlight diverse, robust approaches that deepen our understanding of the ecology and evolution of anti-eavesdropper strategies.

Conclusion

This Research Topic provides a road map of the overarching themes on anti-eavesdropping strategies. We hope this compilation will motivate researchers to investigate the responses of signalers to enemies that exploit their communication systems and further elucidate how their behavior, signals and sensory systems have been shaped by eavesdropping enemies.

Author contributions

Both authors listed have made a substantial, direct, and intellectual contribution to the work and approved it for publication.

Funding

This work was funded by the National Science Foundation (IOS#1433990 and #2054636 to XB) and by the Smithsonian Tropical Research Institute (to RP).

Acknowledgments

We are grateful to all the researchers that contributed to this Research Topic. We particularly appreciate the support from the Animal Behavior Society (ABS) that provided the funds and space for all of us to come together at a symposium on this topic that we hosted at the 55th Annual Conference of the Animal Behavior Society.

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