HOW ENEMIES SHAPE COMMUNICATION SYSTEMS: SENSORY STRATEGIES OF PREY TO AVOID EAVESDROPPING PREDATORS AND PARASITES

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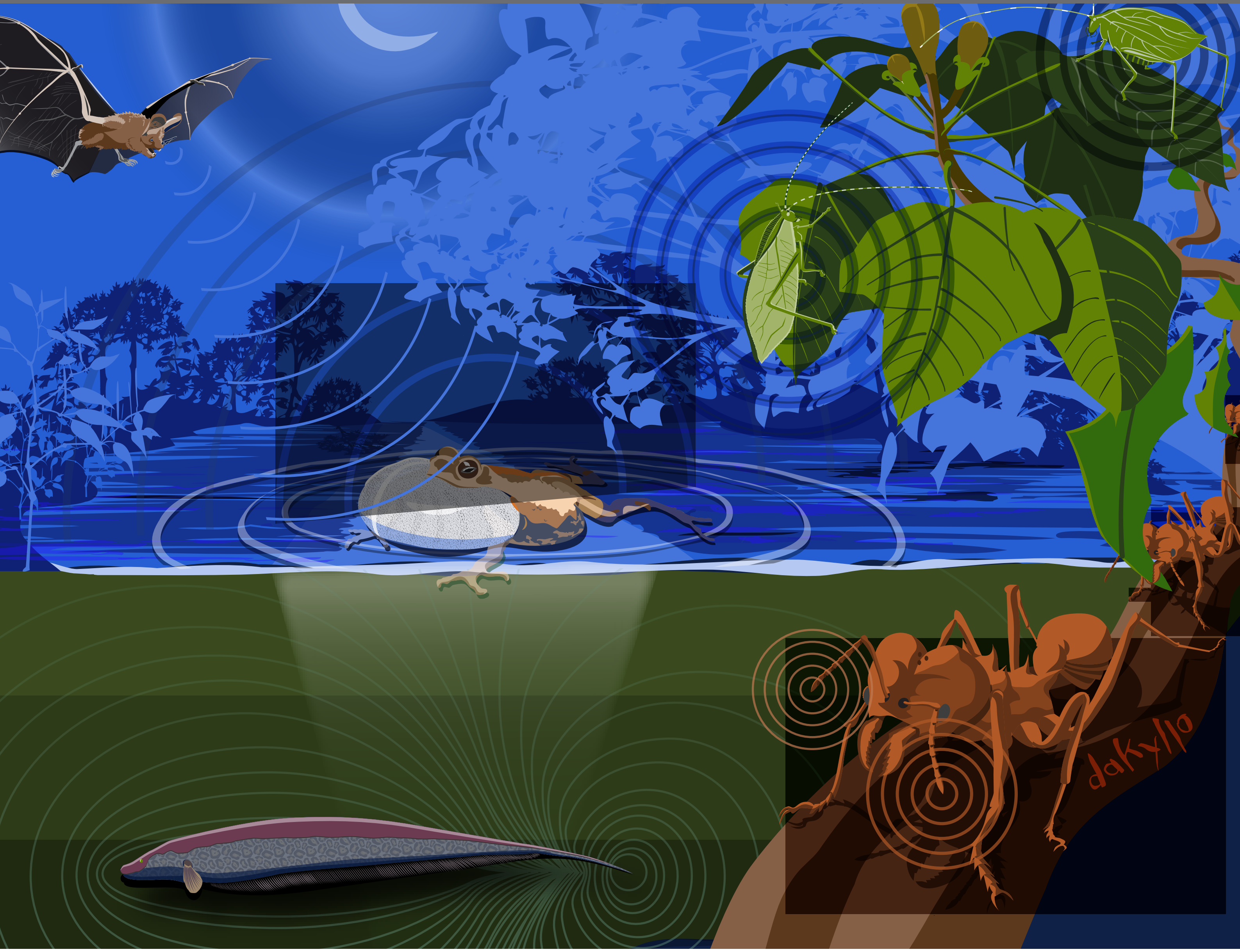

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HOW ENEMIES SHAPE COMMUNICATION SYSTEMS: SENSORY STRATEGIES OF PREY TO AVOID EAVESDROPPING PREDATORS AND PARASITES

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

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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.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Adaptive Strategies in Life-History of Bushcrickets (Orthoptera) and Cicadas (Homoptera) to Parasitoids Pressure on Their Acoustic Communication Systems—A Case for Sociality?

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In sexual reproduction, the search for mating partners elevates the individual's risks of predation and parasitism. One way to increase mate search effectiveness and reduce search costs is acoustic signaling. However, acoustic orienting parasitoid flies exploit singing hosts, leading to high parasitism rates. Aggregations of males and females at mating and singing in choruses might reduce individual risks by dilution and predator saturation. This mini-review reflects on consequences for host's acoustic signaling in choruses using the examples of cicadas and bushcrickets. It concludes that despite antagonistic selection pressure by parasitoids, singing in choruses might select for increased, not reduced signaling in males. The time joining and leaving a chorus might be crucial: once mated, a refractory period will drop males off the signaling pool, preventing parasitism. In a chorus, fast and loud singing might be highly advantageous, supporting the fittest males. Natural selection might have shaped signaling strategies in choruses, which can probably only be understood when applying individual based dynamic modeling.

Keywords: acoustic communication, parasitoid, host finding, host infection, signal plasticity

Mating requires the finding of a partner and the search can expose participants to increased risk of predation, and parasitism (Andersson, 1994). Many animals have, therefore, evolved signaling as a strategy to increase the effectiveness, and simultaneously reduce search costs (Greenfield, 2002). Acoustic communication is a very effective way of sending information and is employed by different insect taxa (Gerhardt and Huber, 2002; Strauß and Lakes-Harlan, 2014). The diversity of potential acoustic options allows for the selection of very specific signals that can create private channels, interfering little with other broadcasters and receivers. Despite the uniqueness of acoustic signals, some parasitoid flies have evolved sensory systems to break into the private communication channel of their hosts and become unintended signal exploiters (Zuk and Kolluru, 1998). Acoustically hunting flies belong to the Tachinidae and Sarcophagidae, with only a few specialized taxa in both fly families. Interestingly, the flies hunt for sound producing hosts from two distinct host taxa: flies of the tribus Ormiini (Family Tachinidae) parasitize singing crickets and bushcrickets (Orthoptera: Ensifera; Lehmann, 2003), while flies of the tribus Emblemasomatini (Family Sarcophagidae) attack cicadas (Homoptera; Lakes-Harlan and Lehmann, 2015). This clear separation of host taxa indicates at least two independent evolutionary processes, each with different adaptations. Neuroanatomy and neurophysiology underline the separate evolution of the hearing sense for host detection (Lakes-Harlan and Heller, 1992; Robert et al., 1992; Lakes-Harlan et al., 2007). The parasitoids are well-adapted to their hosts and are very successful acoustic hunters, resulting in high rates of parasitism (Lehmann, 2008; Lakes-Harlan and Lehmann, 2015).

Within the Ormiini, some radiation might have occurred leading to around 70 parasitoid taxa (including *Ormia*, *Therobia,* and *Homotrixa*) which are specialized on a single species or a limited set of crickets, mole crickets and bushcricket host species (Lehmann, 2003). The radiation could simply be caused by an availability of different host species. Alternatively, avoidance and defense adaptations of hosts to parasitoid pressure could force parasitoid species to a more general host spectrum or a switch of host species. Such adaptations could be realized by satellite males and other alternative behavior (Zuk et al., 1993) and have mainly been reported for crickets and their parasitoids, especially *Ormia ochracea*. Within the Emblemasomatini some parasitoids have multiple host species (Stucky, 2015), whereas the well-investigated *Emblemasoma auditrix* seems to be more selective as it has almost exclusively been found in the cicada *Okanagana rimosa* (Lakes-Harlan et al., 2000). *E. auditrix* shows several host specific adaptations, from ecological preferences to tuning to the auditory cue for host localization and a highly specific host infection behavior (Schniederkötter and Lakes-Harlan, 2004).

We highlight possible processes in the two independent host systems of bushcrickets and cicadas, which are convergently under the risk of parasitism yet share some similarities in the sensory exploitation. One obvious fact is that despite the high parasitism rates, host sensory counter adaptations seem to be less effective in both, the bushcrickets and the cicadas, as host individuals seldom detect approaching parasitoid flies until direct contact. Furthermore, contrary to the selection to reduce calling in some of the *Ormia*-cricket systems, neither the bushcrickets nor the cicadas show signaling reduction as response to the acoustic parasitoids (Lakes-Harlan and Lehmann, 2015). The two host systems share however important life-history aspects; (1) a highly synchronized occurrence of males and females (Williams and Simon, 1995; Lehmann, 2012), including an operational sex ratio close to one (Heller and von Helversen, 1991), and (2) an aggregated occurrence at mating time including chorusing (Lehmann, 1998; Stölting et al., 2004). We review what is known in these systems, and emphasize the importance of social aspects to reduce individual parasitism risk, especially of superior signaling males. Several bushcrickets species of the genus *Poecilimon*, especially those of the *P. propinquus*-group, are well-known hosts of the Ormiini *Therobia leonidei* (Lehmann, 2003). Because of singing, male bushcrickets are under a steady rate of attack from parasitoids, reaching up to a parasitism rate of 65% (Lehmann and Heller, 1998; Lehmann, 2008). Interestingly, bushcricket species of the genus *Poecilimon* hatch, and develop in a highly synchronized manner. Similarly, males show only little protandry, with females following 0.6–3 days after the males, which is extremely short in comparison to other bushcricket species (Lehmann, 2012). Consequently, a close match is found for the time to reach sexual maturation (Lehmann and Lehmann, 2008). However, this pattern of high synchronization is found in all three *Poecilimon* species, with one being a highly parasitized species, the second one a probably parasitized and the third one a species uninfected by the acoustic parasitoid. Hence, environmental factors like the summer drought in Mediterranean habitats depriving the herbivore bushcrickets of their food may select for such synchronization (Lehmann and Lehmann, 2006). Regardless of the ecological drivers, the *Poecilimon* species with unidirectional communication system of signaling males and silent females (Heller, 1984, 1992; Strauß et al., 2014) sing temporarily and locally aggregated. The aggregated males increase singing performance as response to acoustic rivals (Anichini et al., 2018), hence stimulate each other into unstructured choruses (Lehmann, 1998). Such aggregations might increase the total risk for the population but lower the per capita risk of an individual compared to singing in isolation, as found for the cricket-*Ormia* system (Cade, 1981). It has been shown that the acoustically orienting parasitoid *O. ochracea* reduce the propensity of cricket males to sing, especially in the host-parasitoid system on Hawaii (Zuk et al., 2006) where the parasitoid fly seems to be introduced rather recently and have adapted to a new host (Gray et al., 2019). Although no differences in signaling behavior were found between low-risk and high-risk populations in some north American mainland areas attacked by the same parasitoid (Beckers and Wagner, 2012) and predominant parasitism late in the season might even increase not reduce reproductive trait investment (Beckers and Wagner, 2018).

Even with a balancing selection by acoustic parasitoids (Lehmann et al., 2001), *Poecilimon* males increase their investment into songs depending on social environment, such as the number and fitness of competitors, expressed through song parameters (Anichini et al., 2018). Conditionally fitter males (expressed as body mass) produce not only the larger nuptial gifts (Lehmann, 2008; Lehmann and Lehmann, 2009), they also have larger morphological structures for stridulation (Anichini et al., 2017), win song contests against weaker males (Anichini et al., 2018), and are preferred by phonotactic approaching females (Lehmann and Lehmann, 2008). The attractive singers to females might face a dilemma as they are also preferred by the parasitoid flies (Lehmann et al., 2001). We do not know which individual song characters are preferred by females and flies (Lehmann et al., 2001), but in a cross-species comparison the one with the longer songs including several repeated song elements (vs.) is at a much higher risk of infection (Lehmann and Heller, 1998). At first glance this is a paradox as both, sexual and natural selection, seem to act in opposite directions on song characteristics. The solution might lie in the social aspect of a chorus: once a male has attracted a female and mated, it shows a refractory period to produce the massive spermatophore (Lehmann and Lehmann, 2000), which can make up to 30% of a male's body mass as reviewed for the genus (McCartney et al., 2008); consequently it will keep silent for a few days until it is able to remate (Heller and von Helversen, 1991; Reinhold and von Helversen, 1997; Lehmann and Lehmann, 2000). In phonotactic experiments females reach a singing male in less than a minute up to a meter apart (Lehmann and Lehmann, 2006; Lehmann, 2008). However, parasitoid flies are also able to very precisely track and localize a singing bushcricket (summarized in Lakes-Harlan and Lehmann, 2015). Therefore, quick and risky singing might be highly advantageous, if better singers are able to attract conspecific females before a parasitoid localizes them. Once mated, those males drop out of the chorus and are no target of parasitoids anymore lighter, less fit rivals in turn need to continue singing until they attract a female. Mate choice in bushcrickets is best described as a best-of-n search strategy (Lehmann, 2007; Lehmann and Lehmann, 2007); once the fittest male drops out of the chorus, the second best singer will become the favored male (Lehmann, 2007). Females will mate when giving access to a single male (Lehmann and Lehmann, 2008), even if it was the non-preferred singer in a previous phonotactic experiment (Lehmann and Lehmann, unpubl. data). Consequently, the parasitism risk for low condition singers of being parasitized might in fact be even higher when integrated over the reproductive season (**Figure 1**). As *T. leonidei* flies are rarely attracted to loudspeakers (Lehmann and Heller, 1998), we have no direct test for the duration until flies approach their hosts in the field. However, a comparison of the number of mated males per night, estimated to be around 20% (Heller and von Helversen, 1991), with the nightly parasitoid attack rate of 3–7% (Lehmann and Heller, 1998) shows the advantage of mating over parasitism. So, in a simple approximation it is three to six times more likely for a high condition male to attract a female than to be parasitized. This easily would mask the parasitism risk and could also be a pattern found in other taxa.

The cicada *O. rimosa*, as hosts of the fly *E. auditrix*, might show the similar behavioral, and social traits as the bushcrickets. It is under attack by an acoustically orienting parasitoid, possibly influencing signaling behavior. In contrast to Poecilimon not much is known about intraspecific competition and female

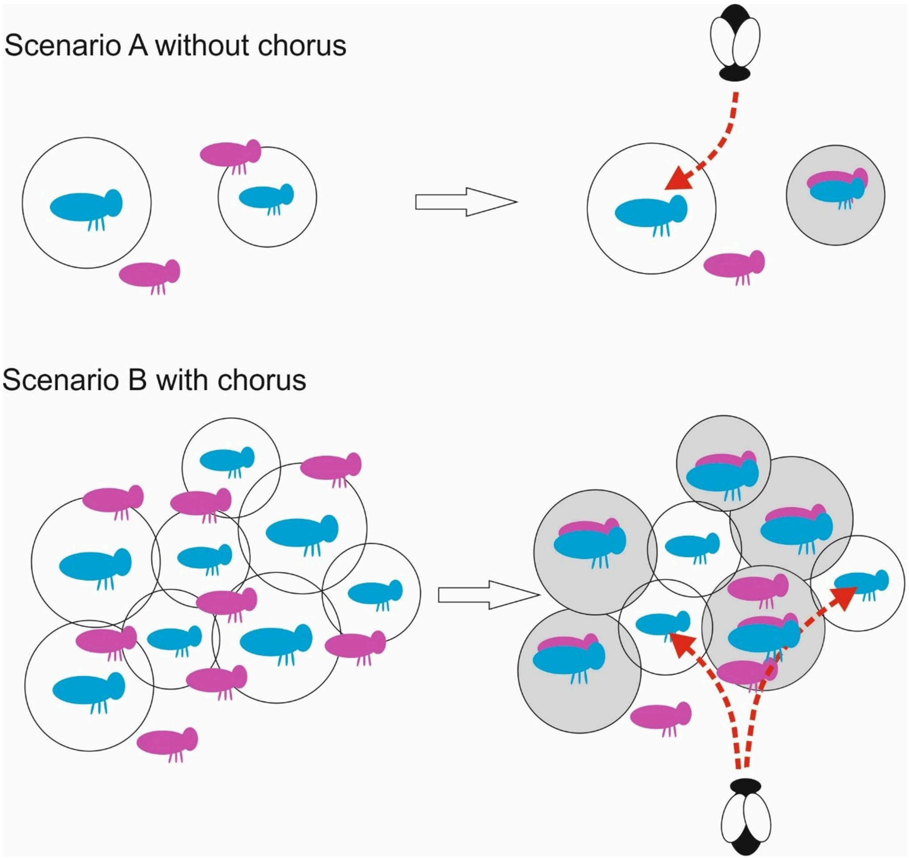

FIGURE 1 | Schematic illustration of possible chorus effect on parasitoids. Singing males (blue) are classified by their sound propagation as superior (large radius) and inferior (smaller radius). Scenario A: In a non-chorus situation, females (pink) may have limited choices, and might mate with an inferior male nearby, due to better sound representation in her nervous system. Overlaid figures indicate mating pairs. This male then stops singing for some time (indicated by a gray circle) and cannot be detected by the acoustically hunting parasitoid. A dipteran parasitoid might then attack the next sound producing male, which might be by chance a superior individual. Scenario B: In a chorus situation males and females are densely packed. Females which are in the broadcasting range of more than one male can select a superior one. As result more superior than inferior males mate and cease song production (gray circle). The parasitoid will affect mostly inferior singers. Some females might remain unmated, as more than one choose the same male (e.g., Lehmann and Lehmann, 2007) or are not in the broadcasting range.

choice. Here we highlight the commonalities and the differences in aggregation calling. Even stronger than in the bushcrickets, the cicada life cycles might have evolved under predation and/or parasitism pressure, having a multi-year life cycle with nymphal stages living several years in the ground (Williams and Simon, 1995). At the extreme end are the periodical cicadas, which emerge in large numbers every 13 or 17 years at a given location (Williams and Simon, 1995). With such prime numbered periodicity, it may be possible to reduce the pressure from predators and parasitoids (Hoppensteadt and Keller, 1976). Modeling confirmed that this prime numbered periodicity could have arisen from such processes (Goles et al., 2001). Connected to the periodical life cycle are mass emergences of adult cicadas, often resulting in large and loud choruses (Williams and Simon, 1995). Such choruses are interpreted as adaptations to predation pressure, as for example birds are saturated due to the high numbers. Chorus synchronization has been reported for the periodical cicada species *Magicicada cassini* (Huber et al., 1990). While not fully periodical, *O. rimosa* populations fluctuate in abundances from year to year making them proto-periodic (Lakes-Harlan and de Vries, 2014). The abundance fluctuations seen today might be an effective measure to reduce parasitization pressure for the cicada, as in poor cicada years the parasitoids quickly become host saturated, which reduces the parasitism risk in the following years. Like the *Poecilimon* bushcrickets, the cicada *O. rimosa* form unstructured choruses where the temporal pattern of the specific calling song is obscured (Stölting et al., 2004). Surprisingly little is known about the auditory behavior of female cicadas acting as receivers. Even simple female phonotaxis is rarely studied in cicadas (but see Doolan and Young, 1989; Daws et al., 1997), and female sexual selection less so. Nevertheless, calling is a prerequisite for *O. rimosa* males to attract females (Stölting et al., 2004) and this signal is similarly exploited by the parasitoid *E. auditrix* (Lakes-Harlan et al., 2000; Tron et al., 2015). Interestingly, the cicada choruses might distract the acoustically hunting parasitoid, as it's phonotaxis is tuned to the temporal structure of an isolated calling song (Lakes-Harlan et al., 2000). Individually calling of single males are noted either in years with low population densities, or early in the season. Such males face strong parasitism pressure, as early in season up to 80% of males have been found to be infected (Schniederkötter and Lakes-Harlan, 2004). *O. rimosa* does not exhibit defense strategies like wing flips or other behaviors to expel the parasitoid (Schniederkötter and Lakes-Harlan, 2004). Individual cicada males cannot reduce the risk of being attacked by a parasitoid by shortening songs, as the parasitoid can detect signals of only 1 s duration (de Vries and Lakes-Harlan, 2003). Chorusing might provide the only possibility to reduce an individual's risk of parasitism (**Figure 1**). The adaptation for chorus calling can be shown by experimentally broadcasting the calling song in silent cicada habitats. If males are present, they produce short calling songs triggered by the stimulus (Stölting et al., 2004), which in turn might result eventually in a chorus. The number of calls increases drastically with start of the chorus, and the number of fly larvae per female *E. auditrix* drops simultaneously by 50–75% (de Vries and Lakes-Harlan, 2005). Interestingly, the success rate of host infection by the parasitoid seems to slow down as the number of larvae per female fly stay constant for the next few days. This finding might be another indication of a protective character of the chorus.

Thus, the cicada chorus with its acoustically hunting parasitoid has several commonalities to the *Poecilimon-Therobia* system and it might serve as testing system for the hypothesis, that successful males are more protected than unsuccessful males. Therefore, we need data on the individual song characteristics of males, the female preferences, interactions within the chorus and preferences of the parasitoid. The same system might also provide the control, as the different abundances between years vary from low density populations with singly calling to high density populations with chorus.

CONCLUSION

Acoustic communication of bushcrickets and cicadas is shaped through selection of acoustic orienting parasitoids. Similar social signaling strategies evolved in the two distinct taxa, which form large choruses. Fitter males might face an advantage through the chorus by mating faster and risking fewer parasitoid attacks as they drop out of the pool of signalers. Thus, this type of sexual communication can be best understood when analyzed in a socially dynamic network, including the individual risk of -and the fitness deprivation by- parasitism. We suggest further cicada experiments to test for a mating advantage of better singers.

AUTHOR CONTRIBUTIONS

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

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REVIEW
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When Does Sexual Signal Exploitation Lead to Signal Loss?

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Evolutionary loss of traits is common over evolutionary time and occurs in diverse taxa. Sexual signals and other non-signal traits should differ in their likelihood of becoming lost because they experience different selection pressures contributing to their diminution or persistence. In particular, conspicuous sexual signals are often exploited by natural enemies; this significant cost can favor signal reduction or loss. Yet sexual signals should also experience strong selection favoring their persistence because they facilitate communication during sexual encounters and their loss would involve changes in both the signaler and receiver. Most examples of sexual signal loss come from phylogenetic studies, so it is difficult to ascertain the context and key factors responsible for their loss. Here, we describe one of the best documented examples of evolutionary sexual signal loss in real time due to signal exploitation: *Teleogryllus oceanicus* (the Pacific field cricket) in Hawaii where many males have lost the ability to sing due to natural selection from a deadly, acoustically-orienting parasitoid fly. Using sexual signal loss in *T. oceanicus* as a model, we identify environmental, social, and genetic factors that appear generally important in driving sexual signal loss due to signal exploitation. We also discuss each putative factor contributing to signal loss more broadly within the context of non-signal trait loss. Overall, the factors that facilitate evolutionary loss of signals and other traits exhibit significant parallels. In general, a significant cost from the environment, weak selection for persistence, and alternative ways of accomplishing the former function appear critical to achieving evolutionary loss of both sexual signals and non-signal traits. However, because few empirical examples of sexual signal loss over contemporary timescales exist, we need more theory and empirical work to better understand the evolutionary dynamics of sexual signal loss.

Keywords: sexual signal loss, trait loss, signal exploitation, signal evolution, sexual selection, natural selection, female mate choice, *Teleogryllus oceanicus*

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EVOLUTIONARY LOSS OF TRAITS AND SIGNALS

How biodiversity is generated in nature is a fundamental question in evolutionary biology. Though research tends to focus on understanding how new traits arise within a population, biodiversity is also created when traits are lost (Johnson et al., 2012; Ha and Nehm, 2014). Research in recent decades, particularly through use of comparative phylogenic methods, has demonstrated that trait loss is common over evolutionary time. Lost traits are diverse, and include the loss of flight in insects and birds (Roff, 1990, 1994), photosynthesis in plants (Merckx and Freudenstein, 2010), lipid synthesis in parasitoid insects (Visser et al., 2010), and eyes and pigmentation in cave-dwelling fish (Jeffrey, 2005; Hyacinthe et al., 2018). One consistent message from trait loss literature is that traits do not become reduced or lost simply because they are no longer needed in a Lamarckian "use and disuse" fashion. Trait loss can only occur when the costs incurred by the trait outweigh its benefits, and then must be possible given genetic and physiological constraints (van der Kooi and Schwander, 2014). At a minimum, all traits bear constitutive costs associated with maintenance and expression of the trait that can favor trait disintegration, but traits often experience additional costs beyond basic maintenance (Lahti et al., 2009). Because traits differ in the balance of selective costs and benefits and genetic and physiological constraints, not all traits should be equally subject to loss.

We suggest that sexual signals, traits important in mate localization and mate choice, should be particularly difficult to lose. Signals are by definition used during communication and mediate the transfer of information between a signaler and receiver (Bradbury and Vehrencamp, 1998). Hence, a drastic change in any signal should also require concurrent changes in the receiver, since otherwise communication will be disrupted. Unless the genes associated with signal production and reception are the same or linked, this will require two separate sets of genetic changes. Furthermore, signals generally evolve because they are mutually beneficial to the sender and receiver. As long as the information communicated by the signal is useful, selection should favor signal persistence. But at the same time, sexual signals can be costly and face strong natural selection limiting their evolution (more below), and phylogenetic studies have demonstrated that sexual signal loss is surprisingly common over evolutionary time (Wiens, 2001).

The goal of this review is to shed light on the drivers of sexual signal loss, particularly when these signals are exploited by eavesdropping natural enemies. We begin by discussing the forces that shape sexual signal evolution and examples of sexual signal reduction and loss. We then highlight a particularly well-documented case of sexual signal loss due to exploitation by a deadly eavesdropper that has been observed in real time (the Pacific field cricket, *Teleogryllus oceanicus*, living in Hawaii). Finally, we synthesize inferences from our empirical case study with other empirical, phylogenetic and theoretical studies of sexual signal loss with work on non-signal trait loss more generally to outline important contributors to the evolution of sexual signal loss in nature.

SEXUAL SIGNAL EVOLUTION AND EXPLOITATION

Sexual signals represent some of the most conspicuous and elaborate traits in nature, and include the iconic peacock train, colorful plumage and mating dances in birds of paradise, and the complex songs of many insects and birds (Andersson, 1994; Zuk and Simmons, 2018). Such signals are critical for securing mates and can play an important role during speciation (Panhuis et al., 2001; Andersson and Simmons, 2006; Safran et al., 2013; Servedio and Boughman, 2017). In general, sexual selection is thought to favor signal elaboration (i.e., bigger, louder, more colorful traits) because the signals are favored by females during mate choice or help males win contests against competitors for access to females (Andersson, 1994). But sexual signals also bear significant costs that can temper this positive, directional selection. For instance, sexual signals are often physiologically costly to produce and maintain, or are difficult to maneuver with when escaping predators (Grafen, 1990; Langerhans et al., 2005; Weaver et al., 2017). Furthermore, because sexual selection tends to favor greater conspicuousness and detectability by conspecifics, sexual signals can also readily capture the attention of unintended receivers such as predators and parasites, which can exploit these signals to localize their prey (Sakaluk and Belwood, 1984; Zuk and Kolluru, 1998; Husak et al., 2006; Heinen-Kay et al., 2015).

Signal exploitation by eavesdropping natural enemies is a major force constraining sexual signal evolution, and includes textbook examples of tradeoffs between natural and sexual selection [reviewed in Zuk and Kolluru (1998)]. For instance, the mating calls of field crickets in North America and Hawaii that attract females is also used by a deadly parasitoid fly to locate its cricket host, which has induced shifts in multiple aspects of cricket song and behavior (Cade, 1975; Zuk et al., 1993; Wagner, 1996). In several species of livebearing fish, males from populations with many predators are less colorful than those in safer populations because the bright colors preferred by females also attract attention from piscivorous fish (Endler, 1980, 1983; Godin and McDonough, 2003; Martin et al., 2014; Heinen-Kay et al., 2015). The vocalizations male túngara frogs use to attract females are also used by frog-eating bats (Tuttle and Ryan, 1981) and blood sucking flies (Bernal et al., 2006) to localize their prey. Sexual signals can even be exploited by eavesdropping humans—bison bellow less in areas where hunting occurs than in protected areas (Sarno et al., 2017). But in most of these cases, even though the signal is reduced or shifted to avoid detection by the eavesdropper, the sexual signal is retained and the communication system remains intact. Does natural selection ever overpower sexual selection and lead to the evolutionary loss of sexual signals?

Looking across phylogenies, both reductions and losses of sexual signals are surprisingly common (Reimchen, 1989; Burns, 1998; Wiens, 2001). This underappreciated trend was highlighted in Wien's (2001) review on the topic, where he showed that loss of sexual signals can be more common than gains over long evolutionary time periods. Since its publication, even more examples of signal reduction and loss have been uncovered. For instance, comparative evidence demonstrates reductions or losses of dorsal crests in newts (Wiens et al., 2011), coo repertoire in doves (de Kort and ten Cate, 2004), song complexity in yellow wagtails (Ödeen and Björklund, 2003), coloration in darters (Gumm and Mendelson, 2011), and digit length in two genera of African frogs (Blackburn, 2009). Such comparative studies using phylogenies are extremely useful in highlighting broad patterns across species lineages. But because these signal loss events happened long ago, we only see the pattern and not the selective forces responsible. In some cases, it is possible to draw inferences based on current species distributions and local ecological conditions. For instance, loss of light flashing in fireflies appears at least partially tied to predation risk (Stanger-Hall and Lloyd, 2015), and loss of sexual ornaments in dragon lizards appears correlated with habitat use (Ord and Stuart-Fox, 2005). But a major limitation of such phylogenetic studies is the inability to ascertain causal agents underlying phenotypic differences with a high level of certainty. It is often impossible to know what causes some sexual signals to disappear while others persist.

What exactly constitutes signal loss is a matter of debate because signal expression within a population occurs along a continuum. For example, signals may merely diminish, rather than completely disappear. Populations may also exhibit polymorphisms, where some individuals express the sexual signal while others do not. For the purpose of this paper, we distinguish between signal reduction and signal loss. In the case of signal reduction, though the trait diminished, it is still present in some form and thus able to be used in communication between the sexes. However, we consider polymorphisms within a population to represent signal loss when some individuals fully lack the trait, yet persist in the population. The complete absence of a signal in at least some individuals is the critical distinction and requires more explanation than trait diminution. Ultimately this can manifest as heritable alternative reproductive tactics. While there has been much informative work on the maintenance of heritable alternative male reproductive morphs (e.g., Sinervo and Lively, 1996), the process by which signals are lost in real time is unclear.

To better understand how sexual signal loss occurs in nature—in particular, when the benefits of sexual signal production fail to outweigh the costs of signal exploitation by natural enemies—we need insight from contemporary systems where sexual signal loss has been observed and the causal driving forces are well-understood. While other ecological agents can impose strong costs that may promote signal loss, including resource limitation and maneuverability within a habitat, we limit our discussion to signal exploitation because this represents a key cost largely restricted to sexual signals. Probably the best documented case of sexual signal loss in real time due to signal exploitation comes from Pacific field crickets (*Teleogryllus oceanicus*) in Hawaii where many males have lost the ability to sing. This system is especially valuable for understanding how signal loss occurs in the wild because the populations have been studied before, during, and after the evolution of signal loss.

CASE STUDY OF SEXUAL SIGNAL LOSS: PACIFIC FIELD CRICKETS (*TELEOGRYLLUS OCEANICUS*)

Pacific field crickets (*Teleogryllus oceanicus*) are native to Australia and South Pacific Islands, and have been introduced to the Hawaiian Islands where they have been studied extensively on Kauai, Oahu, and the Big Island of Hawaii (Otte and Alexander, 1983; Otte, 1994). Like most crickets, *T. oceanicus* males attract females by stridulating, or rubbing together specialized structures on their forewings to produce a long-range calling song and a short-range courtship song, which females use to localize and evaluate potential mates (Zuk and Simmons, 1997; Zuk et al., 2001). In Hawaii, but not elsewhere in its range, *T. oceanicus* co-occurs with an introduced parasitoid fly from North America, *Ormia ochracea*, that uses male calling song to locate its cricket host (Cade, 1975; Zuk et al., 1993; **Figure 1A**). When a gravid female fly locates a calling male, they deposit their free-moving larvae around the cricket, which burrow inside and kill the cricket in approximately a week (Cade, 1975; Adamo et al., 1995). The parasitoid fly presents a major threat to cricket survival—males from parasitized populations tend to be younger on average than crickets from locales where the fly does not occur (Simmons and Zuk, 1994). To cope with this strong natural selection, Pacific field crickets in Hawaii have evolved a number of adaptations to avoid detection by the fly. For example, they exhibit different calling song characteristics and daily calling patterns relative to populations that do not co-exist with the fly (Zuk et al., 1993; Rotenberry et al., 1996).

Around 2001–2003, a novel wing mutation arose and rapidly spread across the island of Kauai that renders male *T. oceanicus* obligately silent (Zuk et al., 2006). These silent male morphs are referred to as "flatwings" because they lack sound-producing structures on their forewings (Zuk et al., 2006; Pascoal et al., 2014; **Figure 1B**). Even though flatwing males still stridulate at approximately the same rate as wild-type males capable of calling (referred to as "normal-wings"), no song is produced (Schneider et al., 2018). By 2003, ~90% of males in the *T. oceanicus* population on Kauai exhibited the flatwing morphology (Zuk et al., 2006; Pascoal et al., 2014). Flatwing crickets are now known to occur on the three Hawaiian Islands that harbor *T. oceanicus*, and have stabilized at different proportions of the population: Kauai ~90%, Oahu ~50%, and Hawaii (Big Island) around 2% (Zuk et al., 2018). The silent phenotypes on Kauai and Oahu are caused by independent mutations at different genomic regions, though both mutations segregate as single loci and are located on the X-chromosome (Tinghitella, 2008; Pascoal et al., 2014). Interestingly, a new population of *T. oceanicus* was recently discovered on the Hawaiian Island of Molokai where many males exhibit an intermediate wing morphology incapable of producing the typical calling song, but instead makes a purring song that is detectable by females (Tinghitella et al., 2018). However, because it is unknown whether *O. ochracea* is present in Molokai and therefore the role of parasitism in the evolution of purring crickets is unclear (Tinghitella et al., 2018), we disregard this population from our discussion of sexual signal loss in Hawaiian *T. oceanicus*.

Though other cricket clades with mute males exist, this is often due to the loss of wings rather than an inability to produce sound. The selection pressures that lead to winglessness are likely distinct from those that drive sexual signal loss, and often are linked to habitat stability and lack of dispersal (Roff, 1990; Wagner and Liebherr, 1992). There are also cricket species, such as *Gryllus ovisopis* in Florida, that lack calling song, but still use courtship song and aggressive chirps to communicate in close proximity, so are not entirely mute (Walker, 1977). This renders the rapid loss of song-production structures in Hawaiian populations of *T. oceanicus* a unique and informative case study to investigate signal loss.

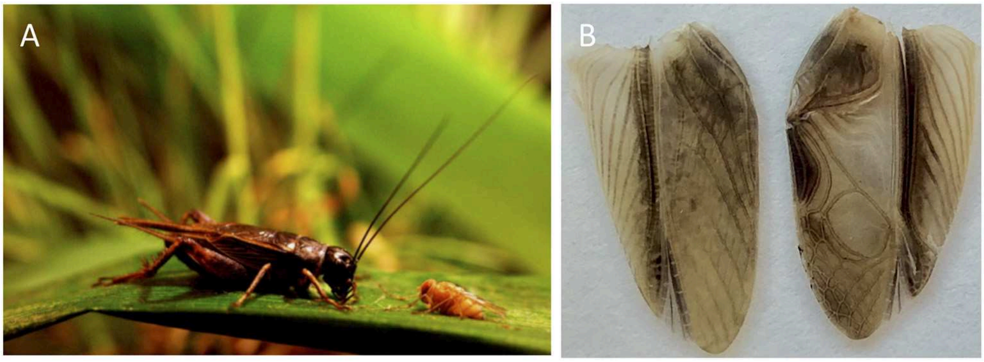

FIGURE 1 | (A) Photograph of *Teleogryllus oceanicus* (left) and *Ormia ochracea* (right); Photo courtesy of N. Lee. **(B)** Photograph of a cricket wing capable of song production (normal-wing; right) and a silent flatwing (left) wing.

What allowed signal loss to occur in Hawaiian populations of *T. oceanicus*? And more generally, in the face of natural selection from sexual signal exploitation, why do some signals persist while others disappear? Below, we describe in detail the environmental, social, and genetic factors that we believe were critical in allowing sexual signal loss to occur in *T. oceanicus*, and that we further assert should be important in driving sexual signal and non-signal trait loss more broadly.

CONTRIBUTORS TO SEXUAL SIGNAL LOSS

Here we discuss key factors that appear to have facilitated sexual signal loss in Hawaiian populations of *T. oceanicus*. The putative causal factors fall into three primary categories first proposed by Wiens (2001)—environmental, social, and genetic. In **Table 1**, we summarize these factors and discuss parallels and differences in their likelihood of driving evolutionary loss of sexual signals and non-signal traits. We bolster these suggestions by drawing on other empirical and theoretical work on sexual signal and trait loss. A recent modeling paper (Weigel et al., 2015) was particularly useful in this regard, as the authors explicitly modeled sexual signal loss under a number of scenarios using digital organisms evolved for many generations under different strengths of female preference, flexibility of the mating system (facultative or obligate signaling), population size, and genetic linkage between preference and signal.

Environmental Factors

Strong, Homogeneous Selection From Signal Exploiter

For a trait to become lost, it must experience significant costs that outweigh the benefits of trait production. In the context of Pacific field crickets, the cost is clear: signal exploitation by a parasitoid fly results in certain death for males. *Ormia ochracea* are extremely adept at localizing calling male crickets. The hearing ability of *O. ochracea* is very similar to that of female crickets, and the flies tend to prefer similar song characteristics as female crickets (Cade, 1975; Robert et al., 1992; Wagner, 1996). Field surveys of Hawaiian populations of *T. oceanicus* prior to the spread of flatwing showed that male crickets experienced high levels of parasitism—for instance, prior to the emergence of flatwing ~25% of calling males captured in Kauai possessed fly larvae (Zuk et al., 1993, 1995). More recent work has confirmed that flatwing males indeed escape parasitism pressure from the fly—only 1 of 121 dissected flatwing males captured in Kauai contained fly larvae (Zuk et al., 2006).

But of course, strong natural selection from signal exploitation does not always lead to signal loss. This is perhaps best exemplified by the fact that other species of field crickets (e.g., *Gryllus rubens*, *G. texensis*, and *G. lineaticeps*) are exploited by *O. ochracea* in North America (Cade, 1975; Walker and Wineriter, 1991; Wagner, 1996), but to the best of our knowledge, this has not resulted in the evolution of obligately silent (flatwing) male morphs. One key difference between the Hawaiian and North American cricket-fly systems is seasonality of cricket and fly prevalence. In Hawaii, *T. oceanicus* breed year-round, and the flies are always present. Many North American *Gryllids*, however, as well as *O. ochracea* in its native range, show stark seasonality in their abundance. North American *Gryllids* do not mate continually throughout the year, and the flies tend to occur at low densities in the spring and peak in the fall (Bertram, 2002). The cyclical nature of crickets and flies in North America introduces heterogeneity in the strength of natural selection, with some periods of relaxed natural selection on cricket song (spring) and other times with strong selection (fall). This late season risk of parasitism was suggested as an explanation for why some parasitized field cricket populations in North America have evolved riskier calling songs and preferences than non-parasitized populations (Beckers and Wagner, 2018). Crickets are thought to benefit by investing heavily in signaling in order to mate before the risk of parasitism becomes strong. Such variation in the strength of natural selection from parasites, however, does not occur in Hawaii. Rather, Hawaiian crickets consistently experience strong and persistent selection from the fly that should favor less risky sexual signals. Furthermore, *T. oceanicus* appears to be the only cricket capable of hosting *O. ochracea* in Hawaii (Otte, 1994), and these flies are highly responsive to song at the frequency range produced by this species (Gray et al.,

TABLE 1 | Summary of key contributors to sexual signal loss and discussion of their general applicability to evolutionary loss of non-signal traits.

Putative contributors to sexual signal loss	Description	Similarities with non-signal trait loss	Dissimilarities with non-signal trait loss
ENVIRONMENTAL			
Signal exploitation	Strong and homogenous natural selection from signal-exploiting natural enemy	NA	Exploitation by natural enemies is a unique environmental cost experienced by sexual signals because they are often highly conspicuous.
SOCIAL			
Weak female preference	Low strength, or absent, sexual selection favoring signal persistence	If selection favoring a trait is weak or absent, it should reduce the relative cost needed to drive trait loss, making it more likely to occur.	Female preference, and selection from social interactions, is unlikely to act as a selection pressure on non-signal traits.
Behavioral flexibility	Use of alternative mating tactics and/or behavioral plasticity to maintain sexual communication	If alternative ways of achieving the same function exist, such behavioral shifts should make the loss of any given trait more likely.	Signal loss may require simultaneous behavioral flexibility in two individuals (signaler and receiver), whereas trait loss should involve a single individual.
Signal compensation	Shift of the relative importance among different signals during sexual communication	Use of an alternative pathway to accomplish the former function of a lost trait appears common, sometimes through a newly established interspecific relationship.	Signal compensation again is involved in communication and requires shifts in two individuals, rather than one for a non-signal trait.
GENETIC			
Single locus	A single locus responsible for presence or absence of signal	A single locus should be more likely to experience a mutation that initiates signal or trait loss than a character controlled by many loci.	NA
Low allelic diversity	Low allelic diversity or small effective population size	Low levels of genetic diversity should allow a novel mutation to quickly sweep through a population regardless of whether evolution is due to selection or drift, and is associated with a signal or non-signal trait.	NA

2007). Meanwhile, on the mainland *O. ochracea* can parasitize multiple cricket hosts (Sakaguchi and Gray, 2011). We suggest that strong and consistent selection from the signal exploiter *O. ochracea* was probably the most important selective force driving sexual signal loss in *T. oceanicus* in Hawaii.

Social Factors

Weak Female Preference

In the presence of a strong environmental cost, reduced or absent selection in favor of signal retention should further facilitate sexual signal loss. This appears true in Pacific field crickets where females, particularly those from Kauai, express relatively weak preferences for male calling song (Tinghitella et al., 2011). This is consistent with Kaneshiro's (1976; 1980) model of female preference in island populations, which suggested that when population size is small and high-quality males are rare, as may occur after colonization of an island, female choosiness will be selected against. If females are very selective and only willing to mate with high quality males, they may never encounter such a male and subsequently fail to reproduce. Thus, when males are rare, selection should favor females that are less choosey about their mates (Kaneshiro, 1976, 1980). Indeed, female *T. oceanicus* from islands, including some where the parasitoid does not occur, exhibit significantly more permissive mating behaviors than those from ancestral, mainland populations in Australia (Tinghitella and Zuk, 2009). Population genetic data also indicate that the Hawaiian Island populations show markers of recent genetic bottlenecks, further bolstering this claim (Tinghitella et al., 2011). The Kaneshiro model has been implicated in sexual signal loss in other species, though to our knowledge not in conjunction with signal exploitation. For instance, the Palaearctic yellow wagtail (*Motacilla flava*) shows dramatic variation in plumage color and song complexity. Reduction in the expression of these sexual signals appears to at least partially result from weak female preferences that emerged during colonization events in conjunction with genetic bottlenecks (Ödeen and Björklund, 2003).

Such permissive female mating behavior in Hawaii is reinforced by socially-mediated behavioral plasticity (see more below). In populations with many silent males, like Kauai, crickets have little exposure to conspecific social cues (i.e., song) that indicate the availability of mates or abundance of competitors an individual can expect to encounter. Female *T. oceanicus* reared in a song-less acoustic environment, mimicking a high proportion of flatwing males, are less choosy about calling song quality during mate choice than females raised with abundant exposure to calling song (Bailey and Zuk, 2008; Swanger and Zuk, 2015; Lierheimer and Tinghitella, 2017). This creates a positive feedback loop where the song-less environment created by the existence of many flatwing males actually renders females more likely to mate with them, further perpetuating the success of silent males. This social plasticity in female preferences existed prior to the emergence of flatwing (Bailey et al., 2008), and therefore helped facilitate signal loss, and did not emerge as a consequence of signal loss. This is an important discovery because in comparative studies, which often represent the only option to study sexual signal loss, it is difficult to determine whether the signal was lost in response to relaxed selection from females, or if female preference weakened after the signal ceased to exist.

Female preference for a sexual signal has been implicated as a driver of signal loss in Weigel et al. (2015) and some, but not all, comparative studies. Weigel et al. (2015) found that it was very difficult to achieve complete sexual signal loss while females expressed any preference for the sexual signal. The only female preference condition under which sexual signal loss spread to fixation was when female preference was completely absent. If female preference for the male signal was present at even low levels, the strength of preference did not influence the prevalence of signal loss. That is, presence vs. absence of female preference was much more influential than whether the preference was weak or strong—signal loss was just as common at 25% strength as it was at 100%. In livebearing fishes that evolved reduced coloration when sympatric with predators, evidence supporting a role for reduced female preference is mixed. Female guppies from high-predation populations do show weaker preference for male coloration than females from populations that lack predators (Endler and Houde, 1995; Schwartz and Hendry, 2007). However, Bahamas mosquitofish females prefer more colorful males regardless of the predation environment in which they evolved (Heinen-Kay et al., 2015). A similar pattern of weak or absent female preferences was found in swordtail species that lack male sexual signals (Morris et al., 2005; Wong and Rosenthal, 2005). It is unclear why the strength of female preferences varies despite a marked reduction in male signal expression, but it is likely due to different costs incurred or benefits gained by females maintaining such preferences.

Sexual signals are sometimes used during both female choice and male-male competition for access to females (Zuk and Simmons, 2018). If signals are used for multiple functions, the strength of selection favoring their persistence should increase. Even if female preferences are weak, if a signal is important in determining the outcome of intrasexual interactions it could be enough to prevent its loss. In theory, if a sexual signal is used only in male-male competition, the same ideas should apply as we described for female preferences. In Pacific field crickets, males use acoustic signals to communicate during aggressive encounters. While male-male signaling can mitigate the cost of conflict (Logue et al., 2010), it apparently was not enough to halt the evolutionary loss of sound production in this system.

Though mating preferences are unlikely to affect the evolutionary trajectory of traits unrelated to mating, non-signal trait loss in general should be facilitated when selection favoring trait persistence is weak or absent. Trait persistence or loss should largely reflect the net balance of selective pressures favoring persistence or reduction.

Alternative Mating Tactics and Behavioral Flexibility

Loss of a sexual signal requires changes in the mating communication system, while non-signal traits can be lost in relative isolation. Perhaps the easiest way to facilitate a shift in communication is through behavioral flexibility (Zuk and Tinghitella, 2008; Zuk et al., 2014). In most crickets, mate localization and evaluation occur through acoustic signaling, where males produce a call that females are attracted to Zuk and Simmons (1997). Because flatwing males cannot produce the typical sexual signal, this creates an impediment to mating. Flatwings appear to overcome this issue by adopting an alternative mating strategy called satellite behavior, which is common in crickets and existed in the *T. oceanicus* behavioral repertoire prior to flatwing (Zuk et al., 2006; Tinghitella et al., 2009). Satellite behavior consists of a non-calling male that hovers near a calling male and attempts to intercept females responding to the caller's song. Flatwing males might be particularly successful acting as a satellite because they are differentially attracted to the same male song characteristics that female *T. oceanicus* prefer in a mate (Olzer and Zuk, 2018). Furthermore, male satellite behavior is enhanced by behavioral plasticity in response to rearing in a song-less environment that occurs as a by-product of the rapid spread of silent males. Males reared in the absence of song are more phonotactic than males reared with exposure to calling song (Bailey et al., 2010). Males from Kauai also walk around more when raised in the absence of calling song, which should increase the likelihood of a chance encounter with a female or calling male (Balenger and Zuk, 2015). As noted above, females reared in a song-less environment are also more phonotactic and express lower mating thresholds (Bailey and Zuk, 2008; Swanger and Zuk, 2015), though they do not show similar flexibility in exploratory behaviors (Heinen-Kay et al., 2018).

Flexibility in the signaling system was also highlighted as an important factor underlying sexual signal loss in Weigel et al.'s (2015) modeling paper. Facultative signaling systems (as opposed to obligate systems, where the signal is required in order to mate), were much more likely to evolve at least some degree of signal loss. This is not surprising, as it highlights the very reason we suggest that sexual signals should be difficult to lose. If the receiver is only willing to mate with individuals that express the signal, even a very costly signal should persist or the population may face local extinction. For instance, if a male signal changes due to strong costs associated with signal exploitation and females are unwilling to mate with males bearing this reduced or absent signal, the population size should dramatically decrease.

Signal Compensation

Another form of behavioral flexibility that may help signal loss occur is signal compensation. Most animals employ multiple sexual signals across a variety of modalities (e.g., acoustic, visual, olfactory), and single signals are often comprised of multiple components (e.g., hue and area of a color patch) that can be differentially targeted by natural and sexual selection (Candolin, 2003; Hebets and Papaj, 2005; Maan and Cummings, 2008). Multiple signals can convey either different or redundant information about the individual bearing the trait (Gomes et al., 2017). The existence of multiple signals, particularly when they are redundant, may provide sufficient flexibility for signal loss to evolve because females could shift the relative importance of the traits they prefer without facing fitness consequences. This could happen if preference for a particular signal weakens for some reason—perhaps if the associated costs begin to outweigh the benefits, or if the information content encoded in the signal becomes unreliable—and the relative importance of a different signal increases as a result. This idea has been referred to as trait switching or trait compensation (Wiens, 2001), and has garnered some empirical support. For example, some *Sceloperus* lizards have lost a conspicuous colorful belly patch used in intrasexual aggressive encounters, probably due to unwanted attention from predators (Wiens, 1999). Lizards lacking the color patch have evolved more dramatic and complex head bobbing displays (Martins et al., 2015) and more robust chemical signals (Hews and Benard, 2001), suggesting that the modality of signal communication has shifted to accommodate loss of a color signal.

At this point, it is unclear whether flatwing *T. oceanicus* compensate for lack of song with an alternate sexual signal. Like most insects, *T. oceanicus* possess cuticular hydrocarbons, long-chain fatty acids expressed on the cuticle that are used for both sexual communication and waterproofing (Ingleby, 2015). Crickets antennate each other prior to copulation and both male and female crickets evaluate cuticular hydrocarbons of potential mates when making mating decisions (Thomas and Simmons, 2009; Simmons et al., 2013). While flatwing males are unable to produce the short-range courtship song typically required in order for the female to mount, if they possessed more attractive chemical cues it could help explain how they are able to achieve matings in the absence of courtship song. Preliminary work suggests that flatwing and normal-wing males express different cuticular hydrocarbon profiles (Simmons et al., 2014), though it is unclear whether females show a preference for singing vs. silent morphs based on these chemical cues (Gray et al., 2014). Cuticular hydrocarbon expression also differs in response to social cues mediated by the acoustic environment experienced during rearing, which could affect the strength of sexual selection on these compounds in the wild (Thomas et al., 2011). However, it is important to note that cuticular hydrocarbons are not detectable over long distances, and therefore would not help females localize males in the absence of calling song. More research is needed to understand whether trait compensation played a role in sexual signal loss of *T. oceanicus*.

Trait compensation appears generally important in facilitating non-signal trait loss. Ellers et al. (2012) suggested that trait loss often goes undetected in natural populations because organisms do not necessarily lose the function accomplished by the lost trait, particularly in species that exhibit close symbiotic relationships with another species. For instance, some parasitic species of fungi have lost the ability to synthesize lipids, and instead extract these compounds from their host (Visser et al., 2010). Additionally, some plants have lost the ability to photosynthesize when they extract nutrients from other species (Merckx and Freudenstein, 2010). In a way, the alternative mating tactics employed by males are analogous to such an interspecific parasitic relationship—flatwing males essentially parasitize the songs of callers, co-opting their sexual signals to attract females and achieve matings.

Genetic Factors

Single Locus of Large Effect

The genetic architecture of a sexual signal should influence the probability of it becoming lost. In *T. oceanicus*, the silent male phenotype is due to a mutation on the X-chromosome that is inherited as a single locus (Tinghitella, 2008; Pascoal et al., 2014). Remarkably, the flatwing morphs on Kauai and Oahu are actually the result of two independent mutations in different regions of the X-chromosome, and are not a product of migration between the islands (Pascoal et al., 2014). The genetic underpinning of the flatwing morph on the Big Island of Hawaii has not yet been investigated because few flatwings are present in the population.

In general, trait or signal loss should be more easily accomplished by a mutation at a locus of large effect, rather than via changes at many loci because selection can be diluted. Indeed, a growing number of studies suggests that single loci of large effect tend to be responsible for rapid evolution and trait loss more broadly (Reznick and Ghalambor, 2001). For instance, a single mendelian genetic factor is responsible for the repeated loss of bony armor across stickleback populations released from predation risk (Cresko et al., 2004). In *Drosophila*, the evolutionary loss of wing pigmentation involved in courtship is caused by a single gene (Prud'homme et al., 2006), and rapid adaptation to a novel thermal environment is due to just two interacting loci (Mallard et al., 2018). Loss of sexual traits due to a transition to asexuality also tends to be caused by a single locus (van der Kooi and Schwander, 2014). While eye loss in cavefish is the product of around 12–15 loci (Protas et al., 2007), the repeated evolution of albinism in cavefish populations is caused by independent mutations in a single gene (Protas et al., 2006). Though evolutionary change in signals should require genetic shifts in both the signaler and the receiver, Weigel et al. (2015) found that genetic linkage between the signaler and receive had little bearing on whether a signal was ultimately lost. This is probably because other factors had a much bigger influence, namely whether the signal was required to initiate mating and whether females exhibited any preference (Weigel et al., 2015).

Low Genetic Diversity in Population

Small population size or low genetic diversity could also create conditions favorable to sexual signal loss because it can increase the chances of a novel mutation sweeping through the population due to selection or drift. In small populations, a trait that is even marginally adaptive could rapidly come to fixation through selection, and deleterious mutations can easily get a foothold through genetic drift. Evidence from *T. oceanicus* populations suggests recent genetic bottlenecks and low allelic diversity in the Hawaiian Islands relative to mainland populations (Tinghitella et al., 2011; Pascoal et al., 2016). Broadly, small population size with opportunity for rapid growth was identified as an important driver of rapid evolution in an influential review on the topic (Reznick and Ghalambor, 2001). However, it is important to note that the link between genetic variation and signal or trait loss may not be so clear because genetic variation, which should be greater in large populations, is necessary to provide the fodder for selection to act on during the establishment of novel traits. In Weigel et al.'s (2015) modeling study, population size did not affect the likelihood of signal loss becoming established in a population, though greater variability was introduced when populations were small. This argues for a more nuanced view on the role of population size and genetic variation during signal or trait loss, and more empirical evidence from natural populations that have experienced trait loss.

CONCLUSIONS

Despite apparent differences in how selection acts on signals and non-signal traits, quite a few commonalities exist regarding the contributors to their loss (**Table 1**). We identified several factors that likely helped drive sexual signal loss due to signal exploitation based on our case study of Hawaiian *T. oceanicus* populations and Wiens' (2001) review on sexual signal loss. For each of our highlighted causal factors, parallel examples exist of similar factors being important in driving trait loss more broadly. Most simply, to achieve evolutionary loss of any trait or signal, there needs to be some kind of major cost, weak or absent selection favoring persistence of the trait, and possibly (but not necessarily) an alternative way of maintaining trait functionality. Genetic architecture and population size may also help tip the balance between trait retention and loss, but are unlikely to represent the primary causal agent. Overall, it seems that no one smoking gun exists for sexual signal loss, but rather that it requires a perfect storm of costs, benefits, and sometimes novel ways of accomplishing the same task.

How sexual signals become lost represents an important issue in the evolution of biodiversity. When looking at particularly biodiverse clades, the distinguishing factors between species are often the sexual signals. Though the vast majority of research on sexual signal evolution focuses on elaboration and gains, sexual signals do not always evolve in a single direction, and instead often involves reduction and loss (Wiens, 2001). Given the important role of sexual signals during the maintenance and formation of species boundaries, it is critical to understand how sexual signals evolve, both in terms of how new traits arise and existing traits diminish (Panhuis et al., 2001; Servedio and Boughman, 2017).

Despite many examples of sexual signal loss over long evolutionary durations, sexual signal loss has rarely been documented on a contemporary timescale. In fact, there are relatively few examples of sexual signal evolution—either elaboration or reduction—on short timescales (Svensson and Gosden, 2007). Because of the paucity of examples, we know surprisingly little about the process of rapid sexual signal evolution. Modeling and experimental evolution should prove especially useful in filling this gap because researchers can exert tight control over which variables are manipulated (e.g., heterogeneity and strength of cost and preference, and other factors described in **Table 1**) to promote sexual signal loss or retention. In the Anthropocene, environmental conditions are changing rapidly and in particular, the composition of ecological communities is shifting due to the rapid spread of invasive and introduced species. Together with rampant habitat fragmentation and loss of genetic diversity in many populations, this may set the stage for new exploitative relationships to develop, and with them, possibly more contemporary examples of sexual signal loss. It is of particular importance that more research capitalizes on these anthropogenic experiments to gain more real-time examples of how sexual signal exploitation influences signal evolution.

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JH-K and MZ together developed the idea and wrote the manuscript.

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METHODS
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Developing a Phonotaxis Performance Index to Uncover Signal Selectivity in Walking Phonotaxis

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Any sensory strategies that prey take to avoid eavesdropping predators will depend on the behavioral decisions of eavesdroppers. As these decisions are guided by the sensory processing of communication signals, accurate measurements of sensorimotor output will provide insights into signal preferences, parameters evaluated for signal recognition, and the perceptual and cognitive capacity of receivers. A number of techniques have been proposed for measuring walking phonotaxis (and taxis behavior more generally). Consistent limitations of such measures are (1) that some animals cannot discriminate alternative signals when they occur simultaneously (i.e., overlapping in the spectral and temporal domain), or (2) some animals respond with low selectivity to stimuli presented in isolation, and (3) identifying appropriate dimensions of response variability is not straightforward. Here we document an approach to develop a sensitive phonotaxis performance index to quantify pulse rate selectivity in two distinct populations of the acoustic parasitoid fly *Ormia ochracea*. Using a spherical treadmill to measure tethered walking phonotaxis, we examined the ability of flies to track a switch in the broadcast location of test songs with varying pulse-rates. By applying an information-theoretic approach, we identified a set of response parameters that best predict a previously described pulse-rate preference. These parameters were incorporated into an index to describe temporal pattern selectivity during walking phonotaxis. Our study also revealed that in Floridian *Ormia ochracea,* the pulse rate preference function is not affected by the locomotor mode (walking vs. flying) used in phonotaxis. Furthermore, we describe for the first time, pulse rate selectivity in Californian *Ormia ochracea*. Both populations have pulse rate preference functions with peak selectivity between 50 and 60 Pulses/s (pps). Previous studies demonstrating natural differences in host song preferences (Floridian *O. ochracea* preferring *Gryllus rubens* and Californian *O. ochracea* preferring *Gryllus lineaticeps* calling songs) may be based on other temporal parameters aside from pulse rate. Finally, we discuss the advantages and limitations of our approach in quantifying signal selectivity. This approach can be applied broadly to study signal preferences in other acoustic parasitoid flies and potentially other eavesdroppers that exhibit taxis behaviors in response to the communication signals of prey.

Keywords: sound localization, song recognition, no-choice paradigm, phonotaxis index, signal preference, tethered walking phonotaxis

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INTRODUCTION

Acoustic communication is widespread in anurans and orthopteran insects (Gerhardt and Huber, 2002). In the context of reproduction, signalers (usually males) produce acoustic signals to advertise to potential mates (Andersson, 1994). As mate choice decisions of intended receivers are often based on assessing conspicuous advertisement signals, these signals are often subject to strong sexual selection to match the psychological landscape of receivers (Guilford and Dawkins, 1991; Wagner, 1998; Miller and Bee, 2012). At the same time, unintended receivers may eavesdrop on the same advertisement signals to locate potential prey or hosts (Cade, 1975; Tuttle and Ryan, 1981; Zuk and Kolluru, 1998). Such eavesdroppers can impose selective pressure for signals to be cryptic or for signalers to adopt alternative behavioral strategies (Zuk and Kolluru, 1998).

Signalers may adopt a number of strategies to avoid eavesdropping by untended receivers. Some of these strategies include changing the spectral and temporal characteristics of communication signals (Lloyd and Wing, 1983; Zuk et al., 1993; Morris et al., 1994; Rotenberry et al., 1996), signaling less often (Morris, 1980; Tuttle and Ryan, 1982; Tuttle et al., 1982; Belwood and Morris, 1987), producing less complex signals (Tuttle and Ryan, 1982), adopting a different communication channel (Belwood and Morris, 1987; Morris et al., 1994), advertising within a chorus (Walker, 1969), and "whispering" to intended receivers (Nakano et al., 2008). Since the behavioral decisions of eavesdroppers are guided by the sensory processing of communication signals, understanding the causes, and consequences of these evasive strategies will depend on sensitive methods for measuring behavior in eavesdroppers.

In acoustically orienting eavesdroppers, investigators can use phonotaxis studies (oriented locomotor responses to sound) that exploit the natural behavioral repertoire of animals to elucidate signal function, information conveyed in signals, and whether a signal is recognized or preferred. There are two general approaches to measuring behavioral preference functions for advertisement signals. The first is to measure the relative attractiveness of two or more signal variants when these are presented simultaneously in a choice paradigm; the second is to quantify the attractiveness of each signal variant when presented alone in a no-choice paradigm, often using a composite measure of phonotaxis (i.e., a performance index). Choice paradigms have been a common strategy to test for discrimination of signals that differ in the relative attractiveness or the role of signals used to facilitate species recognition (Popov and Shuvalov, 1977; Ryan, 1980; Doherty, 1985; Gerhardt and Doherty, 1988; Scheuber et al., 2004). However, in some experimental situations, animals are unable to evaluate small signal differences when confronted with multiple simultaneous signals (Gerhardt, 1982). In these situations, one can adopt a no-choice paradigm and transform a dichotomous outcome into a graded response measure that can describe the strength of preferences and preference functions for different stimuli (Wagner, 1998).

A number of indices have been proposed that incorporate some or all of the following response parameters: response probability, response latency, duration to reach a sound source, distance traveled, meander in walking path, and accuracy (angular orientation and error) (Von Helversen, 1984; Schul et al., 1998; Bush et al., 2002; Schul and Bush, 2002; Bee, 2007). However, the inclusion of specific parameters incorporated in phonotaxis performance indices is rarely justified and the approach to the development of indices is often omitted in the literature. Furthermore, a number of considerations make these approaches difficult to interpret and compare. Response probabilities or latencies can vary with source detectability or motivation to respond (or both) (Bush et al., 2002; Schul and Bush, 2002). Different species may have more direct vs. meandering paths during phonotaxis, making measures based on response duration, distance, or accuracy difficult to compare (Rheinlaender et al., 1979; Rheinlaender and Blatgen, 1982; Schul et al., 1998; Bee, 2007). Differences or ratios comparing responses to reference and test signals can be combined to derive a standardized phonotaxis performance index (Schul, 1998). These measures of phonotaxis are most accurate at capturing large differences in the path length of walking responses that may be specific to the zig-zag approach in localizing a stationary sound source. In animals that localize sound sources with more direct walking paths, finer variation in signal preferences may not be captured.

The acoustic parasitoid fly *Ormia ochracea* is known for its ability to localize sound sources with extreme accuracy. This hyperacute directional hearing allows for walking phonotactic responses to be more direct and with less meander (Mason et al., 2005; Lee et al., 2009). *Ormia ochracea* have evolved directionally sensitive ears for the sole purpose of eavesdropping on the calling songs of field crickets to locate suitable host crickets for the development of their larvae (Cade, 1975). Upon detecting cricket calling songs, gravid female *O. ochracea* perform flying (Cade, 1975; Walker, 1993; Müller and Robert, 2001) and walking phonotaxis (Mason et al., 2001, 2005; Lee et al., 2009) to cricket calling songs. After arriving in close proximity to crickets, *O. ochracea* deposit first-instar planidia (larvae) that burrow into crickets to feed on fat body and muscle tissue for development (Cade, 1975; Wineriter and Walker, 1990; Adamo et al., 1995).

Ormia ochracea occur in several geographic regions in the United States including Florida, Texas, California, Hawaii, and elsewhere (Gray et al., 2007). Most studies have used sound traps in the field to examine the relative attractiveness of songs that differ in duration or duty cycle, rather than specific temporal features underlying song recognition (Wagner, 1996; Zuk and Kolluru, 1998; Gray and Cade, 1999; Wagner and Basolo, 2007). These studies generally show that *O. ochracea* prefer louder songs, with longer chirps at higher chirp rates (Wagner, 1996; Zuk et al., 1998; Gray and Cade, 1999; Wagner and Basolo, 2007). Calling songs are species-specific and differ mostly in the temporal patterning of sound pulses (Gerhardt and Huber, 2002). The fine-scale temporal patterning of sound pulses can differ based on the duration of sound pulses and intervals between sound pulses. Pulse durations and intervals can vary by different amounts to result in songs that vary in duty cycle. Which of these specific temporal parameters are evaluated for species recognition and whether or not different populations of *O. ochracea* evaluate the same temporal parameters are poorly understood. Such signal preferences in eavesdroppers will depend on how their sensory system processes and perceives communication signals. Thus, a complete understanding of how eavesdroppers contribute to shaping the evolution of communication signals will require some knowledge of the perceptual capacity and sensory mechanisms underlying behavioral decisions that determine host selectivity.

In this Methods paper, we describe an approach to develop a phonotaxis performance index sensitive to response variation with less meander relative to the source location. We adapt a no-choice paradigm previously used to study song recognition in field crickets (Weber et al., 1981; Thorson et al., 1982). In this approach, a song model is initially broadcast from one location and subsequently switched to a second location midway through broadcast. The switch in song broadcast location has the potential to capture response variation underlying signal preferences with high sensitivity because animals are forced to actively alter their course of phonotaxis to follow an attractive source to a new location. This allows us to determine whether the rate and accuracy of a switch in orientation depends on specific signal parameters. We also provide the first description of pulse rate selectivity in a population of Californian *O. ochracea*. By using the "source-location tracking" paradigm, we quantify a number of response parameters that vary with stimulus pulse-rate. We incorporate these response features into a newly derived phonotaxis performance index. Preference functions based on this index are a good match with simultaneous choice trials in the field (Walker, 1993), and this method revealed that *O. ochracea* are more selective after they initiate a phonotactic response. Flies discriminated pulse-rate more strongly when they re-oriented to a novel stimulus location than in their initial responses, suggesting an attentional effect contributes to source localization in *O. ochracea*.

MATERIALS AND METHODS

Animals

Experiments were conducted on lab-reared gravid female *O. ochracea* derived from a population originally collected in Gainesville FL and in Thousand Oaks, CA. Flies were maintained in environmentally controlled chambers (Power Scientific, Inc., Model DROS52503, Pipersville, PA) at 25° C and 75% humidity on a 12 h:12 h light: dark regime and fed nectar solution (The Birding Company, Yarmouth, MA) *ad libitum*.

Acoustic Conditions

All experiments were conducted in an acoustically-dampened sound chamber (Wenger Soundlok, USA) at St. Olaf College, Northfield, Minnesota. The standard song, modeled after the natural calling song [mean of 58.6 pulses/s (pps), variance not reported in Walker (1998)] of *Gryllus rubens* found in the autumn in Florida (Walker, 1998), was a trill constructed from 5 kHz tone sound pulses that were 10 ms in duration with 1 ms on/off cosine squared ramps. Each sound pulse was separated by a 10 ms interpulse interval and repeated at 50 pps for a total duration of 1 s. Pulse rate preferences were examined with test songs that ranged from 10 to 100 pps in 10 pps increments (**Figure 1A**). Songs that differed in pulse rates were constructed by adjusting pulse durations and interpulse intervals in equal portions to maintain a constant 50% duty cycle. All test songs were 1 s in duration.

Acoustic stimuli were synthesized in Matlab (R2018a, The MathWorks Inc., USA) with custom software and converted to analog signals using National Instruments hardware (NI USB-6251, 44100 Hz), amplified (Crown XLS1002 Drive Core 2, USA) and broadcast through silk-dome tweeters (1–1/8 Dayton Audio Classic Series DC28FS-8, USA) situated at −45° (left) and +45° (right) relative to the midline of the flies (**Figure 1B**). Sound levels were controlled with programmable attenuators (Tucker Davis Technologies System 3 PA5, USA) and calibrated at the location of the fly using a probe microphone (B&K Type 4182, Denmark) connected to a sound level meter (B&K Type 2250, Denmark).

The level of each speaker was calibrated at the position of the fly to 75 dB SPL (re 20 μPa). Test songs varied in pulse rates (see above). A single standard song that switched in broadcast location was used as the "50 pps" test song. During test song presentations, only one speaker was active at a time.

Experimental Protocol

For each experimental subject, we recorded responses as follows. Presentation commenced with a standard song from the left speaker, followed by a presentation of the standard song from the right speaker (or in reverse order) to ensure that flies were motivated to respond. A test song was then broadcast from one speaker for 500 ms and switched to the other speaker for the remaining 500 ms of presentation. This was followed by 30 s of silence before another test song was presented. The next stimulus presentation was a randomly selected test song. Both the sequence of test songs and the order of first speaker presentation were randomized across flies. Five responses for each test song were collected from Floridian *O. ochracea* while one response for each test song was collected from Californian *O. ochracea*. The entire experimental series (i.e., as above for all test songs), was followed by another two presentations of the standard song (one from each speaker), to allow us to measure any changes in overall responsiveness during the course of the experiment.

Spherical Treadmill

Behavioral measurements were made from tethered flies performing walking phonotaxis on a high-resolution treadmill system situated equidistant (25 cm) from the two test speakers (**Figure 1**). Data collection by the treadmill system was controlled by custom Matlab software (StimProg V6) that interfaced with the National Instruments data acquisition system to ensure synchronous sound presentation and data capture. The treadmill system consists of a light-weight table tennis ball held afloat above a modified optical mouse sensor (ADNS 2620, Avago Technologies, USA) by a constant airstream. Walking responses were transduced as rotations of the treadmill that actuated the optical mouse sensor to record changes in x and y pixel units at a sampling rate of 2160 Hz (Lott et al., 2007). Pixel units were calibrated to actual walking distances by measuring displacement of points on the ball in high-speed video footage (Chronos 1.3

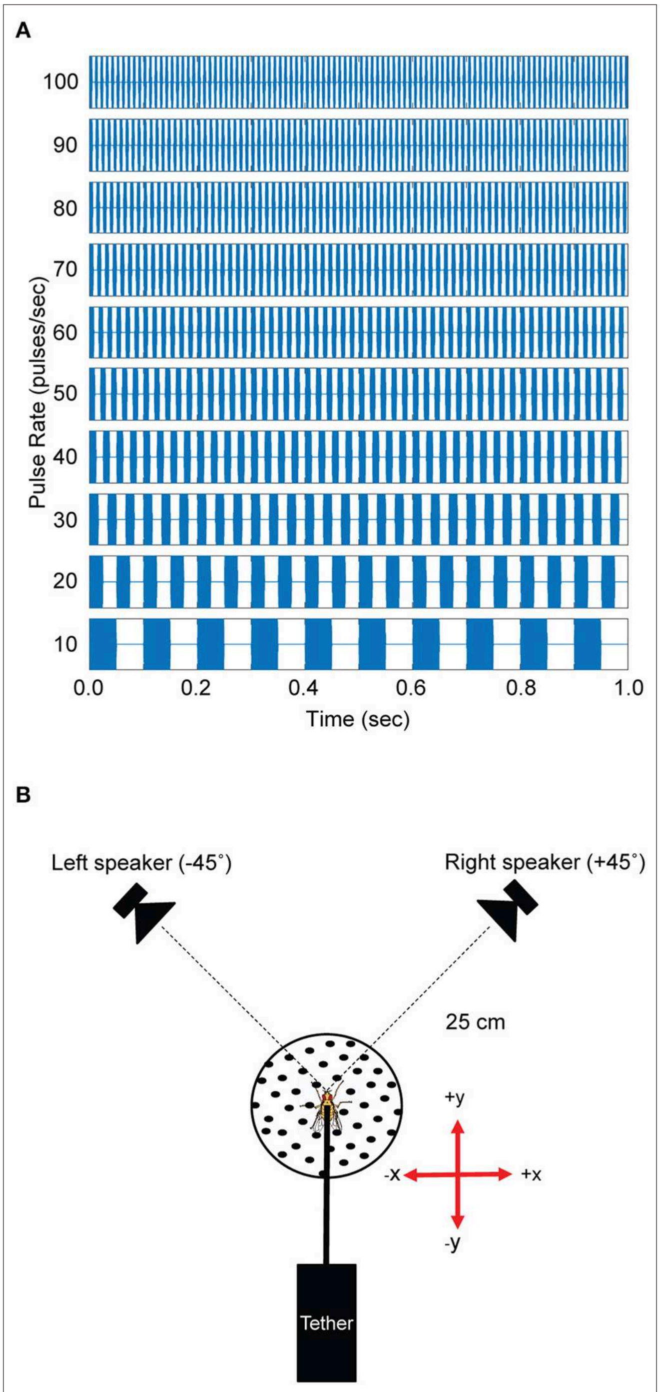

FIGURE 1 | Acoustic stimuli and experimental arrangement. **(A)** Acoustic stimuli used in phonotaxis experiments were 1 s in duration. Test songs varied in pulse rates by changing the pulse duration and interval between pulses in equal amounts to achieve a 50% duty cycle. The 50 pulses/s and 70 pulses/s songs were used as the standard (reference) song in testing responses from Floridian and Californian *Ormia ochracea*, respectively. **(B)** Flies were tethered and held on top of the spherical treadmill system at a fixed position 25 cm away from the left and right speakers. Left and right speakers were positioned at −45° and +45° relative to the midline axis of the fly. Rotations of the treadmill in the forward direction is registered as positive y values while rotations to the right is registered as positive x values and these values can be used to reconstruct virtual walking trajectories.

Highspeed Camera, 1,000 frames per second, Krontech, Canada) that was synchronized to pixel data from the treadmill system. We also calibrated the responses of the treadmill for rotational movements by attaching the spindle of a small DC motor at the position of the fly. Pure rotation around the vertical axis of the treadmill generates a straight trajectory at 90° to the left or right (depending on the direction of rotation). Previous work (Mason et al., 2005) has verified that for tethered flies responding to a sound source at 90° azimuth, treadmill responses are similar to trajectories of freely walking flies.

Flies were presented with attractive stimuli that switched in the broadcast location. The virtual walking trajectory depicted in **Figure 2A** show changes in x and y values throughout the duration of data capture. Before stimulus onset, flies started at a value of 0 cm in the x and y directions. After stimulus onset, flies responded with a 64 ± 3.4 ms (mean ± sem) and cumulative walking distance increased rapidly during stimulus presentation. The rate of change in cumulative distance decreased shortly after stimulus offset, but continued to increase beyond the duration of data capture (**Figure 2B**). When presented with the preferred 50 pps cricket song from the left speaker for the first 500 ms and then subsequently from the right speaker for the remaining 500 ms of broadcast, virtual walking trajectories indicate that flies initially walked left and transitioned to the right (**Figures 2A,C**).

Designing a New Phonotaxis Index

To develop an index that captures signal selectivity, we quantified a range of phonotactic walking parameters and examined how they varied with song pulse-rate. Measured features included: total walking distance during the 1.5 s of data capture; response latencies (time between stimulus onset and first detected change in distance); peak and mean forward and steering velocities to each broadcast location (change in x or y over time, respectively); mean angular heading and error in angular orientation to each broadcast location. The instantaneous angular heading (theta) was determined by converting Cartesian x and y values to polar coordinates by computing the inverse tangent of y divided by x [instantaneous angular heading = arctan(y/x)]. The error in angular orientation was calculated as the difference between the instantaneous angular headings in response to test songs and the mean angular heading to the standard song (reference condition).

To identify response parameters that are most informative of pulse-rate preference, we applied Peng and colleague's Python implementation of max-relevance min-redundancy analysis (mRMR) (Peng et al., 2005). This analysis maximizes feature relevance while minimizing feature redundancy. The mRMR analysis selects features based on their mutual information with a previously established pulse rate preference (Walker, 1993). Response features sharing greater mutual information are better predictors of the pulse-rate preference and are rated as more important provided that they add new information that is not already captured by other features.

Following mRMR (**Table 1**), we applied a follow-up mutual information analysis to rank candidate phonotaxis indices for suitability in describing pulse rate preferences (**Table 2**). This analysis resulted in the selection of one index consisting of

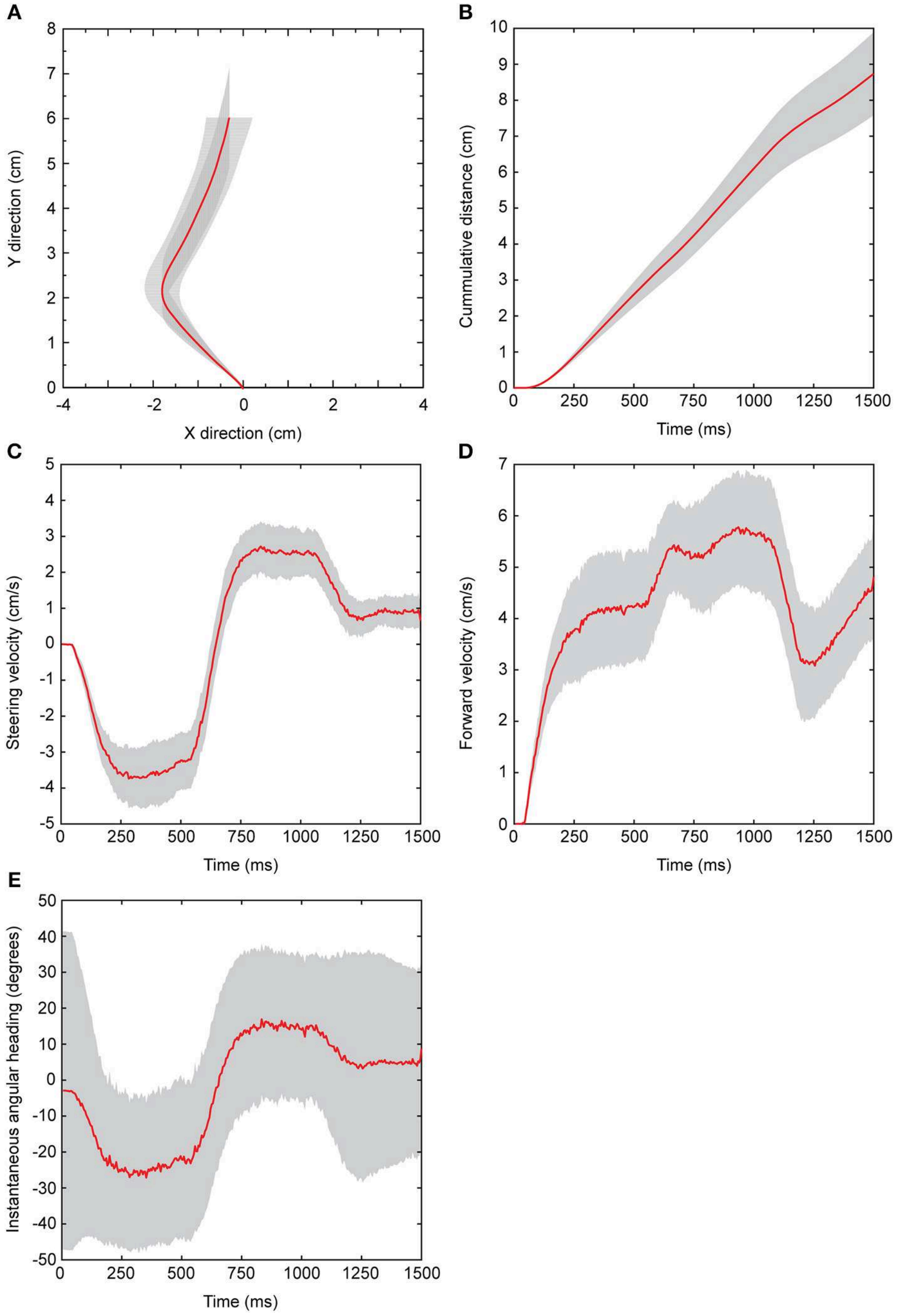

FIGURE 2 | Response features measured from the spherical treadmill system. All data shown are derived from Floridian *Ormia ochracea* in response to a standard attractive cricket song (50 pulses/s) that was broadcast from the left speaker for 500 ms, and then switched to the right speaker for the remaining 500 ms of stimulus presentation. **(A)** Plots of x and y values show a reconstructed virtual walking path. **(B)** Depicts total distance traveled as a function of time. Changes in x and y as a function of time represent steering **(C)** and forward **(D)** velocities, respectively. Instantaneous angular headings **(E)** are derived from converting x and y values from the cartesian plane to polar coordinates. Negative angular headings indicate turning to the left while positive angular headings indicate turning to the right. Red lines represent the grand mean across 16 flies and shaded gray areas represent 95% confidence interval around the mean.

three features: angular orientation, total distance traveled, and steering velocity.

Repeated responses for the same stimulus conditions were averaged within individuals. Index values range from 0 to >1. A phonotaxis performance index of 0 indicates poor performance, 1 indicates performance equivalent to responses to the standard song, >1 indicates performance "better" than responses to the standard song (e.g., higher steering velocity, longer distance). In other words, although the index is defined relative to responses to the reference stimulus, it can nevertheless detect a stronger preference for an alternative signal.

Data Analysis

The numbers of walking responses to the left speaker leading or the right speaker leading were balanced to eliminate any directional biases in broadcast locations. Responses to the right speaker leading were reflected and combined with data in response to the left speaker leading for the final data analysis. Registered changes in x and/or y greater than a calibrated distance of 1 cm were considered valid phonotactic responses. All data are reported as mean ± sem unless otherwise specified.

The effects of song pulse rate on response latencies were statistically analyzed with Friedman's ANOVA as response latencies violated the assumptions of normality and homogeneity of variance. At present, there is no consensus on an inferential statistical approach to analyze repeated measures circular data. Despite violating the assumptions of independence and linearity, some studies have applied linear repeated measures ANOVA to analyze circular data (Mechsner et al., 2007). Here we used a linear repeated measures ANOVA to analyze error in angular orientation and Watson's U^2 Test to analyze angular headings. All other response measures were analyzed with repeated measures ANOVAs and Greenhouse-Geisser corrected if assumptions of sphericity were violated. Bonferroni adjustments were applied to *post-hoc* pairwise comparisons. Statistical analyses were conducted in SPSS Statistics (ver. 19, IBM Corporation, USA).

TABLE 1 | Response features ranked by mRMR feature selection analysis.

Response features	Score
1. Steering velocity	0.453
2. Total distance	0.383
3. Angular heading	0.321
4. Peak forward velocity	0.288
5. Angular error	0.262
6. Forward velocity	0.203
7. Response latency	0.122

Rankings determined from responses obtained from Floridian O. ochracea (n = 16).

RESULTS

We first recorded walking responses from 16 Floridian *O. Ochracea*. Experiments started and ended with testing responses to the standard stimulus, and there was no evidence that flies became less responsive over the course of the experiment. Response latencies differed between speakers [$\mathrm{F}_{(1,15)} = 7.24$, $P = 0.017$], and decreased significantly by the end of experiments [$F_{(1,15)} = 4.58$, $P = 0.05$]. Flies initially responded with a mean latency of 91.44 ± 13.20 ms and 72.03 ± 9.16 ms to the left and right broadcast locations, respectively. By the end of experiments, these response latencies decreased to 61.22 ± 5.25 and 53.52 ± 3.02 ms for the left and right broadcast locations. At the start of experiments, flies walked a mean distance of 7.26 ± 0.52 and 8.65 ± 0.68 cm to localize the left and right broadcast locations. Total walking distances at the end of experiments were 8.58 ± 0.68 and 8.14 ± 0.54 cm for the left and right broadcast locations. These total walking distances did not differ significantly between broadcast locations [$F_{(1,15)} = 1.46$, $P = 0.25$] and did not change between the start and end of experiments [$F_{(1,15)} = 0.66$, P

TABLE 2 | Evaluating candidate phonotaxis indices with mutual information analysis.

Candidate phonotaxis indices	Quantity of information normalized to equation 8 (bits)
1. $\textbf{Angular error}_{\textbf{mean}} = \textbf{cosine}\left(\frac{\overline{\lvert \text{Angular heading}_{\text{test}} - \text{Angular heading}_{\text{reference}} \rvert}}{2}\right)$	0.32
2. $\textbf{Forward velocity}_{\textbf{mean}} = \frac{\overline{\text{Forward velocity}_{\text{test}}}}{\overline{\text{Forward velocity}_{\text{reference}}}}$	0.66
3. $\textbf{Steering velocity}_{\textbf{mean}} = \frac{\overline{\text{Steering velocity}_{\text{test}}}}{\overline{\text{Steering velocity}_{\text{reference}}}}$	0.91
4. $\textbf{Forward velocity}_{\textbf{peak}} = \frac{\overline{\text{Peak forward velocity}_{\text{test}}}}{\overline{\text{Peak forward velocity}_{\text{reference}}}}$	0.44
5. $\textbf{Steering velocity}_{\textbf{peak}} = \frac{\overline{\text{Peak forward velocity}_{\text{test}}}}{\overline{\text{Peak forward velocity}_{\text{reference}}}}$	0.75
6. $\textbf{Total distance} = \frac{\overline{\text{Total distance}_{\text{test}}}}{\overline{\text{Total distance}_{\text{reference}}}}$	0.78
7. Top two features selected by mRMR: $\textbf{Cosine}\left(\frac{\lvert \text{Angular heading}_{\text{test}} - \text{Angular heading}_{\text{reference}} \rvert}{2}\right) \times \left(\frac{\overline{\text{Total distance}_{\text{test}}}}{\overline{\text{Total distance}_{\text{reference}}}}\right)$	0.87
8. Top three features selected by mRMR: $\textbf{Cosine}\left(\frac{\lvert \text{Angular heading}_{\text{test}} - \text{Angular heading}_{\text{reference}} \rvert}{2}\right) \times \left(\frac{\overline{\text{Steering velocity}_{\text{test}}}}{\overline{\text{Steering velocity}_{\text{reference}}}}\right) \times \left(\frac{\overline{\text{Total distance}_{\text{test}}}}{\overline{\text{Total distance}_{\text{reference}}}}\right)$	1.0
9. Top four features selected by mRMR: $\textbf{Cosine}\left(\frac{\lvert \text{Angular heading}_{\text{test}} - \text{Angular heading}_{\text{reference}} \rvert}{2}\right) \times \left(\frac{\overline{\text{Steering velocity}_{\text{test}}}}{\overline{\text{Steering velocity}_{\text{reference}}}}\right) \times \left(\frac{\overline{\text{Total distance}_{\text{test}}}}{\overline{\text{Total distance}_{\text{reference}}}}\right) \times \left(\frac{\overline{\text{Peak forward velocity}_{\text{test}}}}{\overline{\text{Peak forward velocity}_{\text{reference}}}}\right)$	0.82

= 0.43]. Taken together, these data suggest that motivation to respond did not decrease over the duration of experiments.

Response Features to a Preferred Cricket Song

Steering velocity indicates changes in x values as a function of time and is depicted in **Figure 2C**. Shortly after stimulus onset flies track the left speaker location with negative velocities that peaked at −4.54 ± 0.31 cm/s. With a switch in the broadcast location, steering velocities transitioned to positive values that peaked at 3.48 ± 0.36 cm/s. Following stimulus offset, steering velocities decreased rapidly toward baseline values. Forward velocity indicates the speed of movement in the forward direction and is plotted as changes in y values over time (**Figure 2D**). Shortly following stimulus onset, forward velocity increased to about 4 cm/s in response to the first broadcast location. Immediately after the switch in broadcast location, forward velocities were often elevated to beyond 5 cm/s. At the end of stimulus presentation, forward velocities decreased briefly before returning to higher velocities. The apparent decrease in response after stimulus offset followed by a slight increase in activity across several response features (cumulative distance, steering velocity, forward velocity) confirmed that some flies only paused briefly and then continued to walk for some time to search for the source location.

Changes in x and y values can be transformed from the Cartesian plane to polar coordinates and expressed as instantaneous angular headings which indicate the angular direction relative to the starting direction (0°) (**Figure 2E**). As flies turned left, instantaneous angular headings become more negative and reached a peak mean angular heading of −45.02 ± 2.80°. Following the switch in broadcast location, flies transitioned to positive angular headings (**Figure 2E**).

Quantifying Response Features as a Function of Changes in Pulse Rates

We examined how different phonotaxis response features varied as a function of song pulse rates. Response latencies did not significantly differ for songs with different pulse rates (Friedman Test: $\chi^2 = 5.691$, $P = 0.770$, $n = 16$, **Figure 3A**) but total walking distance varied significantly with song pulse rates [$F_{(3.20,\,47.93)} = 37.21$, $P < 0.001$, **Figure 3B**]. Averaged across pulse rate conditions, flies responded with a mean latency of 64 ± 2 ms and a mean total distance of 6.01± 0.46 cm. Walking distances in response to the 60 pps song did not significantly differ from responses to the 50 pps standard song.

Both steering and forward velocities varied systematically and significantly with song pulse rates (steering velocity: $F_{2.92,43.85} = 39.53$, $P < 0.001$; forward velocity: $F_{3.97,\,59.57} = 21.60$, $P < 0.001$, $n = 16$, **Figures 4A,B**). As pulse rates increased from 10 to 40 pps, mean steering velocities increased from 1.12 ± 0.07 to 2.04 ± 0.15 cm/s while forward velocities increased from 2.18 ± 0.18 to 3.42 ± 0.26 cm/s. Mean steering velocity reached a peak of 2.4 ± 0.18 cm/s at 50 pps while mean forward velocity reached a peak of 3.90 ± 0.33 cm/s at 60 pps. Mean steering and forward velocities were reduced in response to songs at higher pulse rates (**Figures 4A,B**). To examine response differences to the initial and subsequent broadcast locations, we calculated mean steering and forward velocities across the first 500 ms (**Figures 4C,E**) of stimulus and across the remaining 500 ms of stimulus presentation separately (**Figures 4D,F**). There was a significant main effect of the initial or subsequent broadcast location on steering and forward velocities (steering velocity: $F_{1,15} = 89.54$, $P < 0.001$; forward velocity: $F_{1,\,16} = 13.03$, $P = 0.03$, $n = 16$). Steering and forward velocities were generally higher in response to the initial source location (steering velocity: 3.37 ± 0.30 cm/s; forward velocity: 1.99 ± 0.13 cm/s) than compared to the subsequent location (steering velocity: 2.67 ± 10.25 cm/s; forward velocity: 1.18 ± 0.08 cm/s) (steering velocity: $F_{1,\,15} = 89.54$, $P < 0.001$; forward velocity: $F_{1,\,15} = 13.03$, $P = 0.03$, $n = 16$).

To determine the angular heading directed at each broadcast location, angular headings were taken from instantaneous angular headings (i.e., **Figure 2E**) at 250 and 750 ms time points. These time points correspond to the middle of stimulus presentation for each broadcast location. Mean angular heading depended on song pulse rate (**Figures 5A,B**). In response to song presentation from the initial broadcast location, flies generally localized a direction that approached the speaker location (left speaker at −45°). For a 50 pps song, flies turned with a mean angular heading of −22.95 ± 2.06°, which is significantly more negative than responses to lower (10 pps: −10.66 ± 2.18° $U^2 = 0.256$, $P < 0.02$, 20 pps: −13.94 ± 2.25° $U^2 = 0.185$, $P < 0.05$) and higher pulse rates (70 pps: −13.80 ± 2.05° $U^2 = 0.231$, $P < 0.02$, 80 pps: −13.43 ± 1.72° $U^2 = 0.344$, $P < 0.002$, 90 pps: −8.26 ± 2.98° $U^2 = 0.307$, $P < 0.005$, 100 pps: $U^2 = 0.292$, $P < 0.005$). Mean angular headings in response to 40 (−21.26 ± 1.88°) and 60 pps (−20.68 ± 1.55°) did not significantly differ from responses to the 50 pps song (50 vs. 40 pps: $U^2 = 0.099$, $P > 0.2$, 50 vs. 60 pps: $U^2 = 0.084$, $P > 0.2$). For songs with less preferred pulse rates, flies exhibited weaker steering responses that resulted in mean angular headings that were closer to the midline (**Figure 5A**). With a switch in the broadcast location, flies exhibited slightly weaker steering responses with smaller mean angular headings that were mostly directed in the forward direction (**Figure 5B**). For a 50 pps song, flies turned with a mean angular heading of 13.78 ± 2.29°, which is significantly more positive than responses to the most extreme pulse rates (50 vs. 10 pps: $U^2 = 0.226$, $P < 0.05$, 50 vs. 100 pps: $U^2 = 0.187$, $P < 0.05$). However, there was a slightly higher tendency for flies to exhibit more positive angular headings toward the subsequent speaker location for songs near the preferred pulse rate.

Angular orientation error represents the angular difference between the mean angular heading in response to the standard song and test songs. The error in angular orientation to each speaker location were taken at 250 (**Figure 5C**) and 750 ms (**Figure 5D**) time points during stimulus presentation. With a switch in broadcast location, error in angular orientation was significantly greater for re-orientation responses than for initial localization responses [$F_{(1,\,13)} = 13.25$, $P = 0.003$]. Error in angular orientation was significantly affected by song pulse-rate [$F_{(4.13,53.70)} = 24.55$, $P < 0.001$]. Pairwise comparisons reveal that flies exhibited significantly greater orientation errors at less

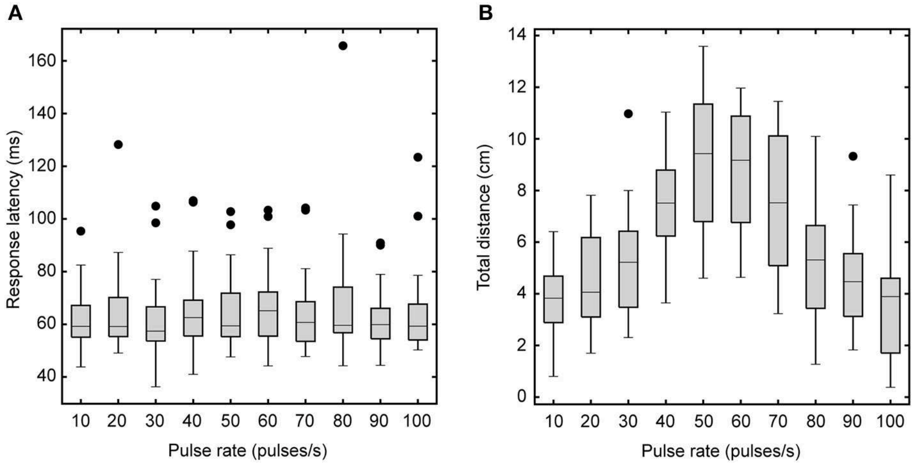

FIGURE 3 | Effects of song pulse rate on response latency and total walking distance. Box plots depict the first and third quartiles and median response latency **(A)** and walking distance **(B)**. Response latencies **(A)** do not vary with song pulse rate. However, total walking distance **(B)** varies with song pulse rate. Flies travel greater distances for the most preferred pulse rates. Whiskers show the most data extreme points that are not considered outliers, and closed circles indicate outliers.

preferred pulse rates (10–40 and 60–100 pps, all *Ps* < 0.001. There was also a significant interaction effect between pulse-rate and presentation order [$F_{(4.77, 61.96)} = 6.04$, $P < 0.001$]. Re-orientation responses to non-preferred pulse-rates (10–40 pps and 60–100) exhibited significantly greater angular orientation error (**Figure 5D**).

Feature Selection and Deriving the Phonotaxis Performance Index

We applied an information-theoretic feature selection analysis (Peng et al., 2005) to objectively select response features to incorporate in our novel phonotaxis performance index. Starting with a list of seven response features, we used mRMR to rank response features that maximize feature relevance while minimizing feature redundancy. The output of the mRMR analysis is presented in **Table 1**. This analysis ranked steering velocity, total distance, and angular heading as top features that significantly predicted pulse rate preference (Walker, 1993) while minimizing correlation between features. These features were incorporated in candidate phonotaxis performance indices that compared responses to test songs relative to responses to the reference 50 pps standard song (**Table 2**). We applied a mutual information analysis to describe the amount of information gained (in bits) about the known pulse rate preference based on evaluating candidate phonotaxis indices presented in **Table 2**. The outcome of this information analysis is the following equation (**Table 2**, Equation 8) to quantify phonotaxis performance:

$$\textit{Phonotaxis Index}= \textit{Cosine}\left(\frac{\left|\textit{Angular heading}_{\textit{test song}}-\textit{Angular heading}_{\textit{reference song}}\right|}{2}\right) \times \left(\frac{\overline{\textit{Steering velocity}_{\textit{test}}}}{\overline{\textit{Steering velocity}_{\textit{reference}}}}\right) \times \left(\frac{\overline{\textit{Total distance}_{\textit{test}}}}{\overline{\textit{Total distance}_{\textit{reference}}}}\right)$$

Other candidate phonotaxis indices that include a greater or lesser number of response features reduced the overall information gained (**Table 2**).

Using the Phonotaxis Performance Index to Capture Signal Preferences

In addition to the 16 Floridian *O. ochracea*, we also examined pulse rate preferences in 16 Californian *O. ochracea*. We found a significant main effect of pulse rate on the phonotaxis performance index [$F_{(9, 270)} = 28.28$, $P < 0.001$, $n = 16$; **Figures 6A,B**]. However, neither the main effect of population nor the interaction between pulse rate and population were significant (population: $F_{1, 30} = 1.42$, $P = 0.24$, population × pulse rate: $F_{9, 270} = 1.41$, $P = 0.18$). The phonotaxis performance index increased gradually for pulse rates between 10 and 40 pps, reached a peak for pulse rates between 50 and 60 pps, and decreased with further increases in song pulse rates. Pairwise comparisons reveal that the 50 pps song resulted in significantly higher index values than compared to all other pulse rates (all *Ps* <0.05). Median index values were fitted with a smoothing cubic spline to generate preference functions (**Figure 6C**). These preference functions suggest that Californian *O. ochracea* exhibit a slightly broader pulse rate preference function than compared to Floridian *O. ochracea*.

DISCUSSION

Developing a Phonotaxis Performance Index to Capture Signal Preferences

In this study, we document an approach (**Figure 7**) for developing a novel method for quantifying taxis behavior, and we use this method to describe pulse-rate preferences in two populations of *Ormia ochracea*. First, this approach relies on some understanding of signal preferences in nature (i.e., pulse rate preference in Floridian *O. ochracea* established from field

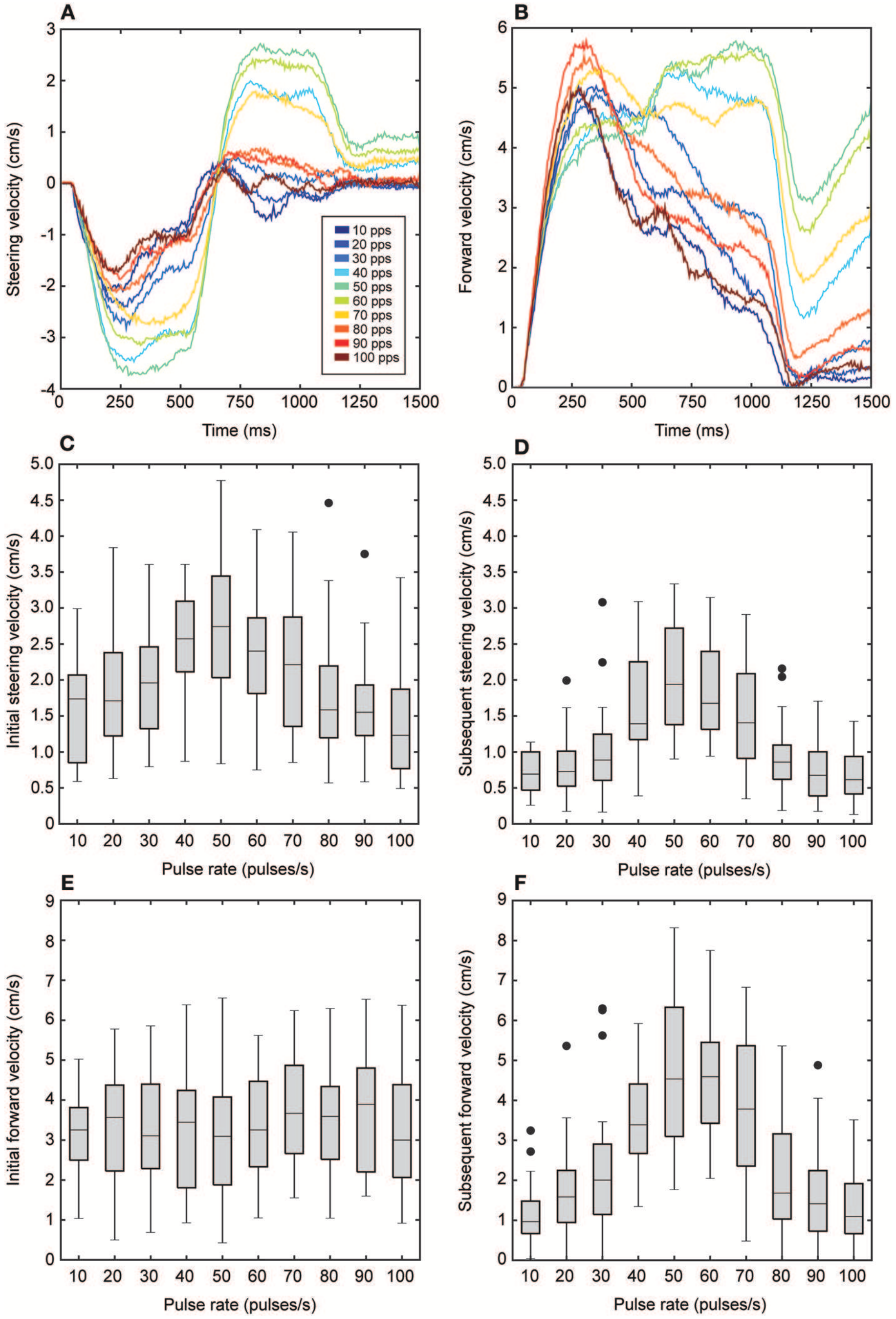

FIGURE 4 | Effects of song pulse rate on steering and forward velocities. **(A)** Flies steered to the left to track the initial 500 ms of song broadcast. This was followed by a steering response to the right to track the switch in broadcast location for the remaining 500 ms of song. The magnitude of steering responses varied with song pulse rate (colors). Steering to the initial broadcast location was less selective while steering to the subsequent location showed greater selectivity to songs with pulse rates that range from 40 to 70 pps. In response to the initial broadcast location, flies exhibited an increase in forward velocity **(B)** that varied as a function of song pulse rate. When the song was switched to the subsequent broadcast location, forward velocity continued to be elevated for the most preferred pulse rates (40–70 pps) but decreased for less preferred pulse rates. **(C–F)** Box plots depict the first and third quartiles and median steering **(C,D)** and forward velocity **(E,F)** values at 250 and 750 ms time points in response the initial **(C,E)** and subsequent **(D,F)** broadcast locations as a function of song pulse rate. In response to the initial broadcast location, mean steering velocity varied with pulse rate **(C)** while mean forward velocity did not vary with pulse rate **(E)**. Flies exhibited greater selectivity in response to the subsequent broadcast location. Steering **(D)** and forward **(F)** velocities reached peaked at the most preferred pulse rates. Whiskers in box plots show the most data extreme points that are not considered outliers, and closed circles indicate outliers.

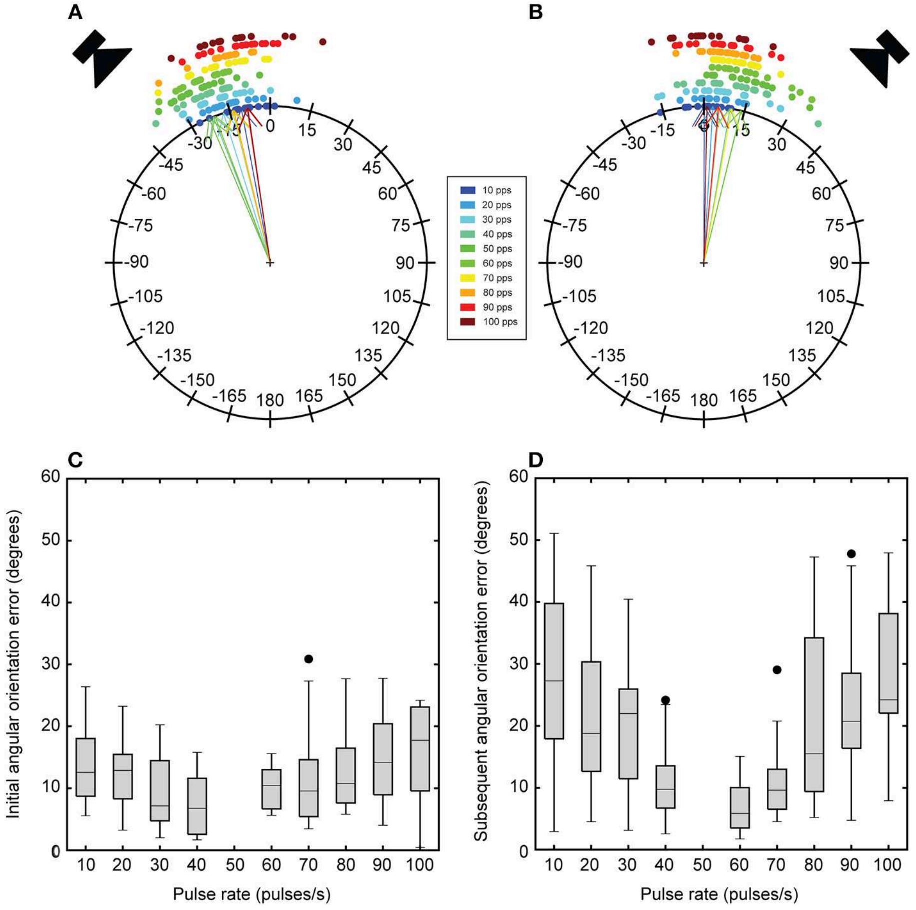

FIGURE 5 | Effects of song pulse rate on mean angular heading and angular orientation error. Circular plots depict the angular headings in response to the initial broadcast location 250 ms into stimulus presentation **(A)** and to the subsequent broadcast location 750 ms into stimulus presentation **(B)**. Dots around the circular plots are mean angular responses in degrees from a single fly to a particular pulse rate (colors). Arrows indicate the grand mean across 16 flies for a particular pulse rate. Initial angular headings vary as a function of song pulse rate. These initial angular headings are generally larger (more negative) and approach the initial broadcast location. Angular headings in response to the subsequent broadcast location are generally more forward directed except for responses to the most preferred pulse rates. These responses exhibit positive angular headings toward the subsequent broadcast location. Box plots depict the first and third quartiles and median angular orientation error in response to the initial **(C)** and subsequent **(D)** broadcast locations. Flies exhibit greater orientation error for songs with less preferred pulse rates and these errors are elevated in response to the subsequent broadcast location. Whiskers show the most data extreme points that are not considered outliers, and closed circles indicate outliers.

experiments) or a predicted salient signal value (i.e., a pulse rate of 70 pps based on the calling song of host crickets parasitized by Californian *O. ochracea*) of a specific signal parameter. Next, response variation to different test signal values are measured relative to reference responses to a salient signal. In our experiments, we examined pulse-rate preferences during walking phonotaxis with an assay that measured the ability of animals to track a switch in the broadcast location for songs that varied in pulse rates. Using the spherical treadmill system, we measured how a range of response parameters (i.e., latency, walking distance, peak and mean steering velocities, and etc.) varied with pulse rate. This was followed by a feature selection analysis to select response features that best predict a known signal preference. We applied mRMR to maximize mutual information while minimizing redundancy of selected features to predict the known pulse rate preference.

In Floridian *O. ochracea*, all these response features varied significantly to changes in song pulse rates. Walking distance increased for pulse rates between 10 and 30 pps, reached a level of saturation from 40 to 70 pps, and decreased with further increases in pulse rate. Similar trends were observed for steering and forward velocities, especially during re-orientation responses to the subsequent broadcast location. Mean angular heading to the initial broadcast location was less selective as flies oriented to a direction that approached the broadcast location for a broad range of pulse rates. Re-orientation responses, however, were more selective and flies most accurately localized the song broadcast following a switch in source location for pulse rates between 40 and 70 pps. Flies steered to track the switch in broadcast location with the smallest orientation error, for this same range of pulse rates when test responses were compared to those of the standard 50 pps song of *G.*

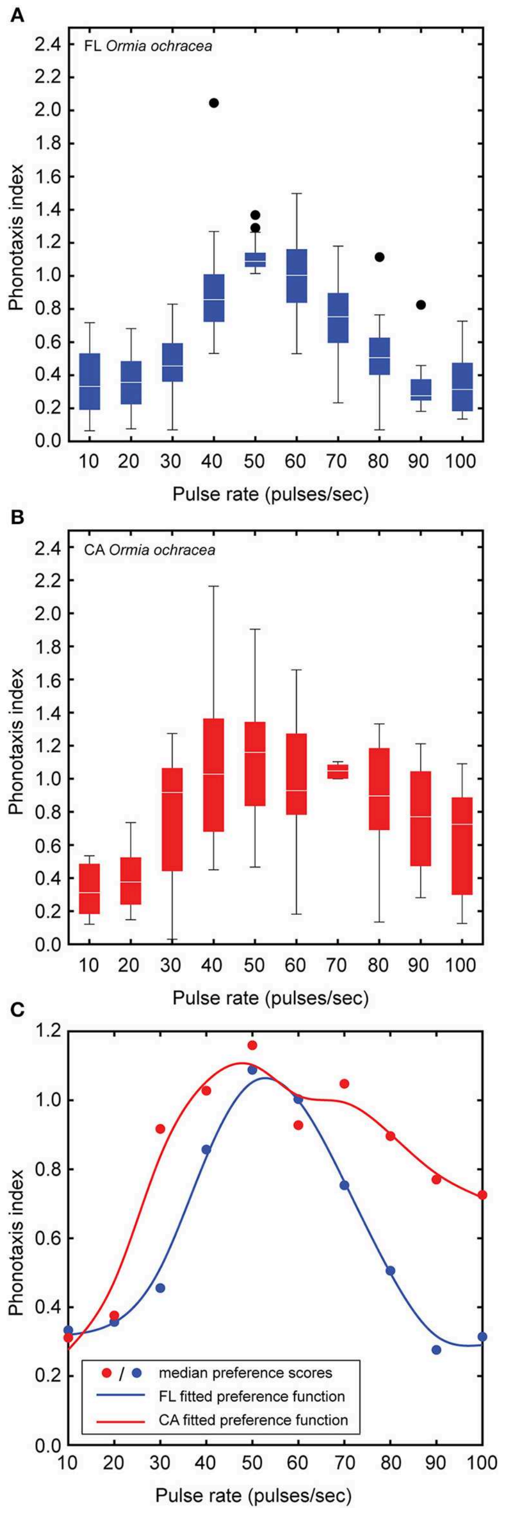

FIGURE 6 | Effects of song pulse rate on the phonotaxis performance index. Box plots depict the first and third quartiles and median phonotaxis index values obtained from Floridian **(A)** and Californian **(B)** *Ormia ochracea*. **(C)** A smoothing cubic spline was fitted to median phonotaxis index values to generate pulse rate preference functions. Whiskers show the most data extreme points that are not considered outliers, and closed circles indicate outliers.

rubens. Above and below the 40–70 pps range, mean steering velocity decreased while orientation error increased. Taken together, the reduced list of features included distance, mean steering velocity and error in angular orientation. These features were suited for inclusion in our novel phonotaxis performance index that compares responses to test signals relative to a reference signal. Based on this index, *O. ochracea* expressed a clear preference function, centered on a pulse rate matching the song of the preferred host for the Florida population, and consistent with results from flying phonotaxis studies (Walker, 1993).

We applied our phonotaxis performance index to examine pulse rate preference in Californian *Ormia ochracea*. Our analysis revealed that Floridian and Californian *O. ochracea* exhibit similar pulse rate preferences. While the pulse rate preference function of Floridian *O. ochracea* is sharply "tuned" to 50 pps, the preference function of Californian *O. ochracea* appear to be more broadly centered around pulse rates that range from 40 to 70 pps (**Figure 6C**). We suggest that this subtle difference in selectivity may relate to differences in the number of potential host cricket species that each population utilizes for reproduction. Floridian, *O. ochracea* is known to mainly parasitize the southeastern field cricket *Gryllus rubens* (Walker, 1986; Walker and Wineriter, 1991; Gray et al., 2007), a species that produces a trilling calling song with a pulse rate of ∼50 pps. In California, *O. ochracea* rely on the variable field cricket *Gryllus lineaticeps* as their preferred host, which produces chirps consisting of ∼8 sound pulses produced at ∼67 pps. However, Californian *O. ochracea* may also utilize the western stutter-trilling cricket *Gryllus integer* and the long-chirp field cricket *Gryllus multipulsator* as potential host species (Weissman et al., 2009; Paur and Gray, 2011b). *Gryllus integer* produces trills with brief gaps separating groups of ∼3 sound pulses at a pulse rate of ∼70–90 pps while *G. multipulsator* produces long chirps with a pulse rate of ∼78 pps (Weissman et al., 2009). Broader pulse rate selectivity may allow Californian *O. ochracea* to potentially exploit a greater number of host species for the development of their larval young.

Field experiments clearly demonstrate differences in host cricket preferences between Floridian and Californian *O. ochracea* (Gray et al., 2007). While the carrier frequency of field cricket calling songs are generally similar, the temporal patterning of sound pulses is species-specific (Gerhardt and Huber, 2002). In addition to differences in pulse rates, cricket songs also differ in the fine scale temporal structure of sound pulses (i.e., pulse durations and the interval between pulses) and larger scale temporal organization of sound pulses into chirps and gaps between and within trills (Hedwig, 2014). In the current experiments, we examined pulse rate preferences in test songs by manipulating pulse durations and intervals by equal amounts to maintain a 50% duty cycle. These experiments were not designed to examine signal selectivity based on differences in the duration of sound pulses, the interval between sound pulses, and the larger temporal organization of sound pulses into songs. Future experiments should directly test for specific temporal features that underlie song preferences in the field.

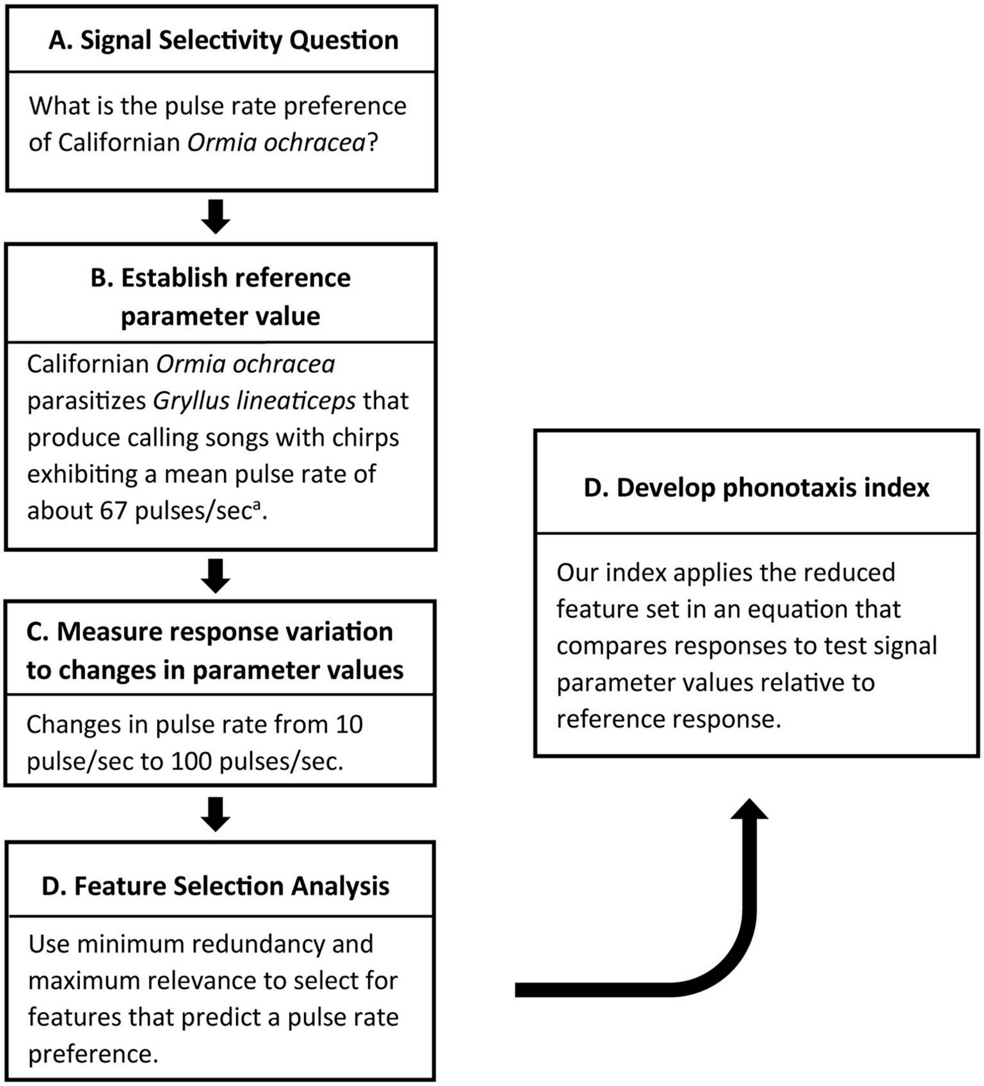

FIGURE 7 | Approach for developing a phonotaxis performance index. Developing a phonotaxis performance index to address a specific question **(A)** with some knowledge of salient signal values of a particular signal feature **(B)** to serve as a reference for comparison. **(C)** Behavioral responses are measured in response to varying signal values. This is followed by a feature selection approach to narrow down the list of response features that predict natural signal preferences. **(D)** These response features are incorporated into a performance index that compares responses to test signals relative to a reference response. [a]Mean pulse rate reported in Wagner and Reiser (2000). Measures of variance not reported.

Advantages and Limitations of the Phonotaxis Performance Index

We have demonstrated that our approach for developing a sensitive phonotaxis performance index can be applied to examine signal preferences exhibited during walking phonotaxis. No-choice paradigms were thought to provide little information regarding song preferences because animals tend to respond with less discrimination when presented without choice (Doherty, 1985; Wagner, 1998). Consistent with Bush and colleagues (Bush et al., 2002), we argue that no-choice paradigms can provide additive information in studying song recognition and signal preferences. In no-choice experiments, Bush et al. calculated a phonotaxis index based on measuring the ratio of response time to reach the source location for a control advertisement call compared to alternative advertisement calls (Bush et al., 2002). This index revealed variation in response timing to changes in pulse rates that facilitate call recognition in two closely related species of treefrogs (*Hyla chrysoscelis* and *Hyla versicolor*). By using a carefully selected phonotaxis task (tracking a switch in source location), our study demonstrates the opportunity to measure variation in tracking performance that is indicative of signal preferences. This preference is quantified using a composite performance index that consists of the most predictive response parameters that results in a heightened sensitivity for detecting a pulse rate preference.

By definition, an index of behavioral performance must be designed to measure task-relevant variability in the behavioral responses. The task, therefore, is to determine which variables best represent the behavior in question. Previously developed phonotaxis performance indices characterized response variation underlying song recognition in orthopteran insects (Schul, 1998) and anurans (Bush et al., 2002). Sound localization behavior in orthopterans and anurans is characterized by turning responses to lateral sound sources resulting in a walking path meandering around a direct route to the source location. Lateralization, because it requires corrective turns to reorient to the source location, causes large variation in the directedness of walking paths, greater total walking distances required to arrive at a source, and increased time required to locate a sound source (Murphey, 1972; Rheinlaender et al., 1979; Gerhardt and Rheinlaender, 1980; Rheinlaender and Blatgen, 1982). In contrast, *O. ochracea* precisely follow a direct walking path in phonotaxis and this renders previous phonotaxis indices unsuitable for quantifying walking phonotaxis in *O. ochracea*. Turns in our study were elicited by requiring flies to track a shift in source location, and steering velocity was a salient response parameter. This may also be the case in other systems, where some measures of phonotaxis have focused on path sinuosity, rather than turning dynamics.

In principle, our approach could also be applied to quantify signal preferences during flight. Flying phonotaxis has been studied in *O. ochracea* using a tethered flight paradigm (Rosen et al., 2009). Similarly to crickets, flies adopt steering maneuvers toward stimuli with the temporal pattern and frequency content of cricket calling songs (∼4.5 kHz), but steer away from stimuli with ultrasonic frequencies (>20 kHz) that are characteristic of bat sonar (Wyttenbach et al., 1996; Rosen et al., 2009). Developing an index to quantify performance in flying phonotaxis would likely involve measuring response latencies and the magnitude of steering maneuvers to (or away from) the source location. In flies and crickets, there appears to be a sharp boundary between two categories along a frequency continuum that distinguishes an attractive cricket host from the echolocation calls of insectivorous bats (Wyttenbach et al., 1996). This frequency based categorical perception of cricket calling songs and bat vocalizations is similar to the human auditory perception of phoneme boundaries that separate /pa/ and /ba/ involved in speech comprehension (Liberman et al., 1957). We expect that our approach can also be applied to other psychoacoustic studies that probe similar perceptual phenomena involved in auditory grouping and sound source segregation.

Walker (1993) documented a pulse rate preference in Floridian *O. ochracea* expressed during flying phonotaxis in response to synthetic cricket songs that varied in pulse rates. By measuring capture rates with an array of sound traps that presented different pulse rate songs, Walker found that highest capture rates occurred at the sound trap presenting the standard 45 pps song. Plotting the proportion of flies captured as a function of pulse rate resulted in a preference function with a "bell-shaped curve" centered between 45 and 50 pps (**Figure 4B** in Walker, 1993). We validated our approach by using identical stimuli in the current study so that pulse rate preferences during walking phonotaxis in the laboratory would be directly comparable to field results. Our results yield a similar preference function for walking phonotaxis, and provide a tractable approach for measuring other dimensions of song preferences and signal features that may be evaluated for song recognition (e.g., pulse duration, duty cycle, etc.).

Given that different populations of *O. ochracea* are locally adapted to parasitize different host cricket species (Gray et al., 2007), our index will also provide a unique opportunity to investigate whether these populations evaluate the same or different signal features for song recognition. Short-term learning of species-specific song patterns based on acoustic experience has been documented in Californian *O. ochracea* and this suggests that the song recognition "template" is malleable to some degree (Paur and Gray, 2011a). Our index can be applied to further examine how learning and memory can shape host choice among different populations and to characterize the extent of learning specific signal features that may limit host switching.

We expect that the current phonotaxis performance index will be directly applicable for quantifying behavior in other acoustically orienting parasitoid flies that eavesdrop on the communication signals of orthopterans or hymenopterans (Lehmann, 2003; Lakes-Harlan and Lehmann, 2015). Some flies in the tribes Orminii and Emblemasomatini (Lakes-Harlan and Lehmann, 2015), making up ∼68 species of acoustically orienting parasitoids, have evolved to eavesdrop on the communication signals of a range of host species with signals that differ in spectral and temporal features (Lehmann, 2003). Some of these flies include tachinids such as: *Ormia depletea* that parasitize mole crickets (*Scapteriscus* spp.) (Fowler, 1987; Parkman et al., 1996), *Ormia linefrons*, *Homotrixa alleni*, and *Therobia leonidei* that parasitize various katydid species (Burk, 1982; Allen, 1995; Shapiro, 1995; Lehmann, 2003) and sarcophagids (i.e., *Emblemasoma auditrix*) that parasitize cicadas (Schniederkotter and Lakes-Harlan, 2004). The evolution of convergent signal preferences between some eavesdroppers and intended receivers (Wagner, 1996; Bernal, 2006; Aihara et al., 2016) suggests that they are solving similar sensory problems: detecting, recognizing, and localizing common communication signals. However, signalers and eavesdroppers likely accomplish these sensory processing tasks with different peripheral and central nervous systems. Applying our phonotaxis performance index along with a phylogenetic approach to investigate signal preferences among eavesdroppers can provide important insights into the diversity of sensory strategies that shape the evolution of host choice.

Although not explicitly tested in this current study, we believe that our approach for developing a phonotaxis performance index is general and should be applicable for measuring stimulus-evoked locomotor behavior in other animals. However, the current index was specifically developed to capture response variation in the relatively more direct phonotactic responses of *O. ochracea*. Consequently, our index may only be applicable for measuring behavior in *O. ochracea* and in other acoustically orienting parasitoid flies.

Avoiding Parasitism From Eavesdropping Acoustic Parasitoid Flies

Crickets parasitized by *O. ochracea* experience almost certain death (Adamo et al., 1995). This strong selective pressure imposed by *O. ochracea* has the potential to drive the evolution of sensory strategies that prey can take to avoid parasitism

(Zuk and Kolluru, 1998). In one striking example, males of the Polynesian field cricket *Teleogryllus oceanicus* has lost the ability to produce calling songs to attract potential mates. This strong selective pressure imposed by *O. ochracea* has led to the proliferation of a single-gene wing mutation in *T. oceanicus* to occur on several of the Hawaiian Islands (Zuk et al., 2006; Tinghitella, 2007; Pascoal et al., 2014). Males exhibiting this mutation are mute and lack the necessary wing morphology to produce calling songs despite trying to do so (Zuk et al., 2006; Tinghitella, 2007; Schneider Will et al., 2018). However, this adaptive response to evade natural selection imposed by *O. ochracea* is balanced by sexual selection that favors the production of calling songs (Tanner et al., 2019) as female crickets discriminate strongly against males that cannot produce calling songs (Bailey and Zuk, 2008; Tinghitella and Zuk, 2009). Crickets with this deficit pay a fitness cost and must rely on alternative mating tactics (i.e., satellite behavior) for reproductive success (Kolluru et al., 2002; Tanner et al., 2019). Whether normal-winged crickets can directly avoid parasitism from *O. ochracea* by altering spectral or temporal characteristics (i.e., pulse durations, interpulse intervals, and pulse rate) of their calling songs remains unknown.

Crickets can avoid parasitism by signaling during periods of low parasitoid activity (Cade et al., 1996; Vélez and Brockmann, 2006), or by producing calling songs that are shorter and less conspicuous (Lehmann and Heller, 1998). However, the effectiveness of interrupted calling may be limited as some parasitoids can estimate host location while in flight and land within centimeters of an attractive sound source (Müller and Robert, 2001, 2002). Alternatively, signalers may adopt the strategy of communicating in a chorus as this can lower the risk of any one individual from being parasitized, or it may confuse eavesdroppers of signaler location (Goodale et al., 2019). Synchronized signaling or the presence of masking noise can lead to the perception of a "phantom" sound source location that does not correspond to the actual signaler location (Lee et al., 2009; Lee and Mason, 2017), but *O. ochracea* can also exploit small time differences between signalers via the precedence effect to locate host crickets (Lee et al., 2009).

Finally, we stress that the effectiveness of behavioral strategies or signal design to avoid parasitism can be evaluated by performing psychoacoustic experiments that measure sensory perception in eavesdroppers. We describe a rigorous approach to developing a measure to quantify signal selectivity. This approach can be generalized to study locomotor responses in acoustically orienting eavesdroppers and the specific index that we present here can be applied across parasitoid flies to investigate sensory strategies that orthopteran and hymenopteran victims can take to avoid parasitism.

AUTHOR CONTRIBUTIONS

NL and AM: conceptualization, writing—original draft, resources, supervision, and funding acquisition. NL, IP, and AM: methodology. NL, AK, KJ, and DK: investigation. NL: data curation and visualization. NL, AK, IP, KJ, and AM: writing—review and editing.

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Maternal Vibrational Signals Reduce the Risk of Attracting Eavesdropping Predators

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Unintended receivers can be an important source of selection on social signals. Vibrational social signals are produced by diverse taxa, but most work on eavesdropping on social communication has focused on airborne signals. Few studies have examined whether predators and parasitoids exploit vibrational social signals, and whether vibrational communication systems have features to reduce apparency to unintended receivers. For a subsocial insect species (Hemiptera: Membracidae: *Platycotis vittata*), we first used a field playback experiment to show that offspring vibrational signals evoke maternal defense, and that maternal signals can inhibit offspring signaling. We next evaluated two potential benefits of inhibiting offspring signaling. We tested whether such inhibition increases the accuracy of offspring signals, as it does in a closely related species. We also tested whether by inhibiting offspring signals, mothers reduce the risk of attracting eavesdropping predators. Using playback experiments, we found that a vibrationally-sensitive predator attends to offspring but not maternal signals. In contrast, we found no evidence that inhibition increases the accuracy of offspring signals. Because predator eavesdropping is a likely cost of social communication for vibrationally signaling animals, we suggest that mechanisms to reduce apparency of such social signals may be common.

Keywords: predator eavesdropping, social signals, vibrational communication, parent-offspring behavior, collective behavior

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INTRODUCTION

Predators and parasitoids eavesdrop on airborne mate advertisement and courtship signals to locate prey and hosts (reviewed in Zuk and Kolluru, 1998; Haynes and Yeargan, 1999), and can act as powerful agents of selection, even driving the evolutionary loss of signaling behavior (Zuk et al., 2006). For animals communicating with substrate vibrations, however, there has been controversy about the potential for predator eavesdropping. Henry (1994) suggested that vibrational communication is essentially a private channel. In contrast, Morris et al. (1994) and (Römer et al., 2010) note that when rainforest katydids switch from airborne to substrate-borne signaling, they avoid eavesdropping bats but remain detectable by nearby spiders. Other authors have argued that substrate vibration is likely to be among the most vulnerable of modalities to unintended receivers, given the wide array of vibrationally-sensitive taxa (Cocroft and Rodríguez, 2005; Cocroft, 2011; Virant-Doberlet et al., 2019). Although Zuk and Kolluru's (1998) review of predator eavesdropping listed no examples from the vibrational modality, more recent studies provide evidence of the importance of unintended receivers in vibrational interactions. To date, however, such evidence is restricted to predator eavesdropping on mate advertisement signals (Narhardiyati and Bailey, 2005; Roberts et al., 2007; Virant-Doberlet et al., 2011) and eavesdropping on incidental vibrational cues by predators (Pfannenstiel et al., 1995; Barth, 1998; Meyhöfer and Casas, 1999) and competitors (Evans et al., 2009).

It is not known if predators eavesdrop on vibrational social signals, as they do on social signals in the other signaling modalities. For example, for airborne acoustic communication, such eavesdropping occurs on aggregating signals (reviewed in Haynes and Yeargan, 1999), offspring begging signals (reviewed in Magrath et al., 2010), alarm signals (Allan et al., 1996), and mobbing signals (Krams et al., 2007). This is unsurprising, as when multiple individuals signal in close proximity, they should provide an amplified and persistent source of information to unintended receivers. However, to our knowledge, there are no examples of predator eavesdropping on social vibrational signals. Yet many invertebrates are group-living for at least one life stage (Costa, 2006), and vibrational communication is widespread in group-living insects (reviewed in Cocroft and Hamel, 2010).

Because eavesdropping predators and parasites can act as strong agents of selection and impose costs on signalers, we should expect to see evidence of such selection in group-living, vibrationally-signaling species. For example, selection might result in strategies to mitigate costs while preserving signal function, such as reducing the apparency of signals to unintended receivers and increasing receiver sensitivity. Here, we test the hypothesis that for an insect species in which mothers and offspring use vibrational communication, maternal signals function to reduce the apparency of their offspring to eavesdropping predators by inhibiting offspring signaling.

In oak treehoppers (Hemiptera: Membracidae: *Platycotis vittata)*, mothers and clustered offspring communicate with one another during predator encounters via substrate vibrations. A family typically consists of 40 to 50 sedentary offspring that live on the new growth tip of an oak branch with their mother (Wood, 1976). Oak treehopper family groups often develop in the presence of invertebrate predators on the same host tree, and even the same branch (**Figure 1**), and all known invertebrate predators of oak treehoppers are vibrationally-sensitive (Hamel, 2011). Predation is likely a strong source of offspring mortality: in one population, all offspring were lost from 45% of families, and invertebrate predators were commonly seen on the same trees as treehopper families (Hamel, 2011). We have observed attacks by invertebrate predators that resulted in 100% mortality.

Predator attacks can be prolonged, and offspring groups produce synchronized vibrational signals throughout such attacks (Hamel, 2011). Mothers defend their offspring from predators (Beamer, 1930), and in response to offspring signals, a mother searches for the predator and produces her own vibrational signals (*this study*). After predator encounters end, mothers produce semi-continuous trains of signals for several minutes, and offspring generally cease signaling.

Here, we first show that offspring collective signals evoke maternal antipredator behavior (Experiment 1), and that vibrational signals by oak treehopper mothers reduce signaling by offspring groups during simulated predator attacks (Experiment 2). We then evaluate two hypotheses to explain why mothers reduce signaling by offspring groups. First, maternal signals may inhibit continued signaling by offspring after attacks end and thereby increase the accuracy with which offspring signals indicate predator presence. Juveniles in closely related thornbug treehoppers (*Umbonia crassicornis*) evoke maternal defense with group vibrational signals (Cocroft, 1996), and often continue signaling after attacks end (Cocroft, 1999a), producing false alarms unless they are inhibited by maternal signals (Hamel and Cocroft, 2012). This hypothesis predicts that maternal signals should reduce offspring signaling when a predator cue is removed. To test this hypothesis, we elicited signaling by offspring groups with simulated predator attacks, removed the predator cue, and then measured continued offspring signaling response as we played maternal signals, silence, or a common source of environmental noise (Experiment 3).

FIGURE 1 | Vibrationally-sensitive insect predators of oak treehoppers **(A–C)** and an oak treehopper family **(D)**. **(A)** Crab spider carrying oak treehopper mother; egg clutch is visible on the branch, underneath the spider. **(B)** Predatory stink bug nymph (introduced by author) feeding on oak treehopper nymph. **(C)** Arboreal ants (*Crematogaster ashmeadii*) preying upon oak treehopper nymphs. **(D)** Oak treehopper mother and late instar nymphs.

We also tested a second hypothesis, that mothers signal to decrease the risk of attracting eavesdropping predators (Experiments 4 and 5). We tested this hypothesis by measuring the responses of one generalist, vibrationally-sensitive predator to offspring and maternal signals. A predatory stinkbug (Hemiptera: Pentatomidae: *Podisus maculiventris*) is an appropriate focal predator because individuals of this species have been observed preying upon oak treehopper juveniles in the field (Mark Rothschild, pers. comm.), and because it uses incidental vibrations to locate caterpillar prey (Pfannenstiel et al., 1995).

Finally, because preliminary observations suggested that offspring and maternal signals differ temporally and spectrally, we characterized maternal and offspring signals recorded during this work.

METHODS

Experimental Settings

We tested the effects of offspring signals on maternal behavior and of maternal signals on offspring behavior with field experiments (Experiments 1, 2, and 3) in 2009 and 2010, at the University of Florida Ordway-Swisher Biological Station (Putnam Co., FL). These three experiments were conducted with a naturally occurring field population of oak treehoppers, and each treehopper family was only used in a single experiment. We located female oak treehoppers on eggs by scanning branches of several oak species (*Quercus* spp.), and we covered each experimental family with a mesh sleeve to prevent predation. All nymphal aggregations tested were between the 2nd and 4th nymphal stages; oak treehoppers develop through a total of five nymphal stages. We tested predator responses to offspring and maternal signals in the laboratory (Experiments 4 and 5) at the University of Missouri.

Detection and Playback of Vibrational Signals

We detected treehopper vibrational signals with an accelerometer (PCB Piezotronics, NY, USA; Model 352A24, weight 0.8 g, frequency range: 0.8 Hz to 10 kHz ± 10% or Vibra-Metrics, NJ, USA; Model 9002A, weight 0.8 g, frequency range: 8 Hz to 18 kHz ± 10%) affixed to the branch $<$ 10 cm from each family using mounting wax and powered by a signal conditioner and power supply (PCB Model 480E09 or Vibra-Metrics Model P5000). We recorded playbacks and signaling responses using a Marantz PMD660 digital audio recorder with a sampling rate of 44,100 Hz. To ensure that playbacks closely matched the frequency and amplitude spectra of original recordings (**Figure S1**), we matched the relative positions of transducer and signal source between each respective stimulus recording and playback. Background noise in vibrational stimuli was minimized, as we recorded stimuli during periods without vibrational noise from environmental factors (e.g., rain and wind), except when the stimuli in question were wind-induced vibrations (see Experiments 4 and 5). In a few stimulus recordings, when unavoidable background noise was present on a stimulus recording but did not overlap with the stimulus, we replaced the background noise with silence of the same duration using Audacity (v. 1.3.13).

For playbacks, we first set up vibration recording and video equipment and allowed each treehopper family 1 h to acclimate. We recorded treehopper and predator behavior using a digital video recorder (Sony Handycam Models HDR-HC7 and HDR-SR11). We scored video of behavioral responses using QuickTime Player (v. 7) and vibrational signaling responses using Audacity (v. 1.3.13). Because substrate-borne vibrations from abiotic factors such as wind can influence treehopper signaling (McNett et al., 2010), we conducted field playback experiments very early in the mornings, when wind is infrequent and occurs at low intensity, and these experiments were situated at a site with minimal anthropogenic noise.

To play vibrational stimuli, we glued a small neodymium magnet (United Nuclear Scientific, Laingsburg, MI) to a branch. We positioned an electromagnet 1 to 2 mm from the magnet so that faces were parallel (Rodríguez et al., 2006). We then played stimuli to the electromagnet from Audacity v.1.3.12 on a MacBook 2.4 GHz Intel Core Duo via a RadioShack 40-watt PA amplifier. To ensure that playback signals had the correct amplitude spectrum, we used a custom program in MatLab v.R2008bSV to assess frequency filtering by the branch and build an inverse filter (Cocroft et al., 2014). We used this inverse filter to filter signals being played through each branch. To ensure we played stimuli at biologically relevant amplitudes, we matched playback peak acceleration to signal peak acceleration from the original field recording. We generated silence for control treatments in audio editing and recording software (Audacity v.1.3.12).

Experiment 1: Do Offspring Vibrational Signals Communicate Increased Risk to Mothers?

To test whether offspring signals evoke maternal antipredator behavior and describe maternal responses, we played offspring vibrational signals to nine oak treehopper families on separate trees (**Supplementary Video 1**), with each family consisting of a single mother and her offspring. Each family was played its own offspring vibrational signals. As a baseline for comparison and to control for effects of observer presence, equipment, and any electrical noise generated by equipment during trials, we also played silence to each family. We controlled for possible carryover effects by alternating the treatment order between families and by waiting 30 min between playback treatments.

Based on preliminary observations, we expected mothers to walk and signal in response to offspring signals. We scored maternal signals using Audacity (v. 1.3.13 beta), and the proportion of time each mother walked in QuickTime Player (v. 7). We compared responses to playbacks of offspring signals against those produced during silence with the Wilcoxon Signed-Rank test; all comparisons were two-tailed. Because we scored both walking and signaling by mothers to test whether offspring signals elicited maternal defense, we adjusted comparison *P*-values for false discovery rate (FDR) (Benjamini and Hochberg, 1995).

Experiment 2: Do Maternal Vibrational Signals Reduce Offspring Signaling?

To test whether maternal signals reduce offspring signaling, we removed the mother from each of 28 oak treehopper families, each of which was located on a separate tree. We then simulated predation to elicit signaling by each offspring aggregation, played either the mother's signals (one of the two maternal signal types, *see below*) or silence, and recorded offspring signals. To obtain vibrational playback stimuli, we recorded each focal mother's signals by simulating predation as described below 1 day before testing each family. When offspring began signaling, the mother patrolled the family, signaled, searched for the source of disturbance, and found the predator cue, which she kicked as she would a predator. As soon as the mother kicked the predator cue, we withdrew it from the aggregation, simulating a predator eviction. Each mother then returned to her typical position at rest at the trunk end of the aggregation and produced steady bouts of signals. Mothers produced short syllables during the early stages of a simulated attack, and long syllables after locating and evicting the simulated predator. We therefore used two vibrational stimulus treatments in this experiment: one with short maternal syllables (hereafter, "early encounter signals"), and one with semi-continuous trains of long and short syllables (hereafter, "post search signals").

We returned to each family the following day, removed the mother, set up vibration recording and video equipment, and allowed the family 1 h to acclimate. We then simulated a predator encounter with only the offspring aggregation, by presenting a predator cue and simultaneously playing vibrational stimuli or silence from the mother's resting position. Our predator cue was a chemical cue from a crushed treehopper nymph (Nault et al., 1974) which reliably elicits offspring signaling (J.H., pers. obs.). We sacrificed nymphs from oak treehopper families not included in an experiment and held them on a stainless steel probe ∼ 1 cm under the center of each aggregation; a different crushed nymph was presented under the nymphal aggregation for the 10 min duration of each simulated attack. Nymphs were humanely euthanized (frozen) before being crushed, and we rinsed the probe with 70% ethanol after each presentation. Mothers were kept in plastic vials during these simulations and returned to their offspring after recording was completed. Because there were three treatments (early encounter signals, post search signals, and silence), we controlled for treatment order effects by randomly assigning families to one of the six possible treatment sequences, and by waiting 1 h between treatments.

We scored offspring group signaling rates in response to each playback treatment. Because we had a larger sample size for this experiment than for Experiment 1, we assessed the effect of early encounter and post-search maternal signaling on offspring signaling with a generalized linear mixed model (GLMM) (package glmmadmb, http://glmmadmb.r-forge.r-project.org/) fitted to the negative binomial error distribution. By using a mixed-effects model, we accounted for experimental design parameters and environmental factors that might have influenced offspring signaling response. The negative binomial was an appropriate distribution choice as the data were counts (i.e., number of offspring group signals per 10 min trial), and this distribution fit the error distribution of the response variable. As fixed effects, we included playback treatment, carryover effects, treatment sequence, temperature, energy from wind-induced vibrations, and interactions between temperature and treatment and temperature and carryover effects. We included family nested within treatment sequence as a random term. We set contrasts in the model to compare responses to playbacks against those from the silence treatment.

Because oak treehopper vibrational signals have not been previously characterized, we took frequency (peak frequency and 90% bandwidth) and temporal (90% duration) measures of maternal and offspring vibrational signals produced during the stimulus recordings for this experiment. Signal analysis was conducted in Raven Pro 1.5, and statistical analyses were conducted with R statistical software, version 2.13.0.

Experiment 3: Do Maternal Vibrational Signals Reduce False Alarms by Offspring?

To assess whether maternal signals reduce group signals in the absence of a predator, we evoked offspring signals from 10 oak treehopper families as described in Experiment 2, but here we withdrew the predator cue after eliciting 10 group signals, rather than leaving the cue in place, as in Experiment 2. As we removed the predator cue, we began playing vibrational stimuli (i.e., maternal signals, silence, or wind-induced vibrations) and recording offspring response.

As in Experiment 2, we first obtained a recording of each mother's signals. For playbacks, our treatments were maternal vibrational signals (post-search), wind vibrations, or silence. Each family received all three playback treatments, and each playback was a loop composed of 30 s of stimulus followed by 30 s of silence. We included silent intervals to facilitate accurate scoring of offspring signaling response, in case the presence of playback signals on the audio track interfered with scoring. However, because offspring group signals contain energy at higher frequencies than do the maternal signals or wind vibrations, we were easily able to score all group signals, including those produced during vibrational stimuli. We controlled for possible effects of treatment order by randomly assigning each family to a pre-determined treatment sequence and by waiting 1 h between treatments.

We scored offspring group signaling rates for each family using XBAT (Harold Figueroa, Ithaca, NY). Because sample size was limited, we compared signaling responses among treatments in both experiments using the Quade test (Quade, 1979), a non-parametric analog of repeated-measures ANOVA, rather than using a mixed-model approach. Statistical tests were conducted with R statistical software, version 2.13.0.

Experiments 4 & 5: Do Offspring and Maternal Signals Attract Potential Predators?

Oak treehopper maternal and offspring signals have different acoustic properties (*see Results*), and may differ in their salience to a predator. Here, we tested the hypothesis that offspring signals, but not maternal signals, attract vibrationally-sensitive insect predators. With two separate experiments, we assessed the responses of predatory stinkbugs (Hemiptera: Pentatomidae: *Podisus maculiventris*) to oak treehopper offspring and then maternal signals in the laboratory.

In both experiments, we allowed juvenile stinkbugs to walk up a thin string tied to the center of a branch of a potted oak (*Q. alba*) sapling (**Figure 2**). Each predator ($N = 30$ for offspring signals; $N = 51$ for maternal signals) received only one playback treatment. Sample size differences are an artifact of the two experiments being done in different years (2010 and 2009, respectively). Here, we wanted to test whether predators

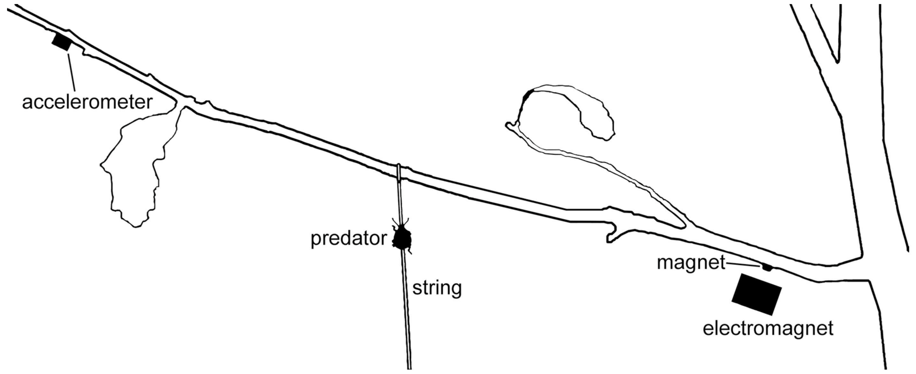

FIGURE 2 | Playback setup for Experiments 4 and 5. Predatory stinkbugs were introduced to string and allowed to walk up to the branch of a potted *Q. alba* sapling. Vibrational stimuli were imparted using an electromagnet driving a magnet attached to the branch at the typical resting location of a female oak treehopper and monitored using an accelerometer.

are attracted to oak treehopper offspring or maternal signals in particular, as compared with vibrations from other sources, such as abiotic factors. We therefore played offspring signals or maternal signals, wind vibrations, and silence for 3 min in continuous loops. We randomized stimulus order and stimulus exemplars. For the first experiment, we recorded two exemplars each of offspring signals and of wind vibrations, and for the second experiment, five exemplars each of maternal signals and wind vibrations. All exemplars were drawn from field recordings of simulated predator attacks and wind vibrations. When playing wind vibrations, we matched peak acceleration to that of the offspring signals being played.

We were provided with stinkbugs by the USDA-ARS Biological Control of Insects Research Laboratory (Columbia, MO). We maintained a laboratory colony at ∼ 25°C on a 14:10 h light:dark cycle. We fed stinkbugs a combination of fourth instar larvae of *Trichoplusia ni* (Hübner) and a zoophytogenous artificial diet (Coudron et al., 2002) and provided water via moist dental wicks (Richmond Dental) in small plastic weigh boats (Fisher Scientific).

We began scoring predator behavior when all of a predator's legs made contact with a branch and ended after 180 s or when the predator dropped from the branch. Stinkbugs detect substrate vibrations with sensory organs in their legs (Čokl and Virant-Doberlet, 2003). Stinkbugs have been shown to remain in the local area of an attractive stimulus (Mazzoni et al., 2017), and pause when attending to attractive vibrational stimuli, as when choosing a direction at a Y-junction (Ota and Čokl, 1991; Čokl et al., 1999). We therefore scored the proportion of time that each predator remained stationary and the time spent on the half of the branch nearest to the playback vibration source as indices of stimulus attractiveness.

To assess the effect of playback treatment on the proportion of time predators remained stationary, we fitted a generalized linear model to the quasibinomial distribution (Warton and Hui, 2011). We set contrasts to compare predator responses during the signal treatment against those during silence and wind vibration treatments. The second response variable, proportion of time spent near the vibration source, had a nearly binary distribution: most (28/30) predators spent very little ($<$ 1/4 of total time) or almost all ($>$ 3/4 of total time) near the vibration source. We therefore treated these responses as binary data (success: predators spend $\geq$ half of observation time near the vibration source), fitted a logistic regression model with contrasts set as in the binomial model, and evaluated treatment level effects with likelihood ratio tests (LRTs). For all three response variables, we first tested for effects of playback exemplars. We found no significant exemplar effects (all $P > 0.15$) and pooled data within each treatment. Because there were three measures of predator attraction, we corrected P-values for false discovery rate (FDR) (Benjamini and Hochberg, 1995).

RESULTS

Experiment 1: Do Offspring Vibrational Signals Communicate Increased Risk to Mothers?

Mothers signaled at a higher rate and walked for a greater proportion of time when offspring signals were played than when silence was played (for both maternal walking and signaling: offspring signals vs. silence, Wilcoxon $W = 0$, $P_{\mathrm{FDR}} = 0.016$, **Figure 3**). The offspring in each family also produced some vibrational signals during trials, but we found no difference in the number of group signals produced by nymphs according to playback treatment (offspring signals vs. silence, Wilcoxon $W = 0$, $P_{\mathrm{FDR}} = 0.125$). Maternal walking and signaling responses did not differ between trials in which their offspring signaled along with playbacks and those with playback signals alone (maternal signaling: Wilcoxon $W = 9$, $P = 0.905$; walking: Wilcoxon $W = 12$, $P = 0.712$).

Experiment 2: Do Maternal Vibrational Signals Reduce Offspring Signaling?

In response to simulated predator attacks, oak treehopper mothers produced vibrational signals consisting of short syllables (69 ± 38 ms) as they began walking, and a combination of short and longer (613 ± 208 ms) syllables after ending their search

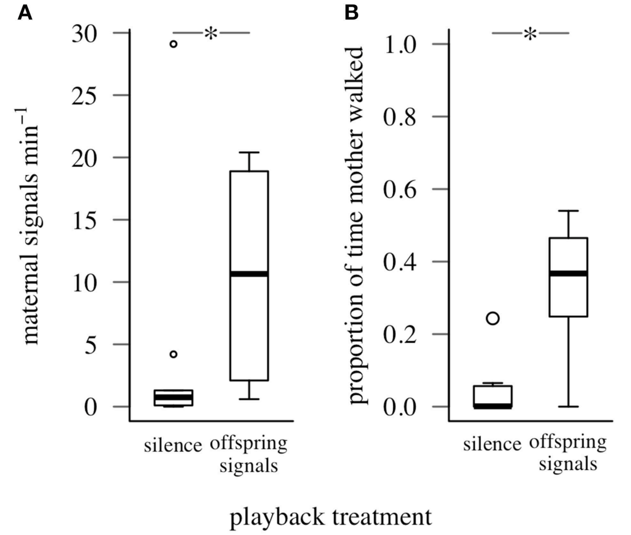

FIGURE 3 | Signaling and walking response of mothers to playbacks of silence and offspring group signals (Experiment 1). *represents PFDR < 0.05, Wilcoxon Signed-Rank Test. Box plots show distributions of **(A)** maternal signaling rate, **(B)** proportion of time mothers walked (minimum, first quartile, median, third quartile, maximum; open circles represent outliers).

and resettling at the base of the offspring aggregation (**Figure 4**) ($N = 11$ females, 7–10 of each signal type were analyzed from each female). Maternal signals then continued at high rates for several minutes. The frequency spectra of both short and long maternal signals were broadband (90% Bandwidth: 1793 ± 862 Hz and 1964 ± 392 Hz for short and long signals, respectively); the frequencies with greatest amplitude were 126 ± 87 Hz (short signals) and 192 ± 57 Hz (long signals).

Offspring produced signals individually and as synchronized groups. Individual signals had a mean duration of 75 ± 26 ms ($N = 11$ aggregations, 7–10 signals analyzed from each). Group signals are formed by overlapping individual signals and have a mean duration of 570 ± 207 ms ($N = 11$ aggregations, 2–10 signals analyzed from each). Group signals have peak amplitude near the midpoint of each signal and a characteristic waveform (**Figure 4**). Frequency spectra of individual and group signals were broadband (90% Bandwidth: individual: 7166 ± 862 Hz; group: 8955 ± 4796 Hz). For group signals, the frequency with the greatest amplitude was 386 ± 299 Hz; for individual signals, it was 83 ± 120 Hz.

Maternal post-search vibrational signals reduced offspring collective signaling during simulated predator attacks. The full model explained 68% of the variation in offspring signaling rate. After accounting for the effect of temperature on offspring behavior (GLMM, coefficient = 0.801, SE = 0.241, $P < 0.001$), offspring aggregations produced fewer group signals during playbacks of maternal post-search signals than during silence (maternal post-search signals: 3.41 ± 3.52 / min; maternal early encounter signals: 5.00 ± 3.37 / min; silence: 6.03 ± 4.56 / min; values are means ± SDs) (GLMM, coefficient = −0.609, SE = 0.195, $P = 0.002$; **Figure 5**). In contrast, offspring aggregations produced similar numbers of group signals during playbacks of maternal early encounter signals and silence (GLMM, coefficient = −0.267, SE = 0.177, $P = 0.130$). The experimental design parameters we expected to influence offspring signaling response accounted for 7.03% of variation (carryover: 4.89%; treatment sequence: 2.14%), and interactions between temperature and design parameters another 11.53%.

Experiment 3: Do Maternal Vibrational Signals Reduce False Alarms by Offspring?

Maternal vibrational signals did not reduce false alarms by offspring after simulated predator attacks: offspring group signaling rate did not differ by playback treatment (Quade $F = 1.519$, $df = 2/18$, $P = 0.25$; **Figure 6**). Offspring aggregations produced group signals at similar (low) rates after simulated attacks, regardless of which vibrational stimulus type was played (maternal post-search signals: 2.25 ± 1.61/min; wind vibrations: 1.75 ± 1.14/min; silence: 2.86 ± 2.57/min).

Experiments 4 & 5: Do Offspring and Maternal Signals Attract Potential Predators?

Playback of offspring signals influenced the proportion of time that predators remained stationary [$N = 30$, $F_{(2,27)} = 8.458$, $P = 0.001$, $P_{\mathrm{FDR}} = 0.003$]: predators were still for a greater proportion of each trial when offspring signals were played than when silence or wind vibrations were played (**Figure 7**; **Supplementary Table 1**). Additionally, the proportion of predators spending more than 50% of the observed time near the vibration source was higher during playback of offspring signals than during silence, although this did not differ between offspring signals (0.70 of individuals) and wind vibrations (0.40 of individuals) (**Figure 7**; **Supplementary Table 1**), and the overall effect of playback treatment on predator location was not significant ($N = 30$, LRT = 5.368, $P = 0.068$, $P_{\mathrm{FDR}} = 0.068$). In contrast, playback of maternal signals did not influence the proportion of time that predators remained stationary [$N = 51$, $F_{(2,48)} = 1.989$, $P = 0.148$, $P_{\mathrm{FDR}} = 0.296$], or the proportion of predators spending $\geq$ 50% time near the vibration source ($N = 51$, LRT = 2.124, $P = 0.346$, $P_{\mathrm{FDR}} = 0.346$) (**Figure 7**; **Supplementary Table 1**).

DISCUSSION

We have established the functions of vibrational signals produced by oak treehopper mothers and offspring in a field population during simulated predator attacks, and we have provided evidence that as with social communication in other modalities, social vibrational signals may be exploited by unintended receivers. Our results also suggest that by reducing offspring vibrational signaling, maternal signaling may reduce the likelihood of attracting invertebrate predators.

Oak treehopper mothers and offspring both produce vibrational signals during simulated predator attacks. Offspring group signals evoke defensive behavior by mothers, and maternal signals inhibit offspring from signaling. Offspring signaling and

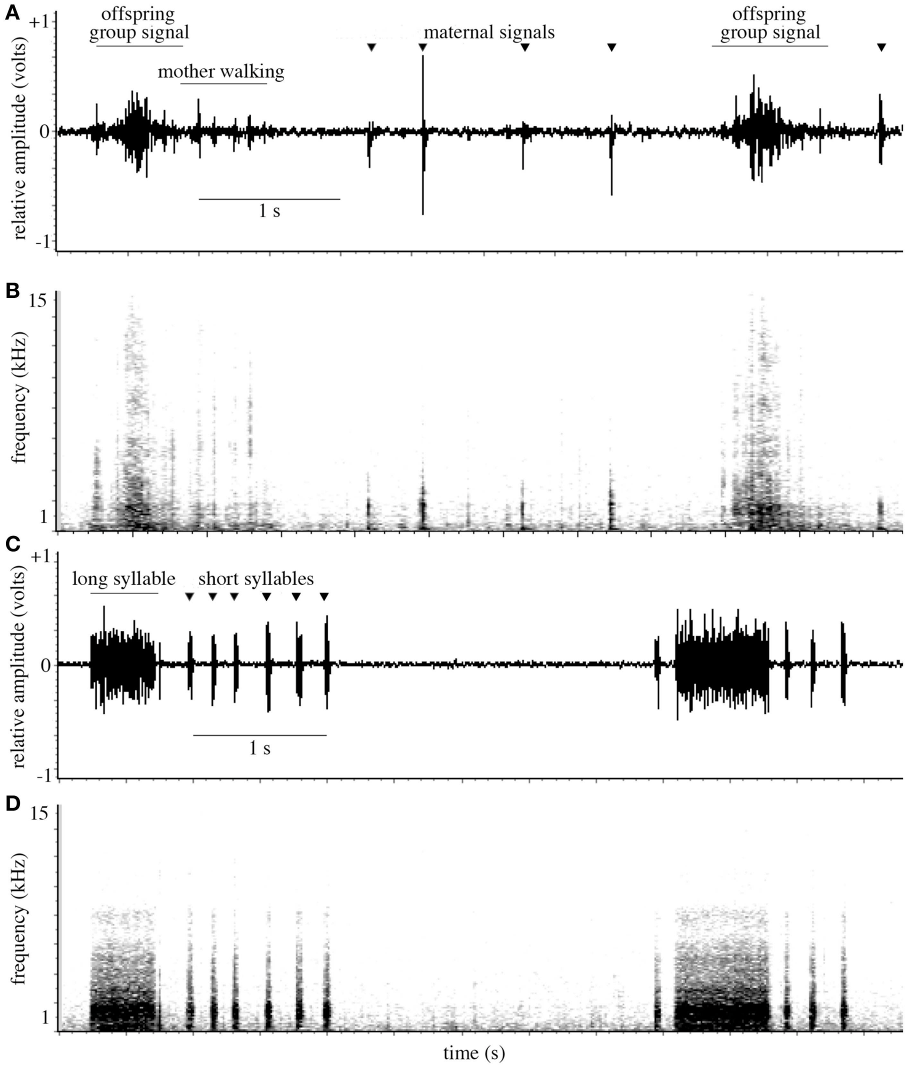

FIGURE 4 | (A) Waveform and **(B)** spectrogram showing oak treehopper offspring vibrational signals; vibrations from mother walking; and maternal early encounter signals (marked with triangular points). **(C)** Waveform and **(D)** spectrogram showing oak treehopper maternal post-search vibrational signals with long and short syllables, produced after a mother has returned to her resting position at the base of the offspring aggregation.

maternal responses to playbacks of offspring signals, including walking and signaling, were all consistent with preliminary observations of familial responses during predator attacks (Hamel, 2011).

We consider our two hypotheses to explain why mothers inhibit offspring signaling, beginning with whether mothers might improve the accuracy of offspring signals. By inhibiting offspring signaling, maternal signals do not reduce the number of false alarms by offspring groups, as they do in a closely related species, in which offspring often continue signaling after predator attacks have ended, and even spontaneously begin signaling again after ceasing (Cocroft, 1999a). Oak treehopper offspring signaled during simulated predator attacks, but they produced very few signals after attacks ended. In other words, they tend not to produce false alarms, whether or not the mother is signaling.

Our second hypothesis was that by silencing offspring, maternal signaling might reduce a family's apparency to predators. A generalist invertebrate predator that locates other species of insect prey via incidentally produced substrate-borne vibrations (Pfannenstiel et al., 1995) attends to oak treehopper offspring signals, but not to maternal signals, with a stationary posture. Although animals adopt stationary postures in response to both attractive stimuli and to perceived threats, the predators in this study also spent more time near the stimulus source when offspring signals were played. In the field, offspring aggregations occur on the same trees, and sometimes the same branches, as vibrationally sensitive invertebrate predators (J.H., pers. obs.). Silencing oak treehopper offspring may therefore reduce the risk of attracting predators occurring in close proximity to relatively immobile offspring groups.

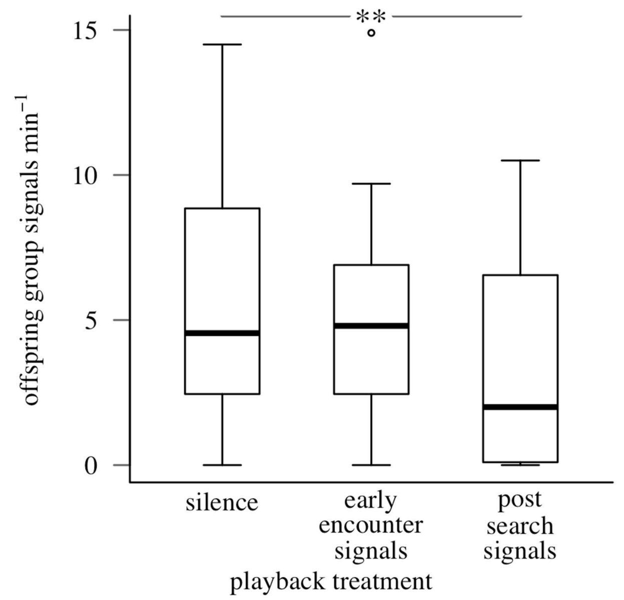

FIGURE 5 | Signaling responses of oak treehopper offspring aggregations to playback of silence, maternal early encounter signals, or post-search signals during simulated predator attacks (Experiment 2). Box plots show distributions of offspring group signaling rate (minimum, first quartile, median, third quartile, maximum; open circles represent outliers). $N = 28$ families. **represents $P < 0.01$, GLMM.

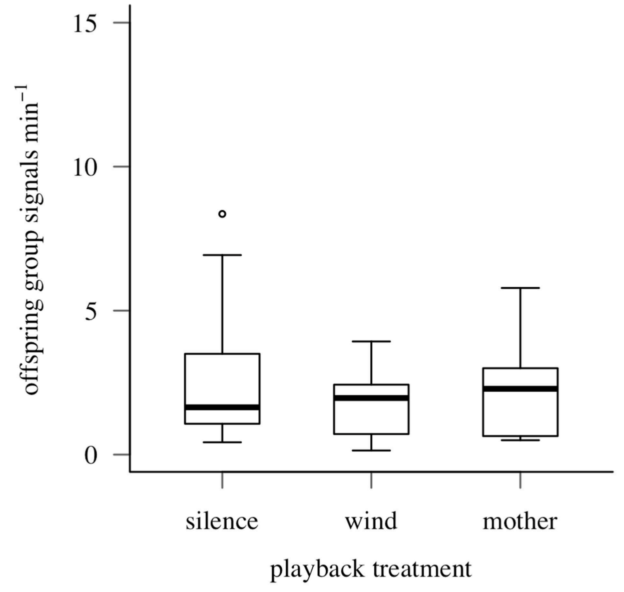

FIGURE 6 | Signaling responses of oak treehopper offspring aggregations to playback of silence, wind vibrations, or maternal post search signals after simulated predator attacks (Experiment 3). Box plots show distributions of offspring group signaling rate (minimum, first quartile, median, third quartile, maximum; open circles represent outliers). $N = 10$ families.

Although the long and semi-continuous signals that oak treehopper mothers produce after evicting predators silenced offspring, the short signals that mothers typically produce while searching for a predator did not inhibit offspring signaling. Interplay between short maternal signals and offspring signals may help the mother locate the source of disturbance. In a closely related species, those offspring closest to the predator are most likely to participate in each group signal, and those farther away are less likely to do so, potentially providing cues to the mother on predator location (Ramaswamy and Cocroft, 2009). However, these position-dependent signaling differences only occur when the mother is present, suggesting that the offspring are responding to some maternal cue, such as vibrational signals.

How Likely Is Predator Attraction by Vibrational Offspring Signals in Nature?

Our findings support work with other animal taxa (Allan et al., 1996; Krams et al., 2007; Magrath et al., 2010) showing that social signals attract predators to groups. Although most studies of predator eavesdropping focus on mate advertisement signals (Zuk and Kolluru, 1998; Haynes and Yeargan, 1999; Peake, 2005), social communication produces a concentrated and persistent source of signals and may be especially vulnerable to eavesdropping. Adaptations to reduce the apparency of social signals to predators and parasitoids are likely to be a general, if often overlooked, feature of social communication. For species with maternal care, offspring signals are produced primarily during periods of social interaction such as soliciting food or protection (Leech and Leonard, 1997; Lingle et al., 2012), and these are the periods of greatest risk of attracting eavesdropping predators (Leech and Leonard, 1997; Wise et al., 1999; Haff and Magrath, 2011). Likewise, signaling by oak treehopper mothers and offspring during predator attacks will make families conspicuous to eavesdroppers, as multiple invertebrate predators often occur simultaneously on the same tree, and even in the same local area on a given tree.

The predators in this study were naïve, lab-reared study animals, and experience may affect predator responses to offspring and maternal signals in the field. For example, female oak and thornbug treehoppers both defend offspring against invertebrate predators with kicks and wing-buzzes, behaviors that effectively deter predators and that are commonly interspersed with maternal vibrational signals (Wood, 1976; Cocroft, 1999b; Hamel, 2011; Hamel and Cocroft, 2012). In laboratory studies, invertebrates associate vibrational cues with both aversive stimuli (Abramson, 1986) and food rewards (Guillette et al., 2009). Therefore, predators may learn to avoid vibrational signals associated with maternal kicks, to approach group signals produced by abundantly occurring offspring aggregations, and to ignore common environmental sources of vibrational noise, such as wind.

Evidence that plant-borne vibrational communication is subject to predator eavesdropping is growing (*reviewed in* Virant-Doberlet et al., 2014). Although the vibrational modality has been hypothesized as a means of escaping eavesdroppers (Henry, 1994; Zuk and Kolluru, 1998), predator eavesdropping on vibrational signals is likely, given the abundance and diversity of vibrationally-sensitive invertebrate predators in the environments where communication occurs (Cocroft and

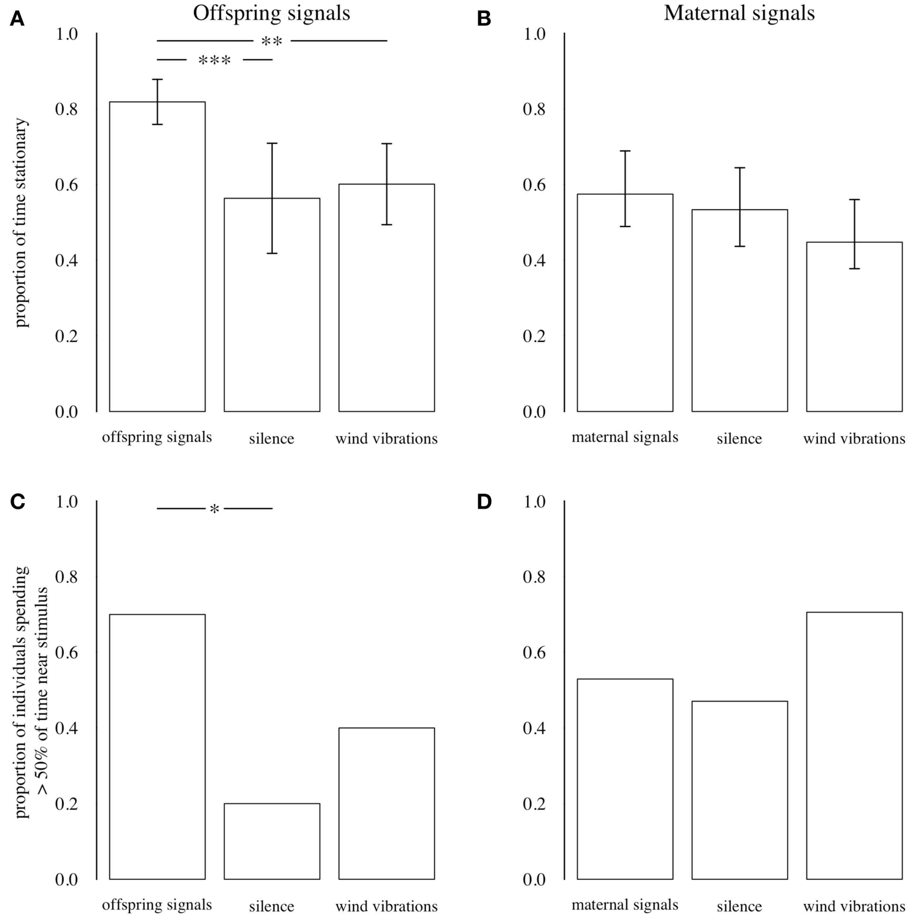

FIGURE 7 | *Top*: Proportion of time that predators remained stationary during playbacks of offspring **(A)** and maternal **(B)** signals, silence, and wind vibrations. Bars show means; error bars are 95% CIs. *Bottom*: Proportion of individuals who spent > 50% of total time near the vibration stimulus during playbacks of offspring **(C)** and maternal **(D)** signals, silence, and wind vibrations. Data from Experiments 4 and 5. $^*P \leq 0.05$, $^{**}P \leq 0.01$, $^{***}P \leq 0.001$, GLMs.

Rodríguez, 2005), and the ability of invertebrate predators to learn associations between vibration cues and food rewards (Guillette et al., 2009). Invertebrate predators can locate prey via incidental vibrations (Pfannenstiel et al., 1995; Barth, 1998; Meyhöfer and Casas, 1999), and invertebrate predators home in on vibrational mate advertisement signals as well (Narhardiyati and Bailey, 2005; Laumann et al., 2007, 2011; Roberts et al., 2007; Virant-Doberlet et al., 2011).

In summary, this study provides evidence that predators can exploit social vibrational signals, and that a benefit of inhibiting offspring signaling may be reducing predation risk. Consequently, we suggest that predator eavesdropping is a probable cost of within-group communication for invertebrate groups using vibrational signals, and such signaling groups may experience strong selection by predators and parasitoids to reduce the apparency of their signals.

AUTHOR CONTRIBUTIONS

JH and RC contributed to the conception and design of the study. JH conducted the experiments, performed the statistical analysis, and wrote the first draft of the manuscript. RC contributed to data collection and analysis and provided extensive and thoughtful revisions to the manuscript. All authors have contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00204/full#supplementary-material

Supplementary Video 1 | Vibrational playback from Experiment 1, in which offspring group signals were recorded from and played back to mothers and offspring of nine oak treehopper families. Here, a mother walks and produces early-encounter signals in response to playback of offspring vibrational signals.

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Predator-Prey Interactions and Eavesdropping in Vibrational Communication Networks

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Due to human perceptional bias in favor of air-borne sounds, substrate-borne vibrational signaling has been traditionally regarded as a highly specialized, inherently short-range and, consequently, a private communication channel, free from eavesdropping by sexual competitors and predators. In this review, we synthesize current knowledge pertinent to the view that most animals live in a rich vibratory world, where vibrational information is available to unintended receivers. In recent years, we realized that vibrational signaling is one of the oldest and taxonomically most widespread forms of communication by mechanical waves and that receptors detecting substrate vibrations are ubiquitous. In nature, substrate vibrations are reliable source of information readily available to all members of the animal community able to detect them. Viewing vibrational communication in more relevant ecological context reveals that animals relying on substrate vibrations live in complex communication networks. Long evolutionary history of this communication channel is reflected in varied and sophisticated predator-prey interactions guided by substrate-borne vibrations. Eavesdropping and exploitation of vibrational signals used in sexual communication have been so far largely neglected; however, existing studies show that generalist arthropod predators can intercept such signals emitted by insects to obtain information about prey availability and use that information when making foraging decisions. Moreover, males which advertise themselves for longer periods than females and with vibrational signals of higher amplitude face higher predation risk. It is likely that eavesdropping and exploitation of vibrational signals are major drivers in the evolution taking place in the vibratory world and we believe that studies of interspecific interactions guided by substrate vibrations will, in the future, offer numerous opportunities to unravel mechanisms that are central to understanding behavior in general.

Keywords: biotremology, vibrational communication, communication network, predator-prey interactions, eavesdropping

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INTRODUCTION

Signals produced by mechanical vibrations and transmitted from the signaller to the receiver through the medium (air, water or solid substrate) via mechanical waves are an important part of animal communication (Bradbury and Vehrencamp, 1998). Speech (i.e., air-borne sound communication) is such an important element of human interactions that our strong bias in favor of this form of mechanical communication is inevitable, in particular, since our hearing also allows us to perceive most of air-borne mechanical waves (i.e., sounds) emitted by other animals. Although cutaneous mechanoreceptors in human skin are capable of detecting substrate-borne mechanical waves (e.g., Brisben et al., 1999; O'Connell-Rodwell et al., 2001; Stuart et al., 2003), our own experience of the vibratory world around us depends almost exclusively on the use of sensitive equipment. It is therefore not surprising that in contrast to air-borne sound, substrate-borne vibrations have been traditionally considered a highly specialized and rare form of animal communication, and consequently, even regarded as an adaptation to avoid detection by eavesdropping enemies (Belwood and Morris, 1987; Lima and Dill, 1990; Henry, 1994; Zuk and Kolluru, 1998; Cooley, 2001; Lang et al., 2005; Römer et al., 2010), at best accessible only to specialized parasitoids (Hughes et al., 2012). Although the evidence emerging in the last decade shows that enemies and rivals use vibrational information available in their environment to guide their behaviors crucial for reproduction and survival (reviewed in Virant-Doberlet et al., 2014), the unfortunate general misconception that vibrational signaling is a private mode of communication (i.e., inaccessible to eavesdroppers sharing the same habitat) is unexpectedly hard to put at rest. This persistence is surprising, since it is widely accepted that incidental vibrational cues induced in the substrates by activities like moving and feeding are used by predators and parasitoids to find their prey or host (e.g., Barth, 1998; Meyhöfer and Casas, 1999; Brownell and van Hemmen, 2001; Devetak, 2014), although such vibrations are generally less conspicuous than vibrational signals used in sexual communication.

Here, we aim to provide a synthesis of the current state of knowledge relevant to the view that the majority of animals lives in a rich vibratory world, where vibrational information is readily available to eavesdroppers. While the body of existing literature supporting this view is large, the available information is scattered across different research topics and often does not directly address the issue of ecological context of vibrational communication. There are so far only a few studies directly dealing with exploitation of vibrational signals used in sexual communication by eavesdropping predators or parasitoids and to challenge the view that vibrational signaling is a safe mode of communication (e.g., Henry, 1994; Zuk and Kolluru, 1998; Hughes et al., 2012), we also review the evidence that substrate vibrations guide many behaviors related to predator-prey interactions. As it has been first proposed by Cocroft and Rodríguez (2005), we argue that in this communication modality eavesdropping may be particularly common and we wish to convey that besides our perceptional bias and general lack of understanding of the importance of the vibrational channel, there is no reason for a persisting view that enemies ignore vibrational signals as a source of information helping them to find their prey or host. In this review, it is not our intention to focus on a distinction between air-borne sounds and substrate-borne vibrations and differences between acoustic and vibrational communication, since this topic has been subject of several commentaries (e.g., Cocroft et al., 2014; Endler, 2014; Hill and Wessel, 2016; Hill et al., 2019) and comprehensive reviews (e.g., Cocroft and Rodríguez, 2005; Hill, 2008; Caldwell, 2014; Yack, 2016).

Due to their diversity, abundance and reliance on substrate vibrations, arthropods are the best animal group to provide an insight into life in the vibratory world and various aspects of their behavior that is guided by substrate vibrations have been studied in detail. In line with the existing literature and our own research, the review is therefore focused primarily on interactions in arthropods; however, we also include the evidence from other animal groups whenever appropriate. Throughout the review, we use eavesdropping in accordance with the existing literature, where it is defined as "extracting information from signaling interactions between others" (McGregor and Peake, 2000). Consequently, we do not consider interactions that do not include interception of vibrational signals used in communication (e.g., incidental vibrational cues, mimicry) as eavesdropping. We further define exploiters as a subset of eavesdroppers that use extracted information to gain advantage over the signallers thus incurring direct or indirect costs (Bradbury and Vehrencamp, 1998). In this context, eavesdropping rivals that may extract from vibrational signals relative information about the size and dominance of signaling males and use this information to avoid direct encounters, are not considered exploiters.

VIBRATIONAL COMMUNICATION NETWORKS

Viewing communication in a more ecological context, it becomes clear that in nature communication occurs not only in a signaller-intended receiver dyad but in a group of several animals within signaling and receiving range of each other (i.e., in a network environment) (McGregor and Peake, 2000; McGregor, 2005; Virant-Doberlet et al., 2014). Taking into account that each signal can be received by several receivers and that each receiver can receive signals from several signallers, an emerging property of the network environment is that signals can be exploited by eavesdropping receivers (e.g., rivals, enemies) (Peake, 2005) (**Figure 1**). The complexity of the overall network structure depends on the identities and numbers of signallers and receivers able to detect the emitted signals (i.e., ultimately on the animal community present in the habitat). The still prevailing perception that vibrational signaling may be a safer communication channel than air-borne sounds (e.g., Hughes et al., 2012; Römer, 2013; Yack, 2016) mainly results from an impression that substrate vibrations are a rare and inherently short-range form of communication and consequently, the opportunities for eavesdropping and exploitation are severely limited. The first step in changing this perception is therefore to raise the awareness that vibrational signaling is one of the most widespread forms of animal communication and that the emitted signals are accessible to many heterospecifics, including potential enemies.

How Common Is Vibrational Signaling and Reception?

As are substrate vibrations ubiquitous in the environment (Hill, 2009; Šturm et al., 2019), so are vibration receptors ubiquitous

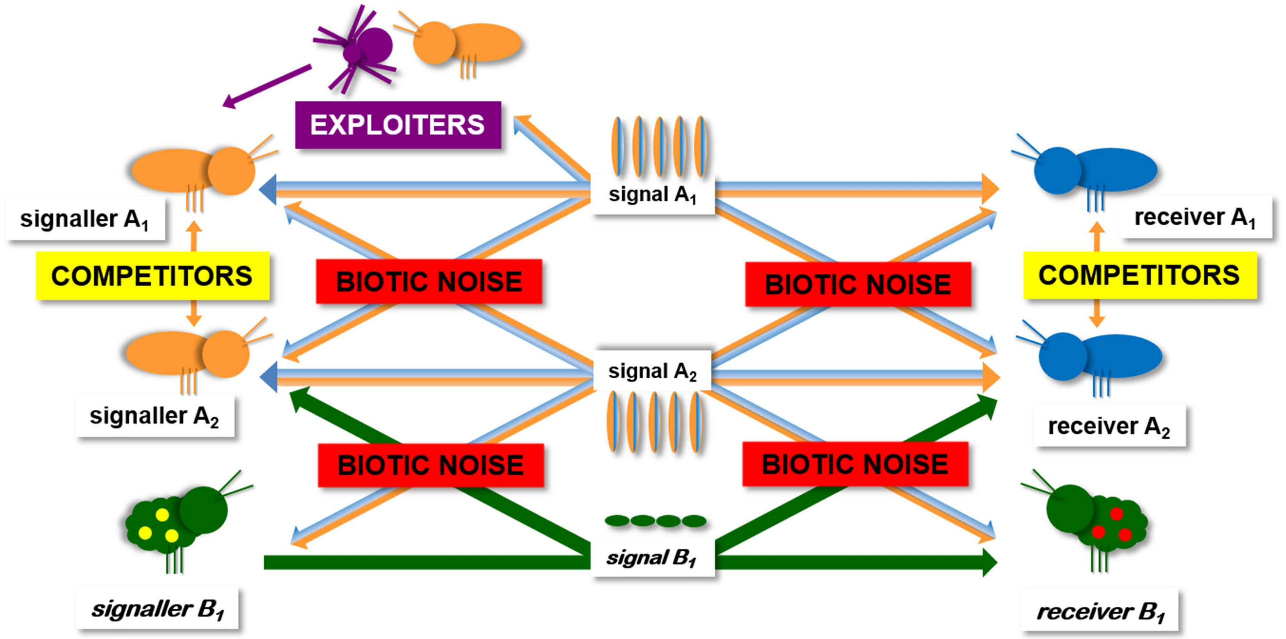

FIGURE 1 | Schematic presentation of insect vibrational communication network. Natural habitat contains other conspecific and heterospecific signallers, as well as eavesdropping exploiters like rivals and enemies. The complexity of any real world communication network depends on the identities and numbers of signallers and receivers able to detect the emitted signals. In a duetting communication system, the same individual is the emitter and the receiver (A1, A2). From potential interactions within such a communication network, it emerges that both, signallers and receivers take on a range of costs and benefits that may have fundamental implications for their communication strategies.

in organisms (e.g., Hill, 2008; Narins et al., 2016; Sugi et al., 2018) and vibrational signaling is now considered one of the most ancient forms of communication (Cocroft et al., 2014; Endler, 2014). It is likely that it is present in bacteria (e.g., Reguera, 2011) and vibrational stimuli affect plants as well (Appel and Cocroft, 2014). So far, behavioral response to vibrational stimuli has been documented in nematodes (Torr et al., 2004), molluscs (Roberts et al., 2015), annelids (Mitra et al., 2009), arthropods (Hill, 2008), and vertebrates (Narins et al., 2016).

Vibrational signaling, vibration reception and behavior guided by substrate-borne vibrations have been best studied in vertebrates and arthropods. In vertebrates, the use of vibrational signaling in intraspecific interactions has been described in all major groups (e.g., Whang and Janssen, 1994; Barnett et al., 1999; O'Connell-Rodwell, 2007; Caldwell et al., 2010a; Ota et al., 2015). The frequency range of vertebrate vibrational signals spans from infrasonic range below 20 Hz up to 1 kHz, with most of the energy found in the range below 500 Hz (Lewis and Narins, 1985; Narins et al., 1992; O'Connell-Rodwell, 2007; Caldwell et al., 2010a; Mason and Narins, 2010; Bishop et al., 2015; Halfwerk et al., 2016). Vertebrates detect substrate vibrations via somatosensory mechanoreceptors in their skin and joints and/or via an extratympanic pathway to their auditory system (reviewed in Hill, 2008; Narins et al., 2016). Greatest frequency and amplitude sensitivity to vibrations is species-specific and usually lies between 50 and 500 Hz, where animals can detect substrate displacements as small as 1 nm (reviewed in Gridi-Papp and Narins, 2010; Mason and Narins, 2010; Narins et al., 2016).

Relying on substrate-borne vibrations to gather information from the environment is particularly common in arthropods. Vibrational behavior is prevalent in insects (reviewed in Virant-Doberlet and Čokl, 2004; Cocroft and Rodríguez, 2005) and spiders (reviewed in Uhl and Elias, 2011). Studies suggest that it may also be common in crustaceans (Taylor and Patek, 2010), scorpions (Brownell and van Hemmen, 2001) and millipedes (Wesener et al., 2011). All arthropods possess sensitive mechanoreceptors to detect substrate vibrations (Hill, 2008, 2009) and it is currently estimated that around 200,000 insect and 40,000 spider species use vibrational communication in a variety of intraspecific interactions (Virant-Doberlet and Čokl, 2004; Cocroft and Rodríguez, 2005; Uhl and Elias, 2011). While many arthropods use vibrational signaling in combination with other modalities, a conservative estimate is at least 150,000 insect species rely exclusively on vibrational communication (Cocroft and Rodríguez, 2005). Vibrational signals used in sexual communication are species- and sex-specific and characterized by their distinct temporal and spectral properties (e.g., Barth and Schmitt, 1991; Čokl, 2008; Cocroft et al., 2010; Elias et al., 2012; Henry et al., 2013; Derlink et al., 2014). Frequency range of insect vibrational signals is usually between 50 Hz and 5 kHz; however, most energy is limited to the frequency range below 500 Hz. The morphological and physiological characteristics of vibration receptors differ greatly among groups (reviewed in Barth, 1998; Brownell and van Hemmen, 2001; Taylor and Patek, 2010; Lakes-Harlan and Strauß, 2014). Arthropods are most sensitive to vibrations below 1 kHz and they can detect displacements in the range of 0.1 nm (e.g., Barth, 1998; Čokl et al., 2006; Eriksson et al., 2011; Lakes-Harlan and Strauß, 2014).

Importantly, besides the signaller's identity, vibrational signals also provide information that enables the receiver to determine in which direction the source of vibration is positioned and to locate the signaller (Barth, 1993; Virant-Doberlet et al., 2006; Hebets, 2008; Gibson and Cocroft, 2018; Prešern et al., 2018). At least in some cases, vibrational signals most likely also enable individuals to estimate the distance to the source (e.g., Lewis and Narins, 1985; Hill and Shadley, 2001; Gridi-Papp and Narins, 2010). In arthropods, the most important directional cues are time differences in a signal's arrival to spatially separated sensory inputs (i.e., vibroreceptors located in each leg) and differences in amplitude resulting from signal damping during propagation through the substrate (reviewed in Virant-Doberlet et al., 2006). Propagation velocity and attenuation depend on signal frequency and signals of lower frequency propagate more slowly and with less attenuation (Michelsen et al., 1982; Barth, 1998; Elias and Mason, 2014; Mortimer, 2017). Vibrational signals are therefore well adapted for transmission through the substrate, as well as creating relevant time delays that can be processed in the central nervous system. Even insects with body size around 1 cm can accurately locate the source of vibrational signals by processing time delays between 0.2 and 0.5 ms (Hager and Kirchner, 2014; Prešern et al., 2018).

Perhaps the most impressive example of versatility of vibrational modality has been described in the blind mole rat *Nannospalax ehrenbergi*. This species produces vibrational signals by striking the head against the tunnel roof and uses these self-generated substrate vibrations to assess the size, physical properties and location of an obstacle blocking its underground tunnel. It can than dig an optimal bypass tunnel around it (Kimchi and Terkel, 2003a,b; Kimchi et al., 2005).

Active Space of Vibrational Signals

The probability that the emitted signal is intercepted by eavesdroppers does not increase only with the number of potential receivers, but also with the distance the signal travels through the habitat. The active space (i.e., effective range) of vibrational signals has been defined as the "area in which the signal amplitude is sufficiently above the detection threshold of potential receivers to have an effect on their behavioral response" (Mazzoni et al., 2014; Šturm et al., 2019). Signal active space therefore depends, on the one hand, on intrinsic factors like the signal amplitude at the source (i.e., "loudness" of the signaller) and the sensitivity of a receiver's vibroreceptors, and, on the other hand, on environmental factors like attenuation of the signal during the transmission through the substrate and the amplitude of interfering background noise. Behavioral studies show that active space of vibrational signals broadly depends on the size of the animal and differs enormously, from a few cm in fruitflies (Mazzoni et al., 2013), to several km in elephants (Narins et al., 2016).

The amplitude of arthropod vibrational signals may be low at the source; however the sensitivity of their vibroreceptors is well above the amplitude of emitted signals (Michelsen et al., 1982). For example, the amplitude of vibrational signals emitted by the green stink bug *Nezara viridula*, recorded from the vibrating body and expressed as velocity is in the range 0.3–0.8 mm/s, while the threshold sensitivity of its receptors in the relevant frequency range is between 0.01 and 0.03 mm/s (Čokl et al., 2007). Nevertheless, the environment imposes severe constraints on the effective range of vibrational signals and, in contrast to air-borne sound, the size and shape of the active space are highly unpredictable.

One limitation is continuity of the substrate. It is generally assumed that for plant-dwelling animals the active space of vibrational signals is limited to the plant on which the animal is signaling. However, at least in meadows, the effective range also extends to the neighboring plants connected by roots and touching leaves (Čokl and Virant-Doberlet, 2003; Šturm et al., 2019) and even across a several-cm-wide air gap between overlapping leaves (Eriksson et al., 2011). Moreover, many small plant-dwelling insects increase the effective range of their vibrational signals using the behavioral strategy "fly/jump-call," where they randomly move through the habitat and emit vibrational signals from different plants (e.g., Šturm et al., 2019). It should also be pointed out that the plant on which the animal is signaling is not necessarily a small herbaceous plant, but can also be a shrub or a tree, and in this case the active space of vibrational signals can extend up to 4 m even within one plant (McVean and Field, 1996; Barth, 2002b).

The effective range of vibrational signals is also limited by damping due to transmission properties of the substrate, which ultimately result in reduced amplitude (Mortimer, 2017). Moreover, heterogeneity of the natural substrates encountered in the habitat imposes unpredictable changes to signal structure observed in selective frequency filtering and temporal distortions (reviewed in Elias and Mason, 2014; Mortimer, 2017). Consequently, the longer the distance a vibrational signal travels from the source, the more likely it will be degraded to the extent that it cannot be recognizable by the receiver. Nevertheless, studies have shown that animal vibrational signals are tuned and adapted to specific transmission properties of their environment (host plants, leaf litter, soil) (Günther et al., 2004; Čokl, 2008; Hebets et al., 2008; McNett and Cocroft, 2008; Elias et al., 2010; Narins et al., 2016). Heterogeneity of the substrate can also affect availability and reliability of directional cues, since besides frequency, signal propagation velocity and attenuation, which create time delays and amplitude differences at sensory inputs, are strongly dependent on physical properties of the transmission medium (reviewed in Virant-Doberlet et al., 2006).

Studies of the natural vibroscape (i.e., vibrations emanating from a given landscape) show that the vibrational channel is dominated by frequencies below 1 kHz. This frequency range also includes the majority of arthropod vibrational signals used in communication (Šturm et al., 2019). In this frequency range,

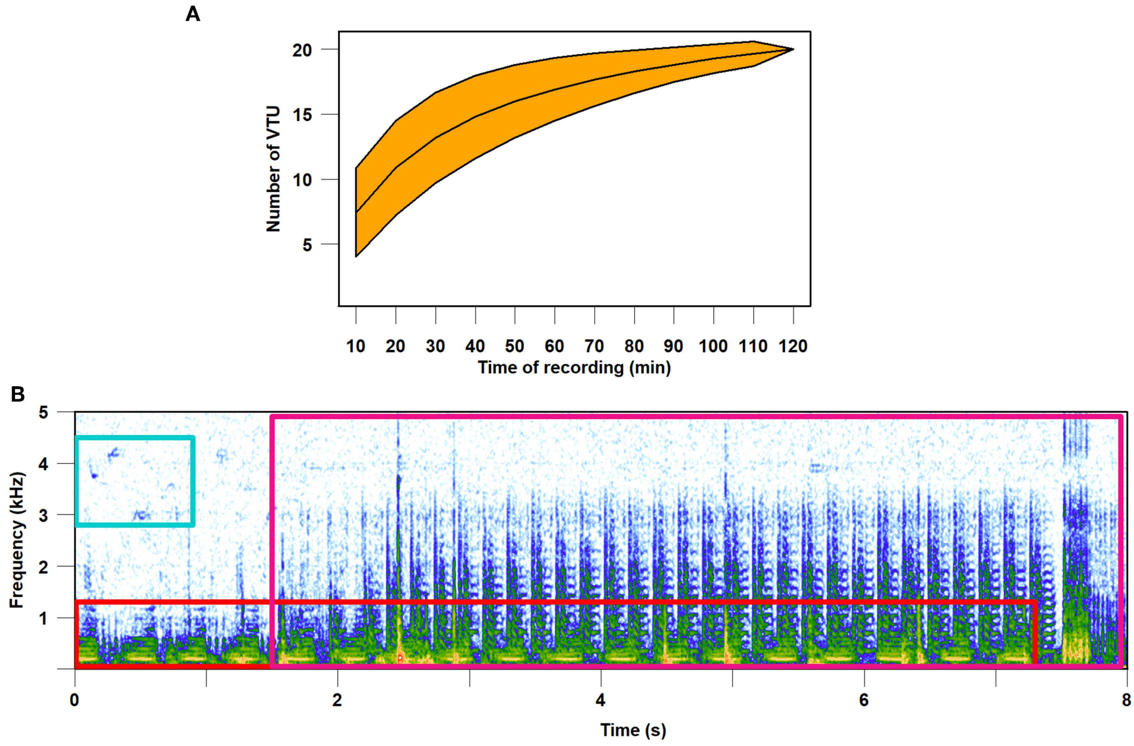

FIGURE 2 | Complexity of meadow vibroscape. Vibrational signals were registered with a laser vibrometer on *Carex hirta* during 2-h (14:30–16:30) recording session on July 9, 2018. **(A)** Species accumulation curve of vibrational taxonomic units (VTU). VTU is equivalent to species and each 10 min of the recording was taken as a sample. Orange area around the curve indicates 95% confidence interval. The curve approaches 20 VTUs; however, it does not reach the plateau. **(B)** Visualization in the form of spectrogram of vibroscape, which includes overlapping vibrational signals of two unknown insect species (red and purple frames) and vibrational component of a bird air-borne song (blue frame).

interfering background vibrational noise results from wind and rain (e.g., Barth et al., 1988; Caldwell et al., 2010b; McNett et al., 2010). Vertebrates and arthropods can distinguish incidental vibrations induced by wind and rain from incidental vibrational cues resulting from animal movements (e.g., Warkentin, 2005; Castellanos and Barbosa, 2006; Guedes et al., 2012). One known exception is the túngara frog *Physalaemus pustulosus*, which appears not to discriminate between vibrations used in intraspecific communication and incidental vibrations induced by rain (Halfwerk et al., 2016). Nevertheless, the frequency overlap of spectra of vibrational signals, vibroreceptor frequency sensitivity and frequency range of abiotic environmental noise indicates that the active space of vibrational signals is likely to be reduced. While it has been shown that wind-induced vibrations had a negative effect on frog and insect vibrational behavior (McNett et al., 2010; Hamel and Cocroft, 2012; Tishechkin, 2013; Halfwerk et al., 2016), current evidence suggests that some arthropod predators exploit background vibrational noise that impairs the ability of prey to detect incidental vibrational cues induced by their approach (Wilcox et al., 1996; Wignall et al., 2011; Soley, 2016).

In summary, laboratory and field studies show that animals live in a complex vibrational environment. The ongoing studies of the natural meadow vibroscape show that substrate vibrations are a constantly available, rich and reliable source of information (Šturm et al., 2019). The complexity of vibrational information available in the environment is best exemplified by the diversity of a vibrational community (i.e., the assemblage of animals in a particular habitat that produce vibrational signals and are active over a specified time). Assessment of species richness reflected in species-specific vibrational signals revealed that on a single plant the vibrational channel can be shared daily by more than 20 species (**Figure 2**).

PREDATOR-PREY AND PARASITOID-HOST INTERACTIONS GUIDED BY SUBSTRATE VIBRATIONS

Taking into account that every movement of the body induces incidental vibrations in the substrate and that animals possess highly sensitive receptors to detect them, it is not surprising that one of the most widespread functions of substrate vibrations in interspecific interactions directly linked to survival and reproductive success is to avoid predators, capture prey or find the host to deposit eggs. In these contexts, detecting, identifying and locating the source is crucial. In this section we provide an overview of interactions guided by substrate vibrations that do not include eavesdropping on prey or host vibrational communication. Humans are aware of such interactions, since we can observe them in the field; either orb-weaving spiders approaching their struggling prey caught in the web, or crickets ceasing singing when they detect vibrations created by our footsteps.

Finding Prey or Host

Arthropod predators often rely on incidental vibrational cues to capture their prey. Spiders and scorpions locate their arthropod prey using incidental vibrations created by prey movements (reviewed in Barth, 1998, 2002b; Brownell and van Hemmen, 2001). Incidental vibrational cues induced by moving prey have, in general, lower amplitude than vibrational signals used in communication and also contain higher frequencies that are subject to stronger attenuation and higher propagation velocities (Barth et al., 1988). Nevertheless, spiders and scorpions can accurately orient toward and locate the source of such vibrations. Although both groups can also use amplitude cues to determine the location of the vibrational source (reviewed in Barth, 1998, 2002a; Brownell and van Hemmen, 2001), at least for scorpions, the more reliable directional cue is the difference in arrival times of a vibrational wave reaching receptors located in eight legs positioned on the substrate and they can detect time delays as short as 0.2 ms. The predatory stinkbug *Podisus maculiventris* (Hemiptera, Pentatomidae) reliably locates the source of vibrations created by chewing caterpillars (Pfannenstiel et al., 1995). The use of incidental vibrational cues to locate endophytic hosts appears to be widespread among parasitoid wasps (reviewed in Meyhöfer and Casas, 1999). However, wasp parasitoids of pupae locate their immobile hosts by using self-generated vibrations induced by tapping the substrate with modified antennae and detecting the echoes with enlarged subgenual vibration receptors in their legs (vibrational sounding) (reviewed in Broad and Quicke, 2000). It was suggested that wasps find the position of a hidden host by analyzing the contrast in resonance between hollow and solid sections of the substrate (Wäckers et al., 1998).

Antlion larvae (Neuroptera, Myrmeleontidae) wait for their prey at the bottom of funnel-shaped pit traps and their reaction to incidental vibrational cues generated by walking prey is to accurately toss the sand in its direction, in order to prevent its escaping from the sand pit (Fertin and Casas, 2009; Devetak, 2014). Moreover, studies show that antlions can associate a behaviourally neutral vibrational cue with the arrival of the prey and that such learning increases fitness by improving their digestive efficiency and, ultimately also decrease the time spent in the larval stage (Guillete et al., 2009; Hollis et al., 2011).

In arthropods, the use of substrate vibrations to catch the prey or find the host can also involve more complex behavioral strategies that do not include accurate location of the prey. The orb weaving spider *Nephila pilipes* uses incidental vibrational cues induced by prey caught in the web to assess the type of prey available in its environment and modify web architecture accordingly (Blamires et al., 2011). Araneophagic jumping spiders from the genus *Portia* produce deceptive vibrational signals to capture their prey (aggressive mimicry) (reviewed in Jackson and Cross, 2013). *Portia* is also well known for its cognitive abilities and uses a trial-and-error approach to generate vibrational signals that elicit appropriate responses from each prey spider species. The aggressive mimicry repertoire includes male vibrational courtship display of another jumping spider species (Jackson and Wilcox, 1990), incidental vibrations induced by prey caught in the web adapted according to the species and size of the spider prey (Jackson et al., 1998; Tarsitano et al., 2000; Jackson and Nelson, 2011), as well as female courtship display by subadult females to prey on conspecific males (Jackson and Cross, 2013). Similarly, the assassin bug *Stenolemus bituberus* (Hemiptera, Reduviidae), which preys on web-building spiders, mimics incidental vibrations generated by struggling prey to attract the spider within striking distance (Wignall and Taylor, 2011). In playback experiments, the ambush bug *Phymata crassipes* (Hemiptera, Phymatidae) alternated with vibrational stimuli and imitated their duration (Gogala et al., 1984). The authors suggested that by imitation of heterospecific courtship vibrational signals this sit-and-wait predatory bug may attract their potential prey; however, this hypothesis was not tested. Acoustic signals emitted by pupae and larvae of the parasitic butterfly *Maculinea rebeli* mimic distinct sounds produced by queen ants, thus providing them superior treatment from workers (Barbero et al., 2009). Although these authors did not describe these stridulatory signals as substrate vibrations, it is likely that this social parasite-host communication is mediated by a vibrational component of these signals (DeVries et al., 1993), since most of the current evidence suggests that ants perceive only substrate-borne mechanical waves (Hunt and Richard, 2013; Golden and Hill, 2016).

Reliance on vibrational cues for finding prey is not limited to arthropods. Entomopathogenic nematodes use vibrational cues induced by insects moving in the soil to locate their hosts (Torr et al., 2004). In vertebrates, the use of vibrational information in prey detection has been documented in reptiles and mammals. The sandfish lizard *Scincus scincus* and sand viper *Cerastes cerastes* detect and locate their prey using incidental vibrations (Hetherington, 1989; Young and Morain, 2002). For the Namib Desert golden mole (*Eremitalpa granti namibiensis*) dune termites that live among the roots of grass are the principal insect prey. The blind and nocturnal golden mole relies on substrate vibrations to locate its food; however, for orientation it uses vibrations created by grass rattling in the wind, since these distinct vibrations with dominant frequency around 300 Hz transmit well through the sand and golden moles may detect them at distances of 20–25 m (Narins et al., 1997; Lewis et al., 2006). Golden moles also possess hypertrophied ossicles in the middle ear and such adaptation enables them better directional hearing in the frequency range up to 300 Hz (Mason and Narins, 2010; Narins et al., 2016).

Avoiding Enemies

While some insects appear to be able to walk near the predator without inducing typical incidental vibrations associated with locomotion (vibrocrypticity) (Barth et al., 1988), remaining still is probably the most common prey behavior in response to incidental vibrational cues arising from a potential enemy, since it also ceases to provide vibrational cues that reveal prey location (e.g., Meyhöfer et al., 1997; Djemai et al., 2001; Kojima et al., 2012a). Wolf spiders freeze in response to perceived presence of a predator and they are not only able to discriminate between incidental vibrations emanating from predators and non-predators, but also can perceive the substrate component of bird calls and use it to differentiate between threatening and non-threatening species (Lohrey et al., 2009; Sitvarin et al., 2016). Interestingly, non-predators can also exploit such a defense freezing response. Pupae of the soil-living beetle *Trypoxylus dichotoma* emit vibrational signals that mimic vibrations induced by a foraging mole to stop burrowing of the conspecific larvae in order to protect themselves from accidental damage to their pupal cell (Kojima et al., 2012a,b). Another form of passive defense is avoidance. Termites rely on avoiding ant predators by hiding behind clay walls and they monitor incidental vibrations generated by ant footsteps and discriminate them from incidental vibrational cues from other sources (Oberst et al., 2017).

Another common reaction is escape behavior that in arthropods includes dropping from the plant (e.g., Losey and Denno, 1998). Larvae of the moth *Semiothisa aemulataria* living on leaves escape invertebrate predators walking on the leaf by hanging from silk threads and they can differentiate between incidental vibrations induced by predator and non-predators or abiotic environmental sources, as well as adapt the length of the thread according to the identity of the predator (Castellanos and Barbosa, 2006). Similar behavior has been observed in treefrog embryos, where vibrational cues emanating from predator attack trigger early hatching and escape behavior from the egg clutch deposited on vegetation, and result in tadpoles falling into the water (Warkentin, 2005; Caldwell et al., 2010b). To avoid false alarms, embryos assess incidental vibrations to distinguish between lethal and benign sources. Earthworms emerge from soil in response to incidental vibrations resulting from digging moles; however, their escape is clearly directional away from the source of vibrations (i.e., a foraging mole) (Catania, 2008; Mitra et al., 2009).

Some animals use vibrational signals as part of an active defense strategy. Kangaroo rats footdrum in the presence of snakes, where drumming functions as a direct signal to the predator. In response to the vibrational component of drumming, snakes cease their stalking behavior (Randall, 2001, 2010). Vibrational signaling is often part of antipredator behavior in group-living insects (reviewed in Cocroft and Hamel, 2010). For example, when attacked by parasitoid wasps, an aphid colony produces coordinated collective kicking and twitching response that induces substrate vibrations. These substrate vibrations play a role in recruiting colony members, synchronizing a defense and potentially also repelling attackers (Hartbauer, 2010). However, besides synchronized signaling within a group, vibrational signaling as part of anti-predator protection has also been described in parent-offspring interactions (Cocroft, 1996; Ramaswamy and Cocroft, 2009; Hamel and Cocroft, 2012), as well as interactions between insects and their ant mutualists, where ant attendance increases the signaller's survival (e.g., Travassos and Pierce, 2000; Morales et al., 2008).

Alarm signals used to inform members of the group about danger can also be considered as a part of defense behavior. Vibrational signals that function to warn conspecifics have been described in termites (e.g., Rosengaus et al., 1999; Hager and Kirchner, 2013; Delattre et al., 2015) and elephants (O'Connell-Rodwell et al., 2007). At present, it is not clear whether footdrumming alarm signals emitted by many mammals in the presence of a predator are perceived as air-borne sound or substrate vibrations, or both (Randall, 2001, 2010).

EAVESDROPPING VIBRATIONAL COMMUNICATION NETWORKS

Eavesdropping in animal communication is defined as "the use of information in signals by individuals other than the primary target" (Peake, 2005) and eavesdropping network applies to situations where, the receiver eavesdrops on the signaling interaction in which it is not directly involved to obtain information (Burt and Vehrencamp, 2005). Due to their reliance on vibrational signals in many intraspecific and interspecific interactions and their highly sensitive vibration receptors, arthropods are the best group to study eavesdropping vibrational communication networks. Besides exploitation of vibrational signaling in the context of sexual communication by enemies (predators, parasitoids), eavesdropping applies also to other interactions like intraspecific competition (Virant-Doberlet et al., 2014).

Intraspecific Eavesdropping

In many species relying on vibrational communication, a coordinated reciprocal exchange of male and female vibrational signals is essential for recognition and successful location of the female (e.g., Derlink et al., 2014; Polajnar et al., 2014; Kuhelj et al., 2015a; Lujo et al., 2016). In leafhoppers (Hemiptera, Cicadellidae), communication is mediated exclusively via substrate vibrations and the male-female vibrational duet appears to be easily exploited by intruding males that silently approach a female duetting with the calling male (Mazzoni et al., 2009a,b; Kuhelj and Virant-Doberlet, 2017). The most important factor in obtaining the female in such a competitive setting appears to be the ability to locate the female before the rival. Evidence shows that intruding eavesdropping exploiters are at a competitive advantage. In the leafhopper *Aphrodes makarovi*, each exchange of male and female vibrational signals is initiated by the male and his walking, associated with the search for the replying stationary female, is limited to the duration of her reply (Kuhelj et al., 2016). In a competitive setting, that included two males and a female, the winners (i.e., males that mated with the female) were males that were better at exploiting female replies emitted in response to the rival's triggering call (i.e., in comparison with their competitors, they more often searched for the female during her reply to the rival's call) (Kuhelj and Virant-Doberlet, 2017). In this species, male signaling effort is negatively correlated with longevity (Kuhelj et al., 2015b) and eavesdropping on a male-female duet maintained by another male allows exploiters to invest less in energetically demanding signaling and to survive longer. In this context, it should be noted, that in the threehopper *Enchenopa binotata*, which also relies on vibrational communication, longevity was the strongest predictor of male lifetime mating success (Sullivan-Beckers and Cocroft, 2010).

Although the role of intraspecific eavesdropping and exploitation of vibrational signaling in the context of sexual communication has only rarely been systematically studied, current evidence suggests that, at least in mating systems based on stereotyped vibrational duets, this may be a widespread strategy to increase male mating success. It may also have important implications for sexual selection and evolution of vibrational communication. In general, in communication systems in which eavesdroppers exploit female replies to signals emitted by another male, males maintaining a duet have no advantage over males exploiting it, since information about the identity and location contained in the female reply is available to all males present in the active space of female signals. So far, in systems based on substrate-borne vibrations, in the perceived presence of an eavesdropping intruding male, the only observed defensive tactic displayed by the calling male was to emit distinct masking signals overlapping the last part of the female reply emitted in response to their own triggering call (Kuhelj et al., 2016; Kuhelj and Virant-Doberlet, 2017). Although the adaptive significance of these masking vibrational signals is not clear, the most likely benefit results from preventing the eavesdropper from locating the female by confounding him with the second vibrational source.

Eavesdropping by Enemies

The fact that we cannot observe by chance predators and parasitoids eavesdropping and exploiting vibrational communication in the field probably underlies our long persisting belief that enemies ignore vibrational signals used by their prey or host in intraspecific communication (Cocroft and Rodríguez, 2005; Cocroft, 2011; Virant-Doberlet et al., 2011, 2014). Arthropod predator-prey interactions usually involve small animals and take place in thick vegetation. Moreover, even when we notice predation, we are not aware that the predator may be exploiting prey intraspecific vibrational communication due to our inadequate perception of substrate vibrations. In previous sections, we reviewed the evidence that in the vibrational channel there are ample opportunities for eavesdropping and that many animals rely on information provided by incidental vibrations to guide their predator-prey interactions. Here below, we focus on the evidence that enemies also exploit prey or host vibrational signaling.

Laboratory studies showed that in the absence of other cues the egg parasitoid *Telenomous podisi* (Hymenoptera: Scelionidae) is selectively attracted to species- and sex-specific female vibrational song of its preferred host, the stink bug *Euschistus heros* (Laumann et al., 2007, 2011). This continuously emitted song composed of repetitive low-frequency pulses provides a reliable directional cue to locate a stationary female. While searching behavior mediated by female vibrational signals may increase the probability of finding egg masses on the same plant, it seems likely that host location is guided by multimodal cues that also include vision and volatile chemical compounds (e.g., Michereff et al., 2016).

Spiders have highly sensitive vibroreceptors and prey detection is commonly mediated by substrate vibrations (Uetz, 1992; Barth, 1998; Roberts et al., 2007). While Morris et al. (1994) suggested that in the Ecuadorean rainforest katydids use low frequency vibrational signaling instead of ultrasonic air-borne sounds in order to avoid eavesdropping by bats, they also observed that many spiders were catching them. Anecdotal evidence from the field and unpublished laboratory results also indicated that jumping spiders may use leafhopper vibrational signals to locate their prey (Narhardiyati and Bailey, 2005). A laboratory study also showed that vibrational signals incorporated into the multimodal courtship display of the wolf spider *Schizocosa ocreata* increased detectability to its predator jumping spider *Phidippus clarus* (Roberts et al., 2007).

Direct evidence that spider foraging behavior is influenced by prey vibrational signals used in sexual communication was obtained in the study of predator-prey interactions between the spider *Enoplognatha ovata* (Theridiidae) and the leafhopper *A. makarovi* (Virant-Doberlet et al., 2011). Using molecular diagnostics to identify *A. makarovi* DNA in the *E. ovata* gut, authors were able to show that in the field predation rate on leafhoppers was significantly higher when signaling adults were present. At that time 25% of spiders were feeding on them. Microcosm and playback experiments showed that spiders caught significantly more males than females and that spider residence time was significantly longer only when a plant was vibrated with the male call. Although taken together results suggest that *E. ovata* spiders exploit prey vibrational signaling primarily to obtain information about prey availability, in response to playback of *A. makarovi* male calls some spiders located the source of vibrations and authors suggested that differences observed in behavior of individual spiders may be attributed to learning and previous experience of *A. makarovi* signals in the field. Importantly, molecular diagnostics also showed that only a few spider species found at the study site were feeding on *A. makarovi* and that *Pardosa* wolf spiders, which were not consuming them in the field, were also ignoring live leafhoppers in microcosms, as well as their vibrational signals in playback experiments.

Avoiding Eavesdropping Enemies

So far, various interactions within vibrational communication network have been studied in more detail only in the leafhopper *A. makarovi*. With our current knowledge we cannot distinguish trade-offs and adaptive behavioral strategies that arise from selection pressure imposed by eavesdropping predators (Virant-Doberlet et al., 2011) from selection resulting from eavesdropping intraspecific competitors (Kuhelj and Virant-Doberlet, 2017), biotic noise and competition for signaling space in the vibrational channel (Šturm et al., 2019), as well as sexual selection and indirect costs due to energetically demanding signaling (Kuhelj et al., 2015b, 2016). This is particularly so, since selection pressures from different sources can reinforce or oppose each other. However, here below, we discuss some potential behavioral strategies in leafhoppers that may also serve as a defense against eavesdropping predators.

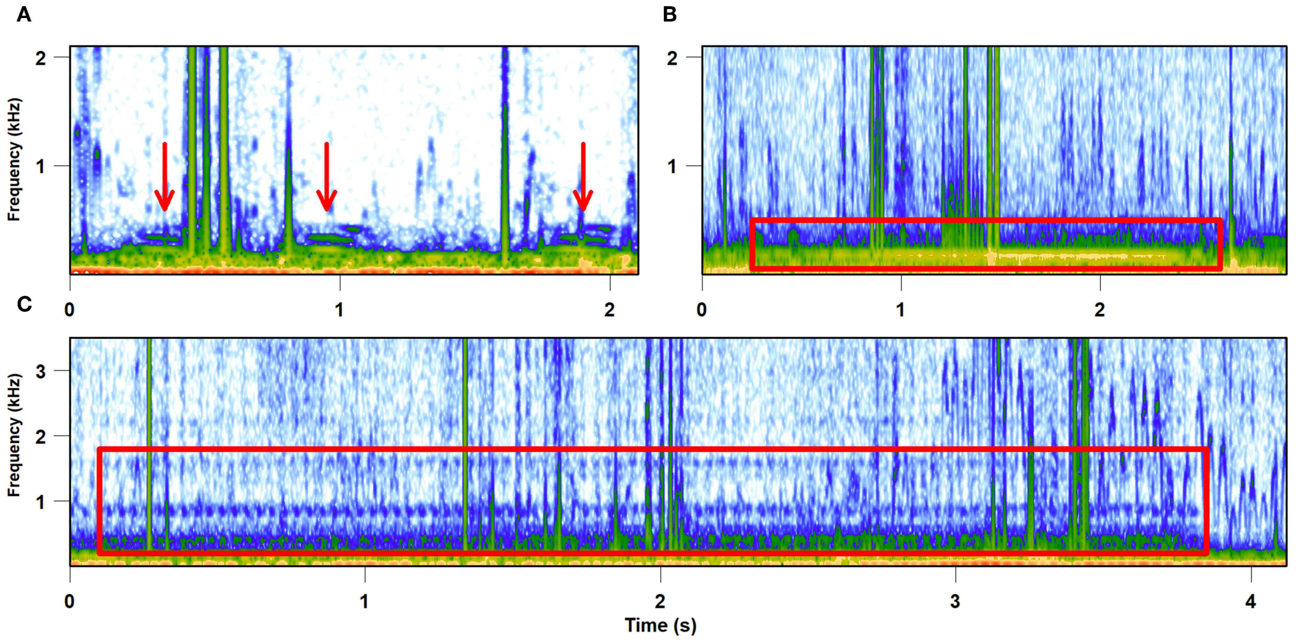

FIGURE 3 | Vibrational signals recorded from spider web. Vibrations were recorded on July 27, 2017 with a laser vibrometer from the web of *Argiope bruennichi* built between several grass stems. **(A,B)** Vibrational signals of two unknown species, **(C)** male advertisement call of the leafhopper *Aphrodes makarovi*.

Taking into account the diversity and density of potential predators in the habitat that exploit leafhopper vibrational signaling, as well as unpredictability in the structure of the predator community at each individual location, it is likely that leafhoppers' behavioral anti-predator strategies would not be adapted to specific predator species and their foraging strategies. The rich and complex vibroscape perceived by predators may provide general information about the food availability important for choosing a good foraging site, as well as directional cues to locate the signallers, depending on the foraging strategy (e.g., Uetz, 1992; Persons and Uetz, 1996). As our own observations in the field show, spider webs attached to several plants also enable the resident spider to eavesdrop on vibrational signals emitted by their potential prey signaling on these plants (**Figure 3**).

The most obvious strategy to avoid enemies eavesdropping on sexual communication would be to emit as few and as quiet vibrational signals as possible without compromising the goal of reliably and quickly finding a suitable partner. In contrast to the majority of mating systems based on air-borne sound communication, where males produce continuous songs and silent females approach them, in mating systems based on substrate-borne vibrations partners exchange signals and males approach stationary females (e.g., Bailey, 2003; Derlink et al., 2014; Polajnar et al., 2014; Gibson and Cocroft, 2018). Duetting, in which both partners coordinate and modify their vibrational signals and behavior according to the partner's reply, is also a communication strategy that enables high signaling activity only at times when a partner is actually present. In the leafhopper *Scaphoideus titanus* the male vibrational repertoire aimed at a female includes several signals. The male emits short and structurally simple calls during the call-fly stage and during the searching phase and starts emitting longer and more complex courtship phrase only after he arrives on the leaf where the female is located (Polajnar et al., 2014). In *A. makarovi*, the long and structurally complex male call is the only vibrational signal directed to the female; however, male calling rate is low during the call-fly stage and increases only after a male receives the female reply (Kuhelj et al., 2015b). After vibrational contact is established, higher calling rate is advantageous and has significant positive effects on the probability to locate a female quickly.

In leafhoppers, pair formation includes male call-fly behavior, as well as a more localized search for the replying female. Hence high predation risk may also result from increased probability of encounters with predators while moving through the habitat. Males can also reduce predation risk by modifying their movements in the perceived presence of the predators. In the treehopper *E. binotata*, male behavioral response to the presence of spider silk was to reduce call-fly behavior but not their calling rate (Fowler-Finn et al., 2014).

In general, males are easier to detect than females, because they advertise themselves over a longer period of time, with more conspicuous signals of high amplitude (Zuk and Kolluru, 1998; Haynes and Yeargan, 1999). However, in duetting systems females are potentially equally exposed to eavesdropping predators as males, not only by proximity to the signaling male, but also because they remain stationary during vibrational exchange and therefore might be easier to locate. Virant-Doberlet et al. (2011) showed that in microcosms predation rate on *A. makarovi* females was also significant. In this study, the natural amplitude ratio between the male call and the female reply remained unchanged. Therefore, the male call which was more effective in increasing residence time of *E. ovata* predators in playback experiments, had higher amplitude. In this species, female vibrational replies can be even longer than male calls; however, their amplitude is always lower (Kuhelj et al., 2016). In this context, the observation that a female mates the first male that locates her may also be a strategy to reduce the duration of exposure to predators.

So far, confounding the conspecific competitors exploiting male-female duets appears to be the only observed defense against eavesdropping (Kuhelj et al., 2016; Kuhelj and Virant-Doberlet, 2017). Duet structures described in some leafhoppers, in which male and female signals share temporal and spectral characteristics and are partly overlapping, or female replies appear randomly among similar elements in male vibrational signals (Mazzoni et al., 2009a; Kuhelj et al., 2016), probably result in difficulties in locating the signallers. In a basically one-dimensional vibrational environment on the plant (de Groot et al., 2011), an eavesdropping exploiter may perceive such duets as one compound vibrational signal arriving from two spatially separated sources and from different directions.

CONCLUSIONS AND SUGGESTIONS FOR FURTHER STUDIES

Despite increased interest in vibrational communication in the last decade and the progress we made in our perception and understanding of this communication modality, vibrational signaling still remains a poorly known and understood mode of communication (Cocroft et al., 2014; Endler, 2019). As it is obvious from this review, vibrational signaling is far from being a safe communication channel, inaccessible to enemies. It is evolutionarily older and more widespread than air-borne sound communication and highly sensitive receptors detecting substrate vibrations are common. Although active space of vibrational signals is undoubtedly more complex and unpredictable than in air-borne sounds, animal vibrational signals are, in general, well adapted to their natural environment and frequency sensitivity of their receptors. As the first studies of the vibroscape show, substrate vibrations are a readily available and reliable source of information, both in intraspecific communication and in predator-prey interactions. Long evolutionary history of this communication channel is also reflected in the breadth of varied predator-prey interactions guided by substrate-borne vibrations. However, our own perceptional bias in favor of air-borne sound communication still hampers our understanding of challenges that animals relying on vibrational signals are facing in their environment. Eavesdropping and exploitation of vibrational signals used in sexual communication have been so far largely neglected; although, it is likely they are major drivers in the evolution taking place in the vibratory world.

What is urgently needed, are more studies on different model species in different environments, since the only existing study providing more comprehensive insight into exploitation of vibrational signaling included one prey species at a single field location (Virant-Doberlet et al., 2011). While leafhoppers provide an excellent model for studying predator-prey interactions within the vibratory world, since their communication is based exclusively on vibrational signals, we should also bear in mind that production of air-borne insect songs also creates a vibrational component of these signals (Caldwell, 2014). In order to establish that exploitation by eavesdropping predators can influence the evolution of vibrational signals, as well as signaling and searching behavior, it is not enough to observe that predation occurs. We must also determine that predation during the mating period occurs frequently enough to be a significant source of mortality and that there is a positive relationship between signaling and risk of predation (Kotiaho et al., 1998; Virant-Doberlet et al., 2011). Moreover, such studies should also be carried out under relevant ecological conditions. As existing data show, when focusing on arthropod predator-prey interactions, it should be also taken into account that only a subset of suitable predators may prey on a particular species (Virant-Doberlet et al., 2011) and that predation behavior can show geographic variation (Jackson and Carter, 2001). Furthermore, experience and learning are also likely to influence prey preference and such selective attention can be formed after a single encounter (Jackson and Li, 2004). We also need to ask whether spiders learn vibrational signals of locally abundant prey species or respond to signal characteristics that are common across many prey species (Cocroft, 2011; Virant-Doberlet et al., 2011). To bridge some gaps in our understanding of vibrational modality, we should also focus on how predators and prey perceive the vibratory world they share. Recent studies showing that plants can also respond to substrate vibrations induced by insects, provide additional evidence about the interconnected complexity of vibrational interactions in nature (Appel and Cocroft, 2014; Veits et al., 2019). Taking into account the long evolutionary history of vibrational communication, we have no doubt that studies of interspecific interactions guided by substrate vibrations will in the future offer numerous opportunities to unravel mechanisms that are central to our understanding behavior in general.

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

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Interspecific Eavesdropping on Ant Chemical Communication

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Chemical communication is a fundamental, highly complex component of social insect societies. Ants in particular employ a remarkable diversity of chemical signals to maintain social cohesion among nestmates, gain essential resources through coordinated foraging, and warn of danger. Although the chemicals used can be functionally specific, they are vulnerable to exploitation by eavesdropping natural enemies (e.g., parasitoids, predators, parasites) and other associates (e.g., myrmecophiles). Ant nests are nutrient hotspots due to their collection of resources warranting keen defense systems; yet the heavily defended hideouts are frequently invaded. Many organisms exploit ant species, but how they locate hosts—including what host-derived cues are used—is still poorly understood. Here, we review current knowledge about how ant chemical communication systems can be exploited by unintended receivers. We take a case study approach and illustrate the diversity of ant associates and host traits that may predispose ants to exploitation. We identify knowledge gaps by reviewing host systems and listing: (1) the types of associates (e.g., fly, wasp, beetle) where eavesdropping is likely occurring, organized by the host communication system that is being exploited; (2) the ant parasites that exploit trail pheromones; and (3) the experimentally determined chemicals (i.e., alarm/defensive pheromones), used by eavesdroppers. At least 25 families of arthropods (10 orders) potentially eavesdrop on ant communication systems and nearly 20 host ant species are vulnerable to trail parasite ant species. We also propose future research that will improve our understanding of community assembly by examining host traits (e.g., latitude, nest characteristics, trail system) that influence their susceptibility to eavesdropping associates.

Keywords: formicidae, symbionts, parasitoids, fungus-growing ants, fire ants, *Azteca*, semiochemical, unintended receivers

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EXPLOITATION OF CHEMICAL COMMUNICATION

In nature, natural enemies impose strong selective pressures on animals. These well-documented interactions drive complex coevolutionary arms races wherein organisms avoid detection by natural enemies that in turn evolve to overcome their victim's defenses. As individuals communicate with conspecifics, they also make information available to natural enemies and other associates that can be used to their advantage. Indeed, signals are often intercepted by unintended receivers who use them to exploit the signaler and ultimately benefit from accessing this communication system (Zuk and Kolluru, 1998; Stevens, 2013). This phenomenon, known as eavesdropping, can occur across sensory modalities in vertebrate and invertebrate communication networks (Otte, 1974; Stowe et al., 1995; Peake et al., 2001; Hamel and Cocroft, 2019). Chemical communication systems in particular, make signalers vulnerable to exploitation by a wide variety of enemies (e.g., parasitoids, predators, cleptoparasites, social parasites) and other associates (e.g., myrmecophiles). The diffusion of chemical signals, albeit less reliable than light and sound signals, can reveal the location of the signaler due to the odor gradients created. Chemical signals can also be made of molecules with low volatility that remain in the environment for days. Most studies investigating eavesdropping by natural enemies, however, have focused on the exploitation of acoustic and visual signals. Here, we evaluate the evidence for eavesdropping on chemical signals with the goal of providing hypotheses for future research that will fill the key gaps in our understanding of this phenomenon. We focused this review on ants (Hymenoptera: Formicidae) given that chemical communication is especially well developed in this insect family, providing an opportunity to cultivate general principles that relate to chemical communication and exploitation of chemical signals more broadly.

Ants are ecologically successful for a variety of reasons, including their social behavior, division of labor among distinct castes, and potentially large colony sizes. Ants communicate with their nestmates and with other organisms using a variety of mechanical (tactile, vibrations), visual, and chemical cues (Hölldobler and Wilson, 1990). However, it is clear that the evolutionary success of ants can be attributed in large part to their efficient chemical communication systems that enables large ant colonies to solve complex problems (Gordon and Mehdiabadi, 1999; Dornhaus et al., 2012). While the average ant worker has seven different glands, 75 different glands have so far been described in the Formicidae (Jackson and Morgan, 1993; Billen, 2009) and many of these secretions provide the basis for chemical communication systems. For example, exocrine secretions are used in defense and communication signals are commonly excreted from multiple glands used in synergy, therefore, the identification of the exact compound that elicits a behavioral response is challenging. Regardless, the literature on ant communication generally centers on detection of volatile emissions, thus we focus on chemical communication as the basis for this review. To our knowledge, all reports of eavesdropping in ants have involved chemical compounds, but tactile and vibrational cues may also be important under certain conditions. We mainly limit this review to sedentary nest-dwelling species because they form a tractable and ecologically relevant subset of the >16,000 known ant species (AntWeb[1] [Accessed 9 September 2019.]). However, we also highlight traits shared among many ant species that are linked with trail pheromone use, defensive substances, and nestmate recognition. We show that, although pheromones are often directed toward nestmates (intended receivers), they can sometimes be detected and used as cues by a diverse array of heterospecifics or non-nestmate conspecifics (unintended receivers).

Trail Pheromones

Ants conspicuously depend on chemical trails when foraging, and these odor-guided recruitment messages are often complex by necessity (reviewed in Morgan, 2009; Czaczkes et al., 2015). A food-bearing ant returning to the nest typically follows a series of chemical signposts including the trail pheromone, home-range markings, nest-marking pheromone, and environmentally derived visual and olfactory landmarks (Hölldobler and Wilson, 1990; Steck, 2012). Multiple species may use the same chemicals as the basis for their trail pheromones (e.g., Z,E-α-farnesene, 2,5-Dimethyl-3-ethylpyrazine), but these are commonly augmented with colony-specific hydrocarbons (reviewed in Morgan, 2009; also see Blomquist and Bagnères, 2010). Moreover, blends of volatile chemicals within trail pheromones can influence different nestmate recruitment functions (e.g., attraction, repulsion, guidance) (Robinson et al., 2005). Some chemical trails are localized and persist for several days (Jackson et al., 2007), providing long-lasting cues that are detected by resource-seeking ant associates (Dejean and Beugnon, 1996). These eavesdroppers subsequently access ant nests or food sources (**Table 1**; e.g., cockroaches, caterpillars, ants) (Moser, 1964; Adams, 1990; Dejean and Beugnon, 1996; Menzel et al., 2010). Indeed, there are many examples of eavesdropping on trail pheromones (**Table 2**), but the specific chemicals underlying these associations remain unknown (see **Table 3**).

Defense Pheromones

Ants release a wide range of volatile chemicals to alert nestmates of impending threats (reviewed in Parry and Morgan, 1979; Attygalle and Morgan, 1984; Jackson and Morgan, 1993; Morgan, 2008). Behavioral responses to these volatiles include increased movement, gaped mandibles, sting extrusion, trail laying, and aggressive postures (Parry and Morgan, 1979). Alarm pheromones are most often produced by the mandibular, poison, or Dufour's glands (Ali and Morgan, 1990), and are frequently used synergistically. Chemicals found in alarm pheromones include straight-chain and cyclic ketones, nitrogenated compounds, and formic acid (Maschwitz et al., 2008; Morgan, 2008; Vander Meer et al., 2010). The volatility of alarm pheromones makes them reliable long-range indicators of host presence, but also makes them spatiotemporally limited. Regardless, many parasitoids and predators of ants eavesdrop on alarm pheromones (**Table 3**) (Feener et al., 1996; Morrison and King, 2004; Witte et al., 2010).

Recognition Pheromones

Nestmate recognition in ants is primarily mediated via "signature mixtures" of branched and unsaturated cuticular hydrocarbons (CHCs) (Wyatt, 2010; Martin and Drijfhout, 2009; Leonhardt et al., 2016; Menzel et al., 2017). These pheromones are distinct from linear compounds with higher melting points, which function mainly to prevent insect desiccation (Howard and Blomquist, 2005; Martin and Drijfhout, 2009; Chung and Carroll, 2015). CHC signals are central to the social organization of

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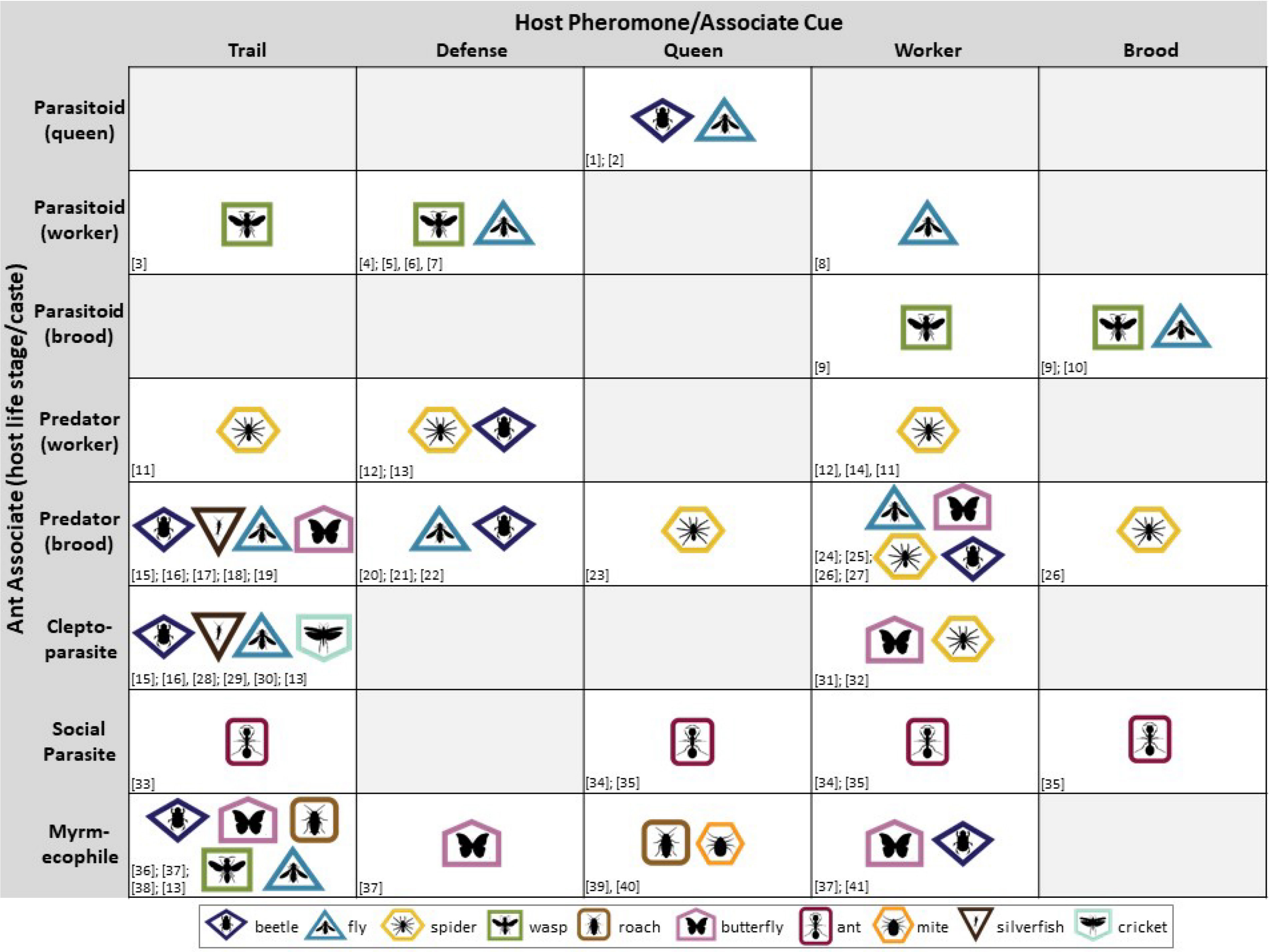
[1] https://www.antweb.org

TABLE 1 | Demonstrated and putative chemical eavesdropping enemies and associates of the ants.



Ant Associate (host life stage/caste)	Host Pheromone/Associate Cue				
	Trail	**Defense**	**Queen**	**Worker**	**Brood**
Parasitoid (queen)			🪲 🪰 [1]; [2]		
Parasitoid (worker)	🐝 [3]	🐝 🪰 [4]; [5], [6], [7]		🪰 [8]	
Parasitoid (brood)				🐝 [9]	🐝 🪰 [9]; [10]
Predator (worker)	🕷 [11]	🕷 🪲 [12]; [13]		🕷 [12], [14], [11]	
Predator (brood)	🪲 ▽ 🪰 🦋 [15]; [16]; [17]; [18]; [19]	🪰 🪲 [20]; [21]; [22]	🕷 [23]	🪰 🦋 🕷 🪲 [24]; [25]; [26]; [27]	🕷 [26]
Clepto-parasite	🪲 ▽ 🪰 🦗 [15]; [16], [28]; [29], [30]; [13]			🦋 🕷 [31]; [32]	
Social Parasite	🐜 [33]		🐜 [34]; [35]	🐜 [34]; [35]	🐜 [35]
Myrm-ecophile	🪲 🦋 🪳 🐝 🪰 [36]; [37]; [38]; [13]	🦋 [37]	🪳 ⬣ [39], [40]	🦋 🪲 [37]; [41]	

🪲 beetle 🪰 fly 🕷 spider 🐝 wasp 🪳 roach 🦋 butterfly 🐜 ant ⬣ mite ▽ silverfish 🦗 cricket

Individuals are categorized by biological lifestyle (left side) and communication system (top) being exploited. Brackets refer to the host life stage or caste (e.g., queen, worker, brood). Where the biological lifestyle is unknown, ant associates are categorized as myrmecophiles. References organized by numbers and separated by either a comma, to indicate the paper is referring to species from different families, or by a semicolon when the paper cited is referring to a new type (e.g., fly, ant, etc.). [1] Hertel and Colli, 1998, [2] Pérez-Lachaud et al., 2017, [3] Staverløkk and Ødegaard, 2016, [4] Durán and van Achterberg, 2011, [5] Mathis and Philpott, 2012, [6] Sharma and Fadamiro, 2013, [7] Witte et al., 2010, [8] Uribe et al., 2016, [9] Fernández-Marín et al., 2006, [10] Brown et al., 2017, [11] Wing, 1983, [12] Allan et al., 1996, [13] Rettenmeyer et al., 2011, [14] Komatsu, 2016, [15] Akino, 2002, [16] Akre and Rettenmeyer, 1968, [17] Cammaerts et al., 1990, [18] Cazier and Mortenson, 1965, [19] Dejean and Beugnon, 1996, [20] Akre et al., 1988, [21] Geiselhardt et al., 2007, [22] Schönrogge et al., 2008, [23] Mello-Leitão, 1923, [24] Akre et al., 1973, [25] Dodd, 1912, [26] Erthal and Tonhasca, 2001, [27] Lenoir et al., 2012, [28] Bhatkar, 1982, [29] Henderson and Akre, 1986, [30] Hölldobler and Kwapich, 2017, [31] Maschwitz et al., 1988, [32] Jackson et al., 2008, [33] Powell et al., 2014, [34] Silveira-Guido et al., 1973, [35] D'Ettorre and Heinze, 2001, [36] Henderson and Jeanne, 1990, [37] Henning, 1983, [38] Moser, 1964, [39] Moser, 1967, [40] Phillips et al., 2017, [41] Hölldobler, 1967.

an ant colony, thus they provide a weakness in colony defense due to the chemical mimicry or camouflage strategies used by nest associates. For example, many social parasites and myrmecophiles invade the ant nest as a "wolf in sheep's clothing" using a CHC-based chemical disguise (Vander Meer and Wojcik, 1982; Lenoir et al., 2001; Akino, 2008; Blomquist and Bagnères, 2010). In such cases, CHC mimicry is not eavesdropping, but an infiltration strategy.

However, CHCs may be used by parasitoids to discriminate among the specific castes and life stages of their ant hosts (**Table 1**) when these chemical signatures function as signals. We define signals as sender-produced actions or structures that alter receiver behavior, and are the product of coevolutionary processes between actors (Maynard-Smith and Harper, 2003). Direct observation indicates ants can readily locate and manipulate their brood in different settings, implying that the same pheromones (and other cues) may be exploitable by brood-specific natural enemies. However, the unambiguous identification of ant brood-specific recognition signals has remained controversial (Morel and Vander Meer, 1988; Casacci et al., 2013). Evidence indicates at least some post-embryonic developmental ant stages emit some form of chemical (Walsh and Tschinkel, 1974; Brian, 1975) and even sound (Casacci et al., 2013). It is therefore possible that these associates

TABLE 2 | Eavesdropping ant species using trail pheromones of distantly related ant hosts.

Subfamily: Trail parasite species	Host species (Subfamily)	Nest sharing	Nest/trail location	References
Dolichoderinae:				
Dolichoderus debilis	*Crematogaster carinata* (Myrmicinae)	Yes	Canopy	Swain, 1980
Dolichoderus cuspidatus	*Polyrhachis ypsilon* (Formicinae)	No	Canopy	Menzel et al., 2010
Formicinae:				
Camponotus beebi	*Azteca chartifex* (Dolichoderinae)	Yes	Canopy	Wilson, 1965
Camponotus blandus	*Pseudomyrmex termitarius* (Pseudomyrmecinae)	Yes	Ground/termite nest	Gallego-Ropero and Feitosa, 2014
Camponotus femoratus	*Crematogaster limata* (Myrmicinae)	Yes	Canopy	Swain, 1980
Camponotus femoratus	*Crematogaster levior* (Myrmicinae)	Yes	Canopy	Swain, 1980
Camponotus lateralis	*Crematogaster scutellaris* (Myrmicinae)	No	Deadwood (tree, log)	Goetsch, 1953; Kaudewitz, 1955
Camponotus rufifemur	*Crematogaster modiglianii* (Myrmicinae)	No	Canopy	Menzel et al., 2010
Camponotus saundersi	*Polyrachis ypsilon* (Formicinae)	No	Canopy	Menzel et al., 2010
Camponotus vitreus	*Crematogaster* cf. *polita* (Myrmicinae)	No	Canopy/stems	Menzel, 2009
Camponotus sp.	*Crematogaster inflate* (Myrmicinae)	No	Canopy	Ito et al., 2004
Camponotus sp.	*Crematogaster coriaria* (Myrmicinae)	No	Canopy/deadwood	Menzel, 2009
Camponotus sp.	*Crematogaster* sp. (Myrmicinae)	No	Unknown/deadwood	Baroni Urbani, 1969
Lasius niger	*Formica rufibarbis* (Formicinae)	No	Underground	Binz et al., 2014
Oecophylla longinoda	*Cataulachus guineensis* (Myrmicinae)	No	Canopy	Dejean, 1996
Polyrachis rufipes	*Gnamptogenys menadensis* (Ectatomminae)	No	Underground	Gobin et al., 1998
Polyrachis sp.	*Camponotus cylindrica* (Formicinae)	Yes	Canopy	Davidson et al., 2007
Myrmicinae:				
Cephalotes maculates	*Azteca trigona* (Dolichoderinae)	No	Canopy	Adams, 1990
Cephalotes specularis	*Crematogaster ampla* (Myrmicinae)	No	Canopy	Powell et al., 2014
Formicoxenus nitidulus	*Formica rufa pratensis* (Formicinae)	Yes	Mound/underground	Elgert and Rosengren, 1977
Pogonomyrmex colei	*Pogonomyrmex rugosus*	Yes	Ground	Johnson et al., 1996

Host and parasite nest sharing is indicated with yes/no and the location of nest and trail are described. Information was gathered from references found with Google Scholar (search words: "ant trail parasites," "ant eavesdropping," "eavesdrop trail," and "trail follow ants"). Additionally, references in each paper were reviewed, as were the papers on the Google Scholar "cited by" function. If there was evidence of heterospecific species trail use in nature, it was included in the table.

eavesdrop upon nestmate recognition pheromones, but may also detect host-derived cues that range across sensory modalities. Determining eavesdropping on CHC signals is technically challenging because decoupling sensory modalities may be difficult, but still worthy of future studies. Host-derived short-range cues (e.g., tactile, chemical and auditory) as well as CHC-based signals are likely part of a complex of features enabling successful host exploitation.

How Enemies and Other Associates Find Hosts

The success of specialized ant associates is dependent on their ability to find hosts (or prey). The first challenge the exploiters face is locating their victim (Encounter Phase, **Figure 1**) (Combes, 2005). Although small ant colonies can quickly relocate in response to predation or disturbance (O'Shea-Wheller et al., 2015), species that invest substantial energy in building elaborate nest structures are often stationary targets (Hughes et al., 2008). In either case, associates locate hosts by using visual and olfactory cues that enable them to orient toward habitats occupied by their hosts (Morehead and Feener, 2000b; Lachaud and Pérez-Lachaud, 2012) (**Figure 1A**). Next, they detect host-derived chemical cues. These may be waste byproducts or long-range chemical signals such as trail, nest-marking and defense pheromones (**Figure 1B**). Once in close proximity, host acceptance prompts the Exploitation Phase. Species identification can be accomplished by detecting species-specific short-range chemical cues; at this stage, eavesdropping is possible if enemies or other associates are intercepting signals (e.g., sex and contact pheromones) (**Figure 1C**) (Bagnères and Wicker-Thomas, 2010). Predatory enemies would consume their prey at this stage. As the Exploitation Phase continues, social parasites (i.e., social species that exploit other social species), parasitoids, and myrmecophiles (i.e., associated organisms that live part or most of its life inside the host ant nest with ants, parasitoids excluded herein), appraise whether an individual or a colony has been previously attacked by conspecifics by detecting oviposition-marking pheromones, to avoid superparasitism (**Figure 1D**). Once the ant enemy or myrmecophile associate invades the organism or ant colony, it may regulate its host physiologically or behaviorally to maximize its own fitness returns (**Figure 1E**) (Vinson, 1976; Henne and Johnson, 2007; Mathis and Philpott, 2012; de Bekker et al., 2018). While we will focus on how olfaction influences host-finding behavior, it is important to keep in mind that multiple sensory modalities are likely at play and will affect ant associate behavior. Determining the role of different sensory modalities and their interaction (e.g., independent, additive, multiplicative) is necessary to test the chemical eavesdropping hypothesis. Furthermore, life experience and learning will also influence the success of host-finding (Vet and Dicke, 1992).

TABLE 3 | Experimentally determined chemicals used by eavesdropping ant associates.

Type, Family: Eavesdropping associate	Host species (Subfamily)	Chemical(s)	Function	References
Fly, Phoridae:				
Pseudacteon brevicauda	*Myrmica rubra* (Myrmicinae)	3-octanone; 3-nonanone; 3-Octanol	Alarm pheromone	Witte et al., 2010
Pseudacteon formicarum	*Lasius* spp. (Formicinae)	HCOOH (Formic acid)	Defense pheromone	Maschwitz et al., 2008
Pseudacteon curvatus	*Solenopsis* spp. (Myrmicinae)	2-methyl-6-alkylpiperidine	Defense pheromone	Sharma and Fadamiro, 2013
Pseudacteon obtusus	*Solenopsis* spp. (Myrmicinae)	2-methyl-6-alkylpiperidine	Defense pheromone	Sharma and Fadamiro, 2013
Pseudacteon tricuspis	*Solenopsis* spp. (Myrmicinae)	2-methyl-6-alkylpiperidine	Defense pheromone	Sharma and Fadamiro, 2013
Pseudacteon curvatus	*Solenopsis* spp. (Myrmicinae)	2-ethyl-3,6-dimethyl pyrazine	Alarm pheromone	Ngumbi and Fadamiro, 2015
Pseudacteon cultellatus	*Solenopsis* spp. (Myrmicinae)	2-ethyl-3,6-dimethyl pyrazine	Alarm pheromone	Ngumbi and Fadamiro, 2015
Pseudacteon obtusus	*Solenopsis* spp. (Myrmicinae)	2-ethyl-3,6-dimethyl pyrazine	Alarm pheromone	Ngumbi and Fadamiro, 2015
Pseudacteon tricuspis	*Solenopsis* spp. (Myrmicinae)	2-ethyl-3,6-dimethyl pyrazine	Alarm pheromone	Ngumbi and Fadamiro, 2015
Pseudacteon spp.	*Solenopsis* spp. (Myrmicinae)	2-ethyl-3,6-dimethylpyrazine	Alarm pheromone	Sharma et al., 2011
Pseudacteon sp.	*Azteca instabilis* (Dolichoderinae)	1-acetyl-2-methylcyclopentane	Alarm pheromone	Mathis et al., 2011
Apocephalus paraponerae	*Paraponera clavata* (Paraponerinae)	4-methy-3-heptanone 4-mehtyl-3-heptanol	Alarm pheromone	Feener et al., 1996
Fly, Syphidae:				
Microdon mutabilis	*Formica lemani* (Formicinae)	methyl-6-methylsalicylate	Alarm pheromone	Schönrogge et al., 2008
Spider, Zodariidae:				
Habronestes bradleyi	*Iridomyrmex purpureus* (Dolichoderinae)	6-methyl-5-hepten-2-one	Alarm pheromone	Allan et al., 1996
Zodarion rubidum	*Lasius platythorax Formica rufibarbis* (Formicinae)	decyl acetate; undecane	Alarm pheromone	Cárdenas et al., 2012

As we have explained above, many ant associates—specifically social parasites, myrmecophiles, and some parasitoids—infiltrate and integrate into the nest by exploiting nestmate recognition signaling systems (Lenoir et al., 2001; Akino, 2008). While eavesdropping involves enemies and other associates detecting host-derived signals during host location (**Figure 1B**) and host acceptance (**Figure 1C**), successful colony infiltration occurs during the host acceptance stage (**Figure 1C**, bottom panel). Detection of host pheromones (i.e., eavesdropping) is distinct from traits that have evolved in response to host resistance (e.g., alteration of CHCs resulting in chemical mimicry). Colony integration, often achieved by the same mechanisms as "infiltration," refers to associates that live for longer periods of time with their host (**Figure 1D**, bottom panel). In this case, they can maintain a chemical disguise and use weaponry to regulate host behavior (**Figure 1E**) while avoiding expulsion from the nest. Although the cuticular hydrocarbon profiles of many ant hosts and their associates have been evaluated, we still do not know how most associates locate their host (**Figures 1A–C**). The examples we present will address chemical eavesdropping during host location and acceptance (**Figures 1B,C**), when essential host-derived pheromones (e.g., defense, trail, nestmate recognition) are detected by the eavesdropping associates.

ENEMIES AND ASSOCIATES OF THE ANTS

Numerous specialized ant associate species exploit individual ants (e.g., parasitoids and predators) or take advantage of shared colony resources (e.g., cleptoparasites, social parasites and myrmecophiles) (**Table 1**). The best-studied enemies are the parasitoid scuttle flies (Brown and Feener, 1991; Brown, 2001; Disney et al., 2006, 2008; Patrock et al., 2009; Morrison, 2012; Pérez-Lachaud et al., 2017) and wasps (Lachaud and Pérez-Lachaud, 2012; Murray et al., 2013) that attack exposed foragers. Other associates consume ant larvae (Masner, 1959; Wing, 1983; Loiácono et al., 2000), attack the queen (Johnson et al., 2002; Barbero et al., 2009; Briano et al., 2012), or are benign myrmecophiles scavenging on waste or taking advantage

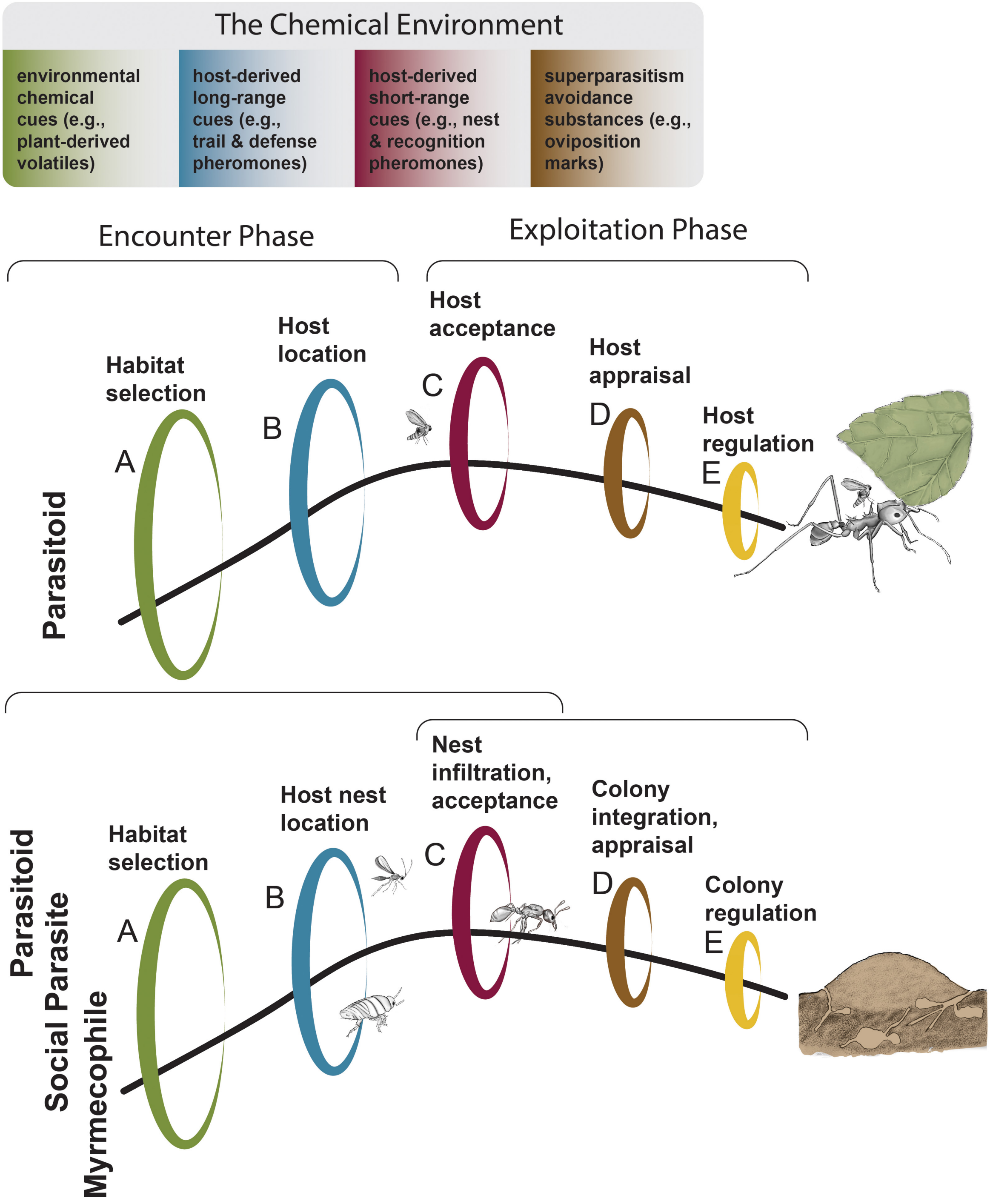
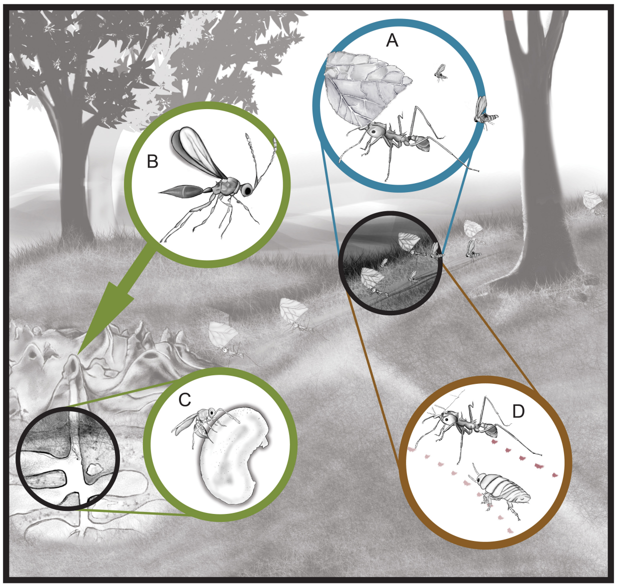


FIGURE 1 | A graphic model of the sequential challenges associates face to successfully exploit an ant host. Different chemical cues can aid the associate in finding and appraising their host. When an enemy is intercepting a signal (e.g., pheromone), this is considered eavesdropping. **(A)** *Habitat selection*. Environmental chemical cues can aid the associate in narrowing search patterns. **(B)** *Host location*. Host-derived long-range chemical cues can guide the ant associate to a host individual (top panel) or nest (bottom panel) after arriving to the host habitat. **(C)** *Host acceptance*. Once the host individual (top panel) or nest (bottom panel) is located, the associate will determine if it is acceptable (e.g., correct species, life stage, caste, etc.). In some cases the associate will infiltrate the nest at this stage (bottom panel). Predators will consume their prey at this stage. **(D)** *Host appraisal*. In order to avoid superparasitism, some associate species are able to detect the chemical signature or oviposition-marking of hetero- or conspecifics, thus avoiding the fitness cost of sharing a host. In some cases this can occur at the same time as colony integration within the nest (bottom panel). **(E)** *Host regulation*. After infecting the host, the parasite can manipulate host behavior or physiology in order to maximize its fitness gains. Sequential challenges were inspired by Vinson (1976) and Mathis and Philpott (2012) whereas the host encounter phase and exploitation phases were inspired by Combes (2005). Illustrations by Rozlyn E. Haley adapted from photographs by Alex Wild.



Taxonomic classification of host
- Leaf-cutting *Atta* and *Acromyrmex* ants (Formicidae: Myrmicinae: Attini: Attina)

Importance (*Atta* and *Acromyrmex*)
- Ecologically significant herbivores, nutrient cyclers, and pests of agroecosystems

Natural history traits (*Atta*)
- Latitude
  - Southern USA to Argentina, tropical forests and savanna
- Host nest
  - *Size* (1-8 million workers, nest mounds can exceed 67 m^2 in area, and have >7,000 chambers up to 8 m deep
  - *Structural complexity* (thousands of chambers and long underground tunnels with multiple nest entrances, external or internal fungus-garden dump)
  - *Location* (underground)
  - *Longevity* (20-30 years)
- Trail system
  - Extensive trails above and below ground
- Species richness or lineage
  - 18 *Atta* species but sister to 33 *Acromymrex* species
- Susceptible communication systems
  - *Trail* (yes, cleptoparasites identified, compounds include 2,5-Dimethyl-3-ethylpyrazine, a known attractant for phorid flies)
  - *Defense* (yes, aggressive defensive behavior, mandibular alarm compounds include 4-Methylheptan-3-ol and 4-Methylheptan-3-one, both are known attractants for phorid flies)
  - *Queen, worker, and brood chemical cues* (yes, caste-specific cuticular hydrocarbons likely used by parasitoids)

Known enemies and associates (*Atta* and *Acromyrmex*)
- Social parasites
  - *Inquiline ants* (Hymenoptera: Formicidae)
- Parasitoids
  - *Scuttle flies* (Diptera: Phoridae)
  - *Diapriid wasps* (Hymenoptera: Diaprioidea: Diapriidae)
- Arthropod predators
  - *Paussine beetles* (Coleoptera: Carabidae: Paussinae)
- Cleptoparasites
  - *Attaphila cockroach* (Blattaria: Polyphagidae)
- Myrmecophiles [partial list, see Waller and Moser (1990)]
  - (Diptera: Milichiidae); (Coleoptera: Alleculidae, Staphylinidae.); (Zygentoma: Atelurinae); (Orthoptera: Myrmecophilae)

Key references: (AntWeb 09/09/2019; Ali and Morgan, 1990; Bragança et al., 2016; Cross et al., 1982; Feener et al., 1996; Forti et al., 2017; Geiselhardt et al., 2007; Hölldobler and Wilson, 2011; Loiácono et al., 2013; Moreira et al., 2004; Moser, 1986, 1963; Norman et al., 2017; Rabeling et al., 2015; Richard et al., 2007; Riley et al., 1974; Schowalter and Ring, 2017)

BOX 1 | Continued

BOX 1 | Leaf-cutting ants and generalized natural history of the associates. Two leaf-cutting genera, *Atta* and *Acromyrmex* use sophisticated chemical communication systems to maintain efficiency, order, and protection for their conspicuous nests and trail systems (ca. 90 m long in *Atta*; Hölldobler and Wilson, 2011). Nest structures with millions of workers are labeled with colony-specific territorial pheromones [e.g., *n*-heptadecane, (Z)-9-nonadecene, 8,11-nonadecadiene] and trail pheromones (e.g., methyl 4-methylpyrrole-2-carboxylate, 3-ethyl-2,5-dimethylpyrazine) with Dufour's gland secretions (Tumlinson et al., 1972; Evershed and Morgan, 1981; Salzemann et al., 1992). Colonies are protected by specialized workers that emit volatilized alarm pheromones (e.g., 4-Methyl-3-heptanol, 3-octanone, 2-heptanone, 4-Methyl-3-heptanone, citral) (Blum et al., 1968; Hölldobler and Wilson, 1990; Norman et al., 2017). **(A)** A phorid fly hovers above *Atta* workers, attracted to trail pheromones. The parasitoid larva will develop and decapitate the host ant just before pupation. **(B)** Diapriid wasp searching for the host nest (e.g., *Acromyrmex*). **(C)** The gravid female searches for brood chamber then lays an egg(s) into a host larva. The parasitoid consumes the host and emerges inside the ant nest. **(D)** *Attaphila* roach following host ant trail (dotted lines). Illustrations by Rozlyn E. Haley adapted from photographs by Alex Wild.

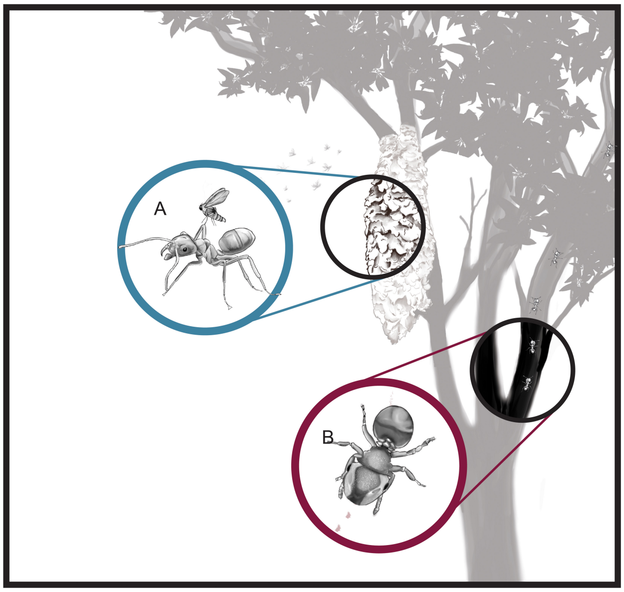
of the protected shelter (Hölldobler and Wilson, 1990). Below we review a diversity of cases where natural history evidence suggests eavesdropping on host-derived communication systems (i.e., trail, alarm and recognition) to locate the host ant, the host nest, or the host brood. We limit the scope to organisms or lineages that are good candidates for hypothesis-driven research testing for chemical eavesdropping on ants.

Parasitoids of Workers

Scuttle Flies (Diptera: Phoridae)

Host-derived ant pheromones are attractants to the so called "ant-decapitating flies" or scuttle flies (Diptera: Phoridae) (**Table 1** and **Boxes 1A**, **2A**). These parasitoids develop in specific body regions of their host ants, with one or more flies emerging per ant. The phorid flies that attack fire ants and leaf-cutter ants (**Box 1A**) have been studied more intensively because their hosts are considered pests (Hölldobler and Wilson, 1990), but many other ant lineages are vulnerable to these parasitoids (Hsieh and Perfecto, 2012). Species in >20 genera of phorids (especially *Pseudacteon, Apocephalus, Eibesfeldtphora, Myrmosicarius, Neodohrniphora*) (reviewed in Folgarait, 2013), collectively attack more than 22 genera of ants in five subfamilies (Mathis and Philpott, 2012). The flies potentially affect colony-level fitness via worker mortality and behavioral changes (e.g., reduced foraging) (Feener and Brown, 1992; Milton and Athayde, 2000; Elizalde and Folgarait, 2011; Hsieh and Perfecto, 2012).

Phorids can often be observed hovering above disturbed ant nests (Witte et al., 2010), injured workers (Brown and Feener, 1991) and foraging trails (Tonhasca, 1996). Trail and alarm pheromones are reliable cues that likely "advertise" host presence, whereas specific ant targets are selected based on short-range chemical and visual cues (Farder-Gomes et al., 2017). In some cases, CHC profiles confirm species identification for final host acceptance by the attacking flies (Mathis and Tsutsui, 2016) (**Figure 1C**, top panel). When searching for an appropriate oviposition point, the flies may detect oviposition -marking pheromones (i.e., used to inform conspecifics of a previously utilized host) or other signs from previous parasitoids



BOX 2 | Pendulous carton forming *Azteca* ants and generalized natural history of the associates. While territorial markings have yet to be discovered, these aggressive arboreal ants maintain foraging territories with trail pheromones from their Pavan's gland and alarm pheromones from the pygidal glands (Adams, 1994). Straight-chain and cyclic ketones (e.g., 2-heptanone and 2-methylcyclopentanone, respectively) act as alarm pheromones attracting nearby nestmates (Wheeler et al., 1975; McCann et al., 2013) while volatile aldehydes and iridoids (e.g., nepetalactol, iridoidal isomers) may simultaneously signal nest location (Adams, 1994; Nascimento et al., 1998). Less volatile chemicals such as cuticular hydrocarbons provide short-range information that allows parasitoids to discriminate between species (Mathis and Tsutsui, 2016). **(A)** A phorid fly hovers outside *Azteca* nest, attracted by alarm pheromones. After locating a suitable host ant, the phorid lays an egg inside her. The parasitoid larva will develop and decapitate the host just before pupation. **(B)** *Cephalotes* cleptoparasite workers follow the trail pheromones (dotted line) of *Azteca* scouts to locate new food sources. Illustrations by Rozlyn E. Haley adapted from photographs by Alex Wild.

Taxonomic classification of host
Pendulous carton forming *Azteca* ants (Formicidae: Dolichoderinae)

Importance (pendulous carton forming *Azteca*)
Numerically abundant, behaviorally aggressive and territorially dominant, potential biological control agents, ecologically significant secondary herbivores

Natural history traits (pendulous carton forming *Azteca*)

Latitude
Mexico to Argentina in tropical forests

Host nest
Size (thousands of workers/nest, carton nests range from 0.5-4 m in length, and one colony can have multiple nests)
Structural complexity (yes, hundreds of entrances on nest under carton flaps, entrances lead to tunnels forming a mosaic that occupies the entire volume of the nest)
Location (hanging from trees or branches)
Longevity (>15 years)

Trail system
Extensive trails mostly on trees and lianas

Species richness or lineage
84 valid *Azteca* species (10 pendulous carton forming)

Susceptible communication systems
Trail (yes, cleptoparasites identified, compounds may include iridodials, 6-methyl-5-hepten-2-one, 2-methyl-1-cyclopentene-carboxaldehyde, and 2-formyl-3-methylcyclopentene-acetaldehyde, but have not been specifically tested)
Defense (yes, very aggressive defense behavior, mandibular alarm compounds include 2-heptanone, a known attractant for phorid flies)
Queen, worker, and brood chemical cues (yes, caste-specific cuticular hydrocarbons likely used by parasitoids)

Known enemies and associates (pendulous carton forming *Azteca*)

Parasitoids
Scuttle flies (Diptera: Phoridae)
Braconid wasps (Hymenoptera: Braconidae)
Chalcidid wasps (Hymenoptera: Chalcididae)

Arthropod predators
Paussine beetles (Coleoptera: Carabidae: Paussinae)

Cleptoparasites
Ants (Hymenoptera: Formicidae)

Myrmecophiles
(Coleoptera: Scarabaeidae: Dynastinae), (Coleoptera: Cetonilinae: Cremastocheilini)

Key references: (AntWeb 09/09/2019; Adams, 1990, 1994; Ali and Morgan, 1990; Alves-Oliveira et al., 2016; Choe et al., 2012; Clay et al., 2013; Davidson et al., 2003; Longino, 2007; Mathis and Philpott, 2012; McCann et al., 2013; Nascimento et al., 1998; Wheeler, 1924, 1986)

BOX 2 | Continued

(**Figure 1D**, top panel). Finally, the developing phorid larva may manipulate the behavior of the host ant until development of the parasitoid is complete (often culminating in decapitation of the host; **Figure 1E**, top panel) (reviewed in Henne and Johnson, 2007; de Bekker et al., 2018). Stages leading to successful exploitation have been studied in various systems where colony size is large and ant nests are permanent (see case studies of *Atta* **Box 1** and *Azteca* **Box 2**) but also in species where workers forage individually (e.g., *Paraponera*) or in large groups (e.g., army ants). Due to their high diversity, the phorid flies are an informative research model for understanding host specificity, and the ecology and evolution of eavesdropping of ant chemical signals.

More than 80 phorid fly species parasitize leaf-cutter ants (i.e., *Atta* and *Acromyrmex*, collectively 51 species) (**Box 1A**) (reviewed in Folgarait, 2013). Phorids frequently attack *Atta* on foraging trails or at refuse piles (Milton and Athayde, 2000; Elizalde and Folgarait, 2012; Folgarait, 2013), and the threat of phorids presumably causes some leaf-cutter species to forage crepuscularly or at night (Orr, 1992). Hovering phorid flies cause reduced foraging activity, and defensive postures in workers that include hitchhiking minima workers riding on leaf fragments (Milton and Athayde, 2000; Elizalde and Folgarait, 2012; Folgarait, 2013). Given that phorid flies target *Atta* on foraging trails (**Box 1A**), it is likely that these parasitoids eavesdrop on trail pheromones (Milton and Athayde, 2000; Elizalde and Folgarait, 2012; Folgarait, 2013). The compound 2,5-dimethyl-3-ethylpyrazine is found in several leaf-cutter trail pheromones (Cross et al., 1982; Morgan et al., 2006), and it is also an alarm pheromone of *Solenopsis* fire ants (Vander Meer et al., 2010) and an attractant for phorid flies (Sharma et al., 2011; Ngumbi and Fadamiro, 2015). Experiments are needed to determine if this compound attracts phorids to *Atta* trails.

To date, only the phorid genus *Pseudacteon* is known to be associated with *Azteca* spp. (Feener and Brown, 1997; Mathis et al., 2011). *Azteca* workers noticeably attempt to dodge phorid fly parasitoids when the nest is damaged or when the ants are otherwise alarmed. The phorids are attracted to alarm pheromones emitted from the nest surface (**Box 2A**) as in other parasitized species (Feener and Brown, 1997; Morehead and Feener, 2000a). Phorids tend to cluster near disturbed workers, and cause reduced survivorship in areas where *Azteca* nests are very dense (Vandermeer et al., 2008; Philpott et al., 2009). As the flies hover to find a suitable host, there is a conspicuous change in ant behavior. Sometimes the ants simply flee, other times they appear to act aggressively toward the flies, as described in other ant-phorid systems (Feener, 1988). The threat of phorid attack also reduces *Azteca* activity at baits, interferes with their ability to protect trophobionts from predators and parasites, and limits their ability to defend plants against herbivores (Philpott et al., 2004; Hsieh and Perfecto, 2012; Hsieh et al., 2012). Knowledge of the chemical ecology of *Azteca* is limited, but three species (i.e., *Azteca instabilis*, *A. nigriventris*, and *A. velox*) release the same cyclopentyl ketones from their pygidial gland as defensive substances (Wheeler et al., 1975; Mathis et al., 2011). Although these species do not build carton nests, similar and overlapping compounds are widespread among *Azteca* spp. (**Box 2**) (Billen, 1986; Nascimento et al., 1998; Longino, 2007; McCann et al., 2013). One *Pseudacteon* species eavesdrops specifically on *cis*-1-acetyl-2-methyl-cyclopentane to locate and attack *A. instabilis* (Mathis et al., 2011). However, there is convincing evidence that visual cues (e.g., motion and ant shape) are also important for host-finding phorids, suggesting that the alarm-defense pheromones are part of multisensory decision making, leading to parasitoid success (Morehead and Feener, 2000b; Mathis et al., 2011).

At least 36 *Pseudacteon* phorid species parasitize *Solenopsis invicta* and *Solenopsis saevissima*; 17 phorid species attack *Solenopsis invicta* alone (reviewed in Chen and Fadamiro, 2018). The small *Pseudacteon* flies are attracted to disturbed fire ant mounds and hover above distressed and alarmed ants. Once the host colony is located, the flies move closer to size-select their victims for optimal offspring development (Morrison and Gilbert, 1999). Despite numerous studies on these flies, exactly how they locate fire ant nests from long distances remains unclear (Mathis and Philpott, 2012). However, piperidine venom alkaloids and 2,5-dimethyl-3-ethylpyrazine are both defensive substances (e.g., venom, alarm pheromones) that attract phorid flies in close-range interactions (Sharma and Fadamiro, 2013; Ngumbi and Fadamiro, 2015). Natural history accounts of the attraction of phorid flies to disturbed nests thus supports the experimental studies concluding that alarm pheromones are involved in host location (Morrison and King, 2004; Sharma and Fadamiro, 2013; Ngumbi and Fadamiro, 2015). The chemical ecology of fire ants is relatively well studied (Tschinkel, 2006), thus they are excellent research models for identifying the exact compounds that lure parasitoids and determining if they are indeed used by eavesdropping enemies and associates.

There are other notable advances in our understanding of chemical eavesdropping by phorid flies in a number of other systems. *Paraponera clavata* (Formicidae: Paraponerinae) are attacked by the phorid *Apocephalus paraponerae*. These phorids are attracted to the two major products of the mandibular glands of *P. clavata*, 4-methyl-3-heptanol and 4-methyl-3-heptanone (Feener et al., 1996). Interestingly, these compounds are found in alarm pheromones of many ant species belonging to other subfamilies (Morgan, 2008), including *Atta* and *Acromyrmex* (Norman et al., 2017). Ant species in the subfamily Formicinae produce formic acid in their venom and this compound is the primary host location cue attracting *Pseudacteon formicarum* to *Lasius niger* and *Lasius emarginatus* (Formicidae: Formicinae) (Maschwitz et al., 2008). Similarly, *Myrmica rubra* produces 3-octanone, non-anone and 3-octanol in their mandibular gland (Cammaerts et al., 1981) and these defense substances serve as attractants for *Pseudacteon brevicauda.* Phorid flies are most often specialists, attacking a single host ant species (Porter, 1998; Weissflog et al., 2008; Witte et al., 2010; Folgarait, 2013) but the chemical attractants of phorids may be more indiscriminate for long-range host localization. Once the fly has entered the habitat and found the nest or trail, they appear to use species-specific hydrocarbons to ensure species specificity (Mathis and Tsutsui, 2016). Phorids are recorded as the most-commonly observed associates among army ant bivouacs, raid trails, and refuse piles (Rettenmeyer and Akre, 1968). Hundreds of species interact with army ants and the genus *Megaselia* is by far the most common. Although observations suggest flies follow trails, eavesdropping on signals has not been formally demonstrated and remains a hypothesis. The great majority of phorid flies associated with army ants are found only in refuse piles, suggesting most species are opportunistic rather than ant-specific associates (Rettenmeyer and Akre, 1968).

Parasitoids of Brood

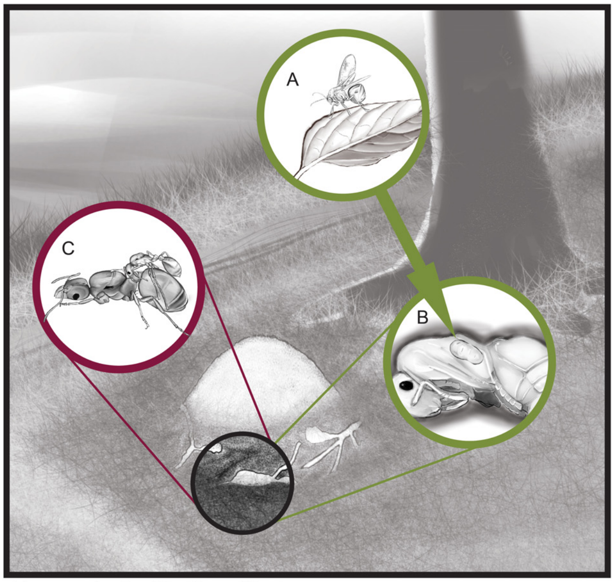
Wasps

Approximately 140 identified endo- or ectoparasitic wasp species (superfamilies: Chalcidoidea, Ichneumonoidea, Diaprioidea) attack ants at different life stages, including brood (**Table 1**) (reviewed in Lachaud and Pérez-Lachaud, 2012). Host-finding strategies vary where some wasps pursue host workers and others seek the host nest, both using host-derived chemicals. Below we present cases where the natural history of the parasitoids suggests that chemical eavesdropping plays an important role in host localization.

Orasema wasps (Hymenoptera: Chalcidoidea: Eucharitidae)

The pantropical wasp genus *Orasema* includes many species that are specialist parasitoids of Myrmicine ants (Heraty, 1994; Murray et al., 2013; Torréns, 2013). They are important natural enemies of ant colonies and specifically attack brood. The cues that guide female *Orasema* wasps to certain plants within their host ant territories currently are unknown (Torréns, 2013), but plant-derived volatiles likely attract the gravid female wasps, as is the case in other parasitoid systems (e.g., Wei et al., 2007). Once the wasps locate their host habitat (**Figure 1A**, top panel) they lay their eggs on specific plant structures (e.g., extrafloral nectaries or leaves) (**Box 3A**) (Heraty, 1994; Carey et al., 2012; Herreid and Heraty, 2017). The active wasp larva is then picked up by, or attaches itself to a host ant forager, suggesting that the wasp larva eavesdrops on CHCs or other host recognition pheromones (**Figures 1B,C**, top panel). While the ectoparasitic larva feeds (**Box 3B**) (Das, 1963), nurse ants tend the parasitoid brood, which are chemically similar to host brood and remain undetected (Vander Meer et al., 1989).

Orasema wasps can be locally common in some regions of South America, with as many as half the fire ant colonies being affected (Varone et al., 2010). Field observations indicate that wasps parasitizing fire ants are often attacked and killed by workers upon emergence (Varone and Briano, 2009). In contrast, other wasp species that attack the brood of *Ectatomma* ants are carried outside the nest by the *Ectatomma* workers and dropped, apparently unharmed (Pérez-Lachaud et al., 2015). *Orasema* and other members of the species-rich wasp family Eucharitidae parasitize multiple ant subfamilies where the phylogenetic relationships within the genera are well understood (e.g., *Ectatomma, Camponotus*, *Solenopsis*) (Shoemaker et al., 2006; Clouse et al., 2015; Nettel-Hernanz et al., 2015). These lineages would be ideal for examining parasitoid-host coevolution or associate richness in the context of eavesdropping of chemical signals (see section Future Perspectives).



Taxonomic classification of host
  Solenopsis fire ants (Formicidae: Myrmicinae: Solenopsidini)
Importance (*Solenopsis invicta*)
  Global invasive pest causing broad socioeconomic damage
Natural history traits (*Solenopsis invicta*)
  Latitude
  Cosmopolitan, invasive across subtropical and tropical regions
  Host nest
    Size (>250,000 workers in largest mounds of 18 cm high)
    Structural complexity (diffuse nests made of soft soil, allowing for rapid vertical migration)
    Location (underground)
    Longevity (Several months to >5 years)
  Trail system
  Extensive underground foraging tunnels, often seen in the open for short distances
  Species richness or lineage
  196 valid *Solenopsis* species (20 fire ants)
  Susceptible communication systems
    Trail (no, mainly underground foragers, Z,E-α-farnesene)
    Defense (yes, aggressive defensive behavior, mandibular alarm pheromones such as 2,5-Dimethyl-3-ethylpyrazine, piperidine venom, both known attractants for phorid flies)
    Queen, worker, and brood chemical cues (yes, caste-specific cuticular hydrocarbons likely used by parasitoids)
Known enemies and associates (*Solenopsis* fire ants)
  Social parasites
    Inquiline ants (Hymenoptera: Formicidae)
  Parasitoids
    Scuttle flies (Diptera: Phoridae)
    Diapriid wasps (Hymenoptera: Diaprioidea: Diapriidae)
    Eucharitid wasps (Hymenoptera: Eucharitidae)
    Strepsipterans (Strepsiptera: Myrmecolacidae)
  Cleptoparasites
    Silverfish (Zygentoma: Nicoletiidae)
  Myrmecophiles [partial list, see Tschinkel (2006)]
    (Diptera: Phoridae); (Diptera: Syrphidae); (Hymenoptera: Diaprioidea: Diapriidae); (Coleoptera: Tenebrionidae)

Key references: (AntWeb 09/09/2019; Ali and Morgan, 1990; Ascunce et al., 2011; Briano et al., 2012; Collins and Markin, 1971; Cushing, 2012; Jouvenaz, 1983; Moser and Blomquist, 2011; Oi et al., 2015; Pitts et al., 2018; Tschinkel, 2006; Vander Meer, 1983; Vogt et al., 2008)

BOX 3 | Continued

BOX 3 | *Solenopsis* fire ants and generalized natural history of the associates. Often foraging underground, fire ants use Z,E-α-Farnesene trail pheromones produced in their Dufour's gland for recruitment and orientation (Suckling et al., 2010). *Solenopsis invicta* dominate habitats by recruiting nestmates with mandibular gland alarm pheromones (e.g., 2-ethyl-3,6-dimethylpyrazine) (Vander Meer et al., 2010) while also using toxic piperidene alkaloid venom against prey and competitors (Greenberg et al., 2008; Lai et al., 2010; Fox et al., 2019). In contrast, to these volatile defense pheromones, cuticular hydrocarbon-based nestmate and species recognition pheromones, primarily function in short-range communication (Leonhardt et al., 2016). **(A)** Eucharitid wasps, specialized parasitoids of ants, lay eggs in or on plant tissue. A 1st instar larvae attaches itself to a foraging ant then is carried back to the nest. **(B)** Once inside, the Eucharitid wasp larva locates, and then feeds on host brood (pupa pictured). **(C)** Inquiline social parasite queen *Solenopsis daguerrei* discovers a host nest, enters, and then attaches itself to the host queen. She will only produce sexual offspring, eventually killing the host colony. Illustrations by Rozlyn E. Haley adapted from photographs by Alex Wild.

Diapriid wasps (Hymenoptera: Diaprioidea: Diapriidae)

The family Diapriidae has an estimated 4,000 species in three subfamilies (Ambositrinae, Belytinae, and Diapriinae) (reviewed in Lachaud and Pérez-Lachaud, 2012). The latter two lineages contain parasitoids of ant species; however, much of their natural history is unknown. Still, morphological adaptations such as winglessness and body sculpturing suggest host specificity and mimicry (Masner and García, 2002). Many species appear to be nocturnal, but those that attack army ants and fungus-growing ants attempt to enter host nests during the day (Masner and García, 2002; Fernández-Marín et al., 2006). Gravid females are challenged with the task of finding their host habitat (**Figure 1A**, bottom panel), then locating and invading the host colony which they presumably accomplish via species-specific nest marking cues (**Figures 1B,C**, bottom panel). They also must distinguish larvae from pupae during oviposition within the dark nest (**Figure 1C**, bottom panel). The young wasps develop amidst ant brood and emerge from the nest as adults seemingly unharmed by the resident ants.

Observations of host and parasitoid diapriid wasps (Hymenoptera: Diaprioidea: Diapriidae) are mainly descriptive accounts of parasitism (Loiácono et al., 2000; Fernández-Marín et al., 2006; Ramos-Lacau et al., 2007; Pérez-Ortega et al., 2010). Still, there are many reports of diapriid wasps associated with the nomadic columns of army ants (Loiácono et al., 2013a), most of which are in the tribe Diapriini; however, they are rarely collected because of their diminutive size. Several diapriids that associate with ants may actually exploit myrmecophiles and not the ants (e.g., dipterans Masner, 1977), thus the mere presence of these wasps in and around a nest is not definitive evidence for ant parasitism.

Diapriid wasp species from multiple genera (e.g., *Acanthopria, Szelenyiopria, Mimopriella, Oxypria*) associate with fungus-growing ant species (Hymenoptera: Formicidae: Myrmicinae: Attini: Attina) (Loiácono et al., 2000, 2013a,b; Fernández-Marín et al., 2006; Pérez-Ortega et al., 2010). In one study, 14 *Cyphomyrmex rimosus* colonies were artificially disturbed and forced to relocate their nests (Fernández-Marín et al., 2006). Males and females of *Acanthopria* wasps were reported to remain close to disturbed ants and brood but no mechanism to explain this close proximity was suggested. If nest disturbance attracts the wasps or induces the emergence of adults, then these individuals could be collected and used in trials with host ant pheromones to test for eavesdropping. The alarm pheromone, 1-octen-3-ol, produced by *Cyphomyrmex rimosus* and *Trachymyrmex cornetzi* (Norman et al., 2017; Hamilton et al., 2018) may be a good compound to explore first. Additionally, the chemical ecology of fungus-growing attine ants has recently expanded (Hogan et al., 2017; Norman et al., 2017; Hamilton et al., 2018) and the phylogenetic relationships within the Attina subtribe are well understood (Branstetter et al., 2017), therefore this lineage of host ants offers great experimental potential for the identification of parasitoid attractants.

Syrphid flies (Diptera: Syrphidae: Microdontinae)

Approximately 20% of all flies are parasitoids (Feener and Brown, 1997). The family Syrphidae (i.e., hoverflies, flower flies) contains ca. 6,000 species globally (Pérez-Lachaud et al., 2014), and includes many important pollinators, parasitoids, and predators (**Table 1**). The syrphid *Hypselosyrphus trigonus* is a neotropical parasitoid that resembles a stingless bee and attacks ponerine ants (e.g., *Neoponera villosa*) (Pérez-Lachaud et al., 2014; Pérez-Lachaud and Lachaud, 2017). Apparently, this is the first parasitoid fly known to attack the brood of ants (Pérez-Lachaud et al., 2014). The gravid female—much like diapriid wasps—seeks host habitat (**Figure 1A**, bottom panel), and then likely uses species-specific host cues to locate and enter the host nest (**Figures 1B,C**, bottom panel). Finally, they are challenged to determine the location of the brood in the nest and oviposit on prepupae (**Figure 1C**, bottom panel) (Pérez-Lachaud et al., 2014). While other microdontine syrphids are known ant brood predators (see below) (Elmes et al., 1999), this case of parasitism is remarkable given that *Hypselosyrphus* females must safely enter the ant colony, presumably undetected. Eavesdropping by these flies is so far untested.

Predators of Both Workers and Brood

Many predacious invertebrates feed on ant workers and brood, including spiders, caterpillars, beetles, and flies (**Table 1**). Just like the parasitoids, these predatory interactions occur both inside and outside of the nest, and have the potential to be facilitated by chemical eavesdropping. They are challenged with encountering their prey where first they locate habitat (**Figure 1A**) then a worker (**Figure 1B**, top panel) or brood within the nest (**Figure 1B**, bottom panel), depending on which life stage they prey on. Finally, they consume their prey (**Figure 1C**).

Paussus Ant-Nest Beetles (Coleoptera: Carabidae: Paussinae)

The paussines or ant-nest beetles are a large subfamily of nearly 800 species that are facultative and obligate associates that prey on the brood and workers of mainly myrmicine and formicine species (**Table 1**) (reviewed in Geiselhardt et al., 2007). They have characteristic adaptations (e.g., morphology, chemical weaponry, sound production) that indicate a long coevolutionary history with ants (Maurizi et al., 2012) but have also undergone rapid adaptive radiation (Moore and Robertson, 2014). While most ant-beetle interactions are described anecdotally in taxonomic papers, some natural history and experimental evidence indicates that paussines eavesdrop on pyrazine trail pheromones (Ali et al., 1988; Cammaerts et al., 1990). Laboratory experiments using glandular extractions of *Pheidole pallidula* trail pheromones showed that adult *Paussus* (*Edaphopaussus*) *favieri* follow host trails (Cammaerts et al., 1990). While inside the nest, the larvae and adult beetles prey on the host ants (eggs, larvae, adults). It is possible that they detect chemicals that mark different areas of the nest (e.g., brood chamber vs. non-brood chamber) (Heyman et al., 2017) or brood-specific contact pheromones (Walsh and Tschinkel, 1974); however, both hypotheses require experimental verification.

Myrmecophagous Spiders

Many spiders use chemical cues to locate mates and prey (Foelix, 2010; Johnson et al., 2011), and chemical eavesdropping on ants occurs, or is suspected to occur in a variety of cases (**Table 1**). The clearest example is the spider *Habronestes bradleyi*, which locates workers of its preferred prey, *Iridomyrmex purpureus* ants, by eavesdropping on their alarm pheromones (**Table 3**) (Allan et al., 1996). Specifically, Allan et al. (1996) experimentally demonstrated that 6-methyl-5-hepten-2-one released by injured or agitated ants is used as a prey location cue by the spider. Although less definitive, several other cases provide circumstantial evidence for chemical eavesdropping on ants by spiders. For example, orb-weaving spiders aggregate near lycaenid butterflies that feed from *Acacia* trees, apparently by detecting pheromones produced by *Acacia*-inhabiting ants (Elgar et al., 2016). In another example, the ant-eating spider *Zodarion rubium* recognizes specific chemical cues produced by glands from formicine ants (Cárdenas et al., 2012). Similarly, prey-seeking behaviors of the ant-eating jumping spider *Habrocestum pulex* are enhanced by exposure to ant chemical cues in soil (Clark et al., 2000). However, in cases where the spiders themselves are vulnerable to predation by ants, ant-derived compounds were shown to elicit habitat avoidance or increased dispersal behavior (Mestre et al., 2014; Penfold et al., 2017).

Syrphid Flies (Diptera: Syrphidae: Microdontinae)

The nearly 350 species of *Microdon* syrphid flies are known only from social insect nests (**Table 1**) (Wheeler, 1908). The gravid females of the myrmecophilous species locate the habitat and seek their host's nest to deposit eggs in or on the nest structure, presumably eavesdropping on species-specific chemicals such as nest-marking pheromones (**Figures 1A–C**, bottom panel) (Akre et al., 1988). The oddly flattened larvae complete the host acceptance phase when they migrate into the nest (infiltration and integration), then to the brood chambers to consume larvae and pupae (Garnett et al., 1985). *Microdon piperi* larvae live inside the nest of *Camponotus modor*, where they feed on host brood. Adults of this species are attracted to excited host workers spraying formic acid alarm pheromones (Akre et al., 1988), suggesting that males and females may use host pheromones to find nests and potential mates, but this was not experimentally determined. *Microdon mutabilis* specifically attacks the larvae of the alpine ant *Formica lemani* (Elmes et al., 1999). Females of *M. mutabilis* extend their ovipositor when exposed to volatile odors from *F. lemani* colonies, suggesting that they use host-derived pheromones to locate the host nest before laying their eggs. The active compound was experimentally demonstrated to be methyl-6-methylsalicylate from the ants' head extract (**Table 3**) (Schönrogge et al., 2008). This compound occurs in pheromones of various ants [e.g. *Camponotus* (Torres et al., 2001); *Tetramorium* (Morgan et al., 1990)], and therefore should be used in additional studies to determine eavesdropping in other systems.

Lycaenid Caterpillars (Lepidoptera: Lycaenidae)

Of the estimated 6,000 species of lycaenid butterflies, over 600 species (10 genera) associate symbiotically with ants, but the total number of myrmecophilous species is presumed to be much larger (reviewed in Pierce et al., 2002). These include a number of obligate parasitic or mutualist ant associates, and at least 10 species feed on brood inside ant nests (**Table 1**) (Pierce et al., 2002). Even where not strictly myrmecophilous, lycaenid associates display adaptations (both as caterpillars and adults) that protect them from ant aggression (Pierce et al., 2002), suggesting a long coevolutionary history between Lycaenidae and the Formicidae. Some myrmecophilous lycaenids eavesdrop on host trail pheromones (Dejean and Beugnon, 1996). The lycaenid caterpillars *Euliphyra mirifica* and *E. leucyana* for instance live inside the ant nest of *Oecophylla longinoda* and follow their trail pheromones (Dejean and Beugnon, 1996). In contrast to other lycaenid species, these are commensals and do not impose a significant fitness cost to the ants. Similar chemical eavesdropping by other lycaenid species is likely but in the context of predation (e.g., *Liphyra brassolis*) (Dodd, 1912) and warrants more research.

Resource Exploitation by Cleptoparasites, Social Parasites, and Myrmecophiles

Many ant species use chemical trails to recruit nestmates to food resources (Hölldobler and Wilson, 1990). While host ant colonies must rely on these trail systems, other organisms use them as highways to ambush foragers or to find and invade host nests (**Table 1**). The marked diversity of trail following eavesdroppers (e.g., roaches, caterpillars, and ant species) illustrates the risk associated with ant chemical communication. Direct observations of trail following myrmecophiles and cleptoparasites are plentiful (**Table 2**) but there is a noticeable gap in evidence demonstrating trail following in other types of parasites. Furthermore, the chemical composition of trail pheromones has been determined for many species, but the specific components are often difficult to synthesize (reviewed in Morgan, 2008, 2009). Thus experimental studies commonly rely on glandular extractions to demonstrate eavesdropping (note, despite our literature review, we could not find studies that directly test specific trail pheromone compounds and therefore none could be included in **Table 3**).

Trail Following Cleptoparasites

Long-lasting trail systems present an apparent vulnerability in host ant colony defense (**Tables 1**, **2**). A comprehensive list of the cleptoparasites of ants (i.e., parasites that steal food from their hosts inside or outside the nest) is beyond the scope of this review; however, we present a few examples backed with experimental evidence for trail-following as a host-association mechanism. The natural history of cleptoparasites is partly determined by the location of host food sources, including (1) colony nest stores; (2) from workers via trophallaxis (i.e., mutual exchange of regurgitated liquids); and (3) at food sources or trails outside the nest. Cleptoparasites stealing food from inside the host ant nest are faced with the challenge of habitat and nest location (**Figures 1A,B**, bottom panel). By contrast, those stealing food from outside the nest must locate the habitat and intercept the host ants on trails to gather resources (**Figures 1A,B**, top panel). Regardless, eavesdropping cleptoparasites illustrate how the structure of social insect colonies (i.e., fixed nest location and central-point foraging) provide variable access to resources that potentially influences parasite community structure.

Cockroaches (Blattaria: Polyphagidae)

An emblematic example of a trail-following nest associate is provided by cockroaches living with leaf-cutting ants (**Table 1**). At least six species of *Attaphila* (Blattaria: Polyphagidae) cockroaches live in *Atta* and *Acromyrmex* nests (Rodríguez et al., 2013). These cockroaches are small (ca. 3.5 mm) and wingless with reduced sensory and glandular systems (**Box 1D**) (Brossut, 1976; Wheeler, 1900). They live in the ants' fungus garden, where they graze (Wheeler, 1900; Phillips et al., 2017) and acquire nest-specific cuticular hydrocarbon signatures (Nehring et al., 2016) while behaving as cleptoparasites (**Table 1**). *Attaphila* climb onto virgin *Atta* queens just before they leave the nest, and remain attached until they are brought into the new host nest. This suggests that the roaches can differentiate between castes, and may use queen-specific pheromones (Dietemann et al., 2003). Phillips et al. (2017) suggested that the young cockroaches use host queens for dispersal and habitat location (**Figure 1A**, bottom panel) but can also move to more established nests by following *Atta* trails (**Figure 1B**, bottom panel) (Moser, 1964). *Atta texana* use methyl 4-methylpyrrole-2-carboxylate as their volatile trail pheromone (Tumlinson et al., 1972), but the concentration and exact trail components used by these cleptoparasites and other *Atta* myrmecophiles (**Box 1**) (Waller and Moser, 1990) deserve further exploration.

Ants (Hymenoptera: Formicidae)

Some cleptoparasite ants eavesdrop on trail pheromones of other ant species to access food (**Tables 1**, **2**) (Gobin et al., 1998; Powell et al., 2014). Such trail parasitism is best known among arboreal species, and is not limited to closely related or parabiotic (i.e., nest sharing) species (**Table 2**). For example, some *Cephalotes* and *Camponotus* species are conspicuous trail parasites of *Azteca* (**Box 2B**) (Wilson, 1965; Adams, 1990). Specifically, *Cephalotes maculatus* follows *Azteca* trail pheromones and coexists undetected at food resources with *Azteca* workers (Adams, 1990, 2016). Data from multiple surveys of >150 trees in Panama showed that *Azteca trigona* co-occurs more frequently with *Cephalotes maculatus* than expected by chance (Adams et al., 2017). A similar phenomenon was shown between the highly aggressive *Crematogaster ampla* host and the comparably demure *Cephalotes specularis* trail parasite (Powell et al., 2014). While the host actively defends foraging territories, the trail parasite eavesdrops on the host's trail pheromones, locates, and then exploits the food resources. A remarkable 89% of the host territories contained the parasites, and host ants showed no aggression toward them. Trail pheromone eavesdropping behavior clearly is widespread in ants (**Table 2**), and hosts and parasites often belong to different ant subfamilies.

Trail Following Social Parasites (Hymenoptera: Formicidae)

Social parasitism has evolved independently numerous times among the Formicidae (Buschinger, 2009). While there are many types of social parasites (e.g., inquilines, slave-makers, thief ants, guest ants) they are faced with the same challenges. They must locate the habitat and nest of their host (**Figures 1A,B**, bottom panel), infiltrate the colony (**Figure 1C**, bottom panel), and extract colony resources (e.g., food and brood) (**Figures 1C–E**, bottom panel). Unfortunately, host nest searching behavior is infrequently observed in social parasites. *Mycocepurus castrator* inquiline parasites experimentally placed near a host nest quickly entered the nest signifying that they are able to sense their host (Rabeling and Bacci, 2010). Dulotic slave-making species and *Megalomyrmex* agro-predator raiders also find host colonies as young queens or later as scout workers (Boudinot et al., 2013; Ruano et al., 2013). This suggests they are using host-derived chemical cues to find the host nest and brood (**Table 1**). Trail pheromones and nest-marking pheromones with low volatility are found around host nesting areas (Hölldobler and Wilson, 1986; Cammaerts and Cammaerts, 1998; Steck, 2012) and likely play an important role in the host-finding of many ant associates (**Table 1**), not only cleptoparasites (**Table 2**). Eavesdropping on host-derived signals may be most effective when used in concert with nest searching behavior. For example, *Gnamptogenys hartmanni,* which are social parasites of *Trachymyrmex* and *Sericomyrmex* fungus-growing species, will search small holes near host nests (Dijkstra and Boomsma, 2003). Nest-searching behavior by scout ants coupled with the detection of host-derived trail and nest-marking pheromones likely work synergistically for host nest invasion. Finally, dulotic slave-maker parasites have evolved independently at least 10 times (reviewed in D'Ettorre and Heinze, 2001). A comparative study examining eavesdropping across lineages would offer great insight into which host traits leave host ants vulnerable to colony invasion.

Like slave-makers and agro-predators, socially parasitic inquiline queens also seek and invade host nests alone. *Pogonomyrmex colei*, an inquiline of *Pogonomyrmex rugosus*, finds its host colony by following host trunk trails with or without host workers, suggesting eavesdropping on host trail pheromones (Johnson et al., 1996). Another inquiline is the well-studied *Solenopsis daguerrei*, which lacks a worker caste. Young queens invade a fire ant colony and firmly attach to the functional host queen (**Box 3C**) (Calcaterra and Briano, 1999). The parasites lay eggs that are intermingled with eggs from the host queen and are reared by host workers, ultimately resulting in the production of parasitic males and females. This intimate and intricate association presumably involves eavesdropping at different levels. While host nest mounds (**Box 3**) and other environmental cues may aid in habitat location, trail or alarm pheromones may attract the host-seeking parasite queen. She likely locates the queen within the nest by eavesdropping on queen-specific pheromones as this level of recognition is essential for her success. *Solenopsis daguerrei* can parasitize a number of fire ant species that are chemically distinct (Fox, 2018) suggesting that ant chemical mechanisms for invasion are not species-specific. This also implies the "encounter phase" (**Figures 1A-C**, bottom panel) may involve host cues (e.g., nest-marking, trail, and alarm pheromones) that are shared among host species. As it stands, the chemical mechanisms for this intricate symbiosis warrants further studies but the known natural history points to eavesdropping as an essential component of social parasite success.

Trail Following Myrmecophiles

While myrmecophiles associate with countless ant lineages, the army ants likely host the most species that are currently known (Rettenmeyer et al., 2011). Indeed, the vast array of ant associates makes their functional classification exceptionally difficult (Gotwald, 1995). Here, we use "myrmecophile" in cases where the nature of the association is not well defined or is deemed commensal, but fundamentally involves any organism that lives at least part of its life associated with ants (see **Table 1**).

Trail-following army ant associates are easily observed in the field, thus contributing to the large list of taxa in this category (**Table 1**). However, identifying species remains a significant challenge (von Beeren et al., 2018). Many associates specifically follow ant trails, and some myrmecophiles are more sensitive to trail pheromones than are the ants (Akre and Rettenmeyer, 1968). All of the ca. 30 known species of *Vatesus* beetles (Staphylinidae: Tachyporinae) are army ant associates (von Beeren et al., 2016) whose adults and larvae follow ant trails (Akre and Rettenmeyer, 1968; Akre and Torgerson, 1969). While the nature of the association is often unknown, some beetles consume army ant booty (i.e., cleptoparasites) and dead army ant brood (i.e., commensals) (Akre and Torgerson, 1969).

Tiny myrmecophilous crickets are wingless ant symbionts comprising some 60 described species that span the temperate and tropical regions of the world (Kistner, 1982). These cricket species associate with ant species in multiple genera (e.g., *Atta, Formica, Pogonomyrmex*) (Wheeler, 1900; Waller and Moser, 1990). Some crickets are known to be egg predators or cleptoparasites, where they either disrupt food exchange between ants, or are directly fed (Henderson and Akre, 1986). In most cases, the natural history of the crickets is unknown, thus they are simply categorized as myrmecophiles. Host specificity differs where some species are ant generalists and others have traits that suggest a long coevolutionary history with their host (e.g., trail following, chemical integration strategy) (Wheeler, 1900; Akino et al., 1996; Wetterer and Hugel, 2008; Komatsu et al., 2013). *Myrmecophila manni* (Orthoptera: Gryllidae) live with *Formica obscuripes*, the western thatch ant, and follow their host trails after colony migration to a new nest, suggesting eavesdropping on trail pheromones (Henderson and Akre, 1986). However, the host-finding mechanisms used during the encounter phase (**Figures 1A–D**) of most ant-associated crickets is unknown, and the generality of trail following is in need of further study.

CONCLUSION

Successful antagonistic interactions are initiated by host-finding mechanisms that lead to efficient exploitation tactics. We have illustrated a parasitological framework to summarize the necessary encounter and exploitation phases used by ant enemies and other associates (Combes, 2005). We move beyond the initial stage of habitat location to focus on the stages where eavesdropping on host-derived pheromones is most likely to occur (**Figures 1B,C**). We distinguish between associates that attack individual ants outside the nest (e.g., phorid flies) and those that breach the protected fortress to reach ant colony resources (food, brood, workers, queen) (e.g., social parasites). Regardless of the initial target (individual or nest), associates locate their host using either long- or short-range chemical cues (**Figure 1**). We found that nine out of 10 different organism types (i.e., beetle, fly, spider, wasp, cockroach, butterfly, ant, silverfish, and cricket) may follow their host's trail pheromones (**Table 1**). These include parasitoids, predators, and parasites (i.e., social parasites and cleptobionts), although more experimental work is needed to support this hypothesis. However, a number of cleptoparasite ant species have been shown to be "trail parasites" that tend to nest in the forest canopy (**Table 2**).

Another form of chemical communication dispersed by host ants is alarm pheromones. The volatile nature of alarm pheromones may contribute to the fact that most of the putative eavesdropping associates are flying insects (**Table 1**), likely detecting the compounds in air currents. Interestingly, alarm/defensive pheromones were the only experimentally determined compounds used by eavesdropping associates (**Table 3**). We also found that a single species may eavesdrop on multiple pheromones emitted by their host. For example, they may initially follow trail pheromones, then use recognition pheromones and contextual cues to locate the queen, workers, or brood (see **Boxes 1B**, **3C**). We conclude that although there is extreme diversity in the organisms that exploit ants (25 families or arthropods in 10 orders; **Table 1**), the stages of successful exploitation (**Figure 1**) and host-finding mechanisms are shared among many.

The extensive natural history of host ant species and their associated parasitoids, predators, parasites, and myrmecophiles provides the needed groundwork for hypothesis-driven studies on chemical eavesdropping. The frequency and abundance of ant associates varies among host lineages, perhaps due to heritable traits that make some species more prone to eavesdroppers than others. More research is needed to identify these traits, and the specific compounds that natural enemies exploit. Determination of the key compounds, and their physiological and behavioral effects, will provide a foundation for comparative studies (e.g., Ngumbi and Fadamiro, 2015). Such studies will clarify the evolutionary trajectories of specific compounds (Norman et al., 2017; Brückner et al., 2018; Hamilton et al., 2018) and improve our understanding of their perception by ant associates. Finally, an evolutionary approach to ant chemistry and eavesdropping will provide a basis for understanding how eavesdroppers and other ant associates, can shape the evolution of pheromone profiles.

Future Perspectives

Are Eavesdropping Coinfection Rates (i.e., Associate Richness) Due to Predictable Host Traits?

Chemical communication structures communities in part by mediating species interactions. Ants are key components of most terrestrial ecosystems (Gao et al., 2016) and a tractable model for exploring the details of chemical communication systems. This review revealed that we know relatively little about the basics of eavesdropping on ant pheromones, and far less about its broader ecological consequences. We propose that ant-specific traits, including their communication systems, influence their susceptibility to eavesdropping associates. Inspired by parasitological theory (Combes, 2001, 2005; Poulin, 2007), below we outline some testable hypotheses that have the potential to advance this field. We encourage an integrative approach applied to multiple host-associate systems to account for confounding variables, and we identify lineages where comparative research is likely to be especially fruitful. We expect that DNA barcoding (Baker et al., 2016) and network-based approaches will facilitate more sophisticated studies, enhancing the understanding of the ecological impact of these associations (reviewed in Ivens et al., 2016).

We suggest that the traits of some ant species will determine their susceptibility to diverse associates including parasitoids, cleptoparasites, social parasites, myrmecophiles, and some predators (**Table 1**). We tailored our trait-linked hypotheses to address associate richness in the context of host-seeking strategies that involve eavesdropping on ant chemical communication.

Latitudinal gradient

Associate diversity varies with latitude. Given that ant species richness increases from the poles to the tropics (Willig et al., 2003; Economo et al., 2018), the potential for symbiotic interactions should also increase. Few studies have addressed this hypothesis in non-ant hosts (e.g., Salkeld et al., 2008; Torchin et al., 2015); to our knowledge, no one has investigated this pattern in ants despite prevalent lists of ant-nest associates (Hölldobler and Wilson, 1990; Waller and Moser, 1990; Schmid-Hempel, 1998; Navarrete-Heredia, 2001; Rettenmeyer et al., 2011; Briano et al., 2012). Studies involving host species that span broad latitudinal gradients would be ideal. Alternatively, comparative studies of host lineages that contain species with similar natural history traits may also prove useful. *Key prediction*: Per-host associate richness is relatively higher in tropical regions.

Diverse microhabitats

Associate diversity is affected by the structural complexity of the host nest. Ant nests are compartmentalized into different chambers containing the queen, brood, workers, food, and detritus. For example, leaf-cutter ants have four kinds of nest chambers (empty, garden filled, dirt/sand filled, and detritus filled chambers) (Moser, 2006; Forti et al., 2017) whereas other species may have 3-4 (entrance, queen, worker with brood, worker without brood) (Heyman et al., 2017), providing vastly different microhabitats. Ants often maintain unique chemical signatures in different chambers, providing spatiotemporal guidance for workers (Heyman et al., 2017). It seems likely that nest associates use these chemical cues to differentiate among regions of the complex nest structure. Refinement of associate niche axes based on subtle but consistent differences in chemistry within an ant nest presumably leads to increased associate richness. To test this hypothesis, ant associate abundance can be evaluated in comparative studies where similar species vary in nest complexity (single chamber e.g., *Acromyrmex* vs. complex nests e.g., *Atta*). *Key prediction*: As host nest structure increases, associate species richness increases.

Long-lived large colonies/gregariousness

Ant associates have more opportunities to detect alarm, nest, and trail pheromones from large, long-lived ant colonies. Eusocial insects, specifically queens, have increased longevity compared to solitary insects (Keller and Genoud, 1997) where some live up to 30 years (**Boxes 1**, **2**) (Hölldobler and Wilson, 1990). These large old colonies can therefore accumulate numerous associates, as they provide resources and homeostatic conditions (Hughes et al., 2008). Territoriality behavior is often expressed in workers of large colony species, and disputes with competing hetero- and conspecifics are frequent (Adams, 2016). While conflicts may cause the ants to emit alarm pheromones, nest- and trail-marking pheromones allow species to partition rival nests in space; together these pheromones leave large, persistent colonies vulnerable to nest-seeking associates that can eavesdrop on these chemical cues (Orr et al., 2003). To test this hypothesis, ant associate abundance can be compared in young vs. old or large vs. small colonies. *Key prediction*: As host colony size and age increases, associate species richness increases.

Nest migration/extensive trail systems

Species with frequent nest migration are more likely to be discovered by ant associates. Army ants are constantly laying trail pheromones (Oldham et al., 1994), and excrete volatile alarm substances when in conflict (Brückner et al., 2018). They do not construct permanent nests, but instead have statary (i.e., stationary) and nomadic phases (Gotwald, 1995). Regardless, if workers are leaving the bivouac to conduct daily raids or the colony is migrating at night, trail and alarm pheromones may enhance their vulnerability to new associates. *Eciton* army ants and leaf-cutter *Atta* species are known for their large colony sizes and numerous and diverse nest associates; however, unlike army ants, *Atta* colonies are stationary and maintain the same trail systems for years (**Box 1**) (Kost et al., 2005). Future studies comparing *Atta* and *Eciton* could test if repeated nest migrations or widespread trail systems are responsible for their susceptibility to arthropod associates. *Key prediction*: Life histories that involve frequent nest migration with extensive trail systems have higher associate species richness.

Nesting location

Nesting habit influences the conspicuousness of ant colonies and their corresponding communication channels. Underground: Many ant species nest underground where communication systems are buffered by soil, thereby limiting associate encounter rate. Leaf litter: The physical structure of leaf litter changes almost daily and is three-dimensionally complex at small spatial scales (Yanoviak and Kaspari, 2000). Thus, ant pheromone trails are less reliable, short-lived and presumably harder to follow. However, the transitory nature of the substrate causes species to frequently move nest locations (also see Kaspari, 1996), which can expose them to opportunistic parasites [e.g., phorids attacking brood (Brown et al., 2017)]. Arboreal: Some arboreal species construct single or multiple visually conspicuous nests in trees (e.g., Wheeler, 1986; Adams and Longino, 2007). These ant species lay trails on vines, branches, and trunks that are exploited by cleptoparasite caterpillars (Dejean and Beugnon, 1996) and ants (**Box 2** and **Table 2**) (Powell et al., 2014). It is probable that the location of trail systems determines the likelihood that they are exploited by eavesdroppers. For example, an underground trail system presumably is less likely to be detected by potential associates than an exposed arboreal trail system. Future studies contrasting closely related species with different trail strategies (e.g., arboreal versus leaflitter dwelling *Cyphomyrmex* species) (Weber, 1941; Adams and Longino, 2007) would be ideal to test this hypothesis. *Key prediction*: Associate species richness correlates with nest type and location.

Extant species-rich host lineage

The potential for host switching increases if the host lineage has many species with similar pheromones (e.g., alarm, trail pheromones, etc.) (Blum and Brand, 1972). While work centered on host ant preference by various associates is important foundational research [e.g., Eucharitidae wasps (Murray et al., 2013); *Paussus* ant-nest beetles (Moore and Robertson, 2014); phorid flies (Mathis and Philpott, 2012; Chen and Fadamiro, 2018); social parasites (Lenoir et al., 2001; Buschinger, 2009)], this hypothesis shifts the focus to the associate community where network-based analyses will prove useful (Ivens et al., 2016). In order to investigate this hypothesis, we must begin with host lineages having (1) a well-resolved phylogeny, (2) a well-studied communication system, and (3) numerous known associates. Although a daunting task, research programs focusing on ant lineages that contain pest species (e.g., *Solenopsis*, *Atta*) would be most promising. *Key prediction*: Associate richness is higher in host lineages with many closely related extant species.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to this work. RA originally drafted the Introduction, fungus-growing ant sections, Conclusion, and Future Perspectives. EF originally drafted the *Solenopsis* section. SY, RW, and CF originally drafted the *Azteca* section. EF, RW, and RA assembled the tables. RA designed the figures. All authors finalized the text in all sections.

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REVIEW
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Predation and Crypsis in the Evolution of Electric Signaling in Weakly Electric Fishes

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Eavesdropping by electroreceptive predators poses a conflict for weakly electric fish, which depend on their Electric Organ Discharge (EOD) signals both for navigation and communication in the dark. The EODs that allow weakly electric fish to electrolocate and communicate in the dark may attract electroreceptive predators such as catfishes and Electric Eels. These predators share with their prey the synapomorphy of passive electric sense supported by ampullary electroreceptors that are highly sensitive to low-frequency electric fields. Any low-frequency spectral components of the EOD make weakly electric fish conspicuous and vulnerable to attack from electroreceptive predators. Accordingly, most weakly electric fish shift spectral energy upwards or cloak low-frequency energy with compensatory masking signals. Subadults and females in particular emit virtually no low-frequency energy in their EODs, whereas courting males include a significant low-frequency component, which likely attracts females, but makes the signals conspicuous to predators. Males of species that coexist with the most predators tend to produce the least low-frequency signal energy, expressing sexual dimorphism in their signals in less risky ways. In these respects, electric signals follow the classic responses to opposing forces of natural and sexual selection, as exemplified in the visual signals of guppies and the acoustic signals of Túngara frogs. Unique to electric fish is that the electric signal modifications that help elude detection by electroreceptive predators are additions to the basal signal rather than losses of attractive components. These enhancements that enable crypsis are energetically costly, but have also provided the evolutionary substrates for subsequent sexual selection and species identity characters.

Keywords: catfish, electroreception, Gymnotiformes, Mormyridae, predation, sensory drive, signal diversity

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INTRODUCTION

Reproductive signals may be subject to balancing selection wherein sexual selection favors extravagant signals, while natural selection by predators provides a moderating counterforce (Maan and Seehausen, 2011). Researchers have documented a catalog of mechanisms by which animals reduce the problem of hostile eavesdroppers. Among these, shifting signal modes or signal frequencies are the most common ways to evade eavesdroppers of mate attraction signals. Hostile eavesdropping by predators has been speculated to lead to evolutionary arms races, wherein the signaler shifts its signal frequency out of the sensory range of the predator, and the predator falls under selection to shift its sensory range to continue detecting its prey (Verrell, 1991; Zuk and Kolluru, 1998). Such pressures can become extreme; unable to win a sensory arms race against parasitoid flies which locate field crickets by sound (Cade, 1975; Robert et al., 1992; Adamo et al., 1995), crickets in Hawaii evolved defective wing combs that render them totally silent in areas where the flies are common (Zuk et al., 2006).

Electric communication was discovered just over half a century ago (Lissmann, 1958), and is less well-studied than the other sensory modalities. However, electric communication signals appear to parallel the trends found for visual and acoustic signals with regard to the balance between conspicuous and cryptic signal forms. These patterns constitute the classic signature of opposing pressures between sexual selection and predation as forces shaping the signals. This research area remains fertile for discovery. The limited sensory physiology data on electric signals suggests vulnerability of some electric waveforms to predation, but the critical sensory information derives from study of temperate catfish species (rev. Finger, 1986) and are lacking for electrosensory systems of key tropical predators. Females of many extant electric fish species appear less conspicuous to predators than males, but we have no field observations showing preferential predation on males based on their signals. Stomach contents of electroreceptive predatory species sometimes suggests specialization on electric fish, but we do not have data showing that the predation is cued by the electric signals. Many electroreceptive predators have been overfished in their native habitat (Petrere et al., 2004), and their scarcity has made them hard to lure in the field with electric stimuli. Despite the gaps in our collective knowledge, in this paper we lay out the evidence we do have, that signals of electric fish have been, and continue to be, shaped by electroreceptive predators.

Electrogenic fish have evolved repeatedly, including torpedoes, skates, stargazers, gymnotiforms, several independent catfish lineages, and mormyroids (Bennett, 1970, 1971a; Bass, 1986; Hagedorn et al., 1990; Baron, 1994; Baron et al., 1994; Alves-Gomes, 2001). The Gymnotiformes radiated in South America, reaching from Mexico to Argentina (Albert and Crampton, 2005). The unrelated Mormyroidea (Osteoglossiformes) are found across sub-Saharan Africa, with the Mormyridae having radiated particularly broadly in western Africa (Sullivan et al., 2000). The Gymnotiformes and the Mormyroidea make up the weakly electric fishes, with each group counting around 200 species.

Weakly electric fish generate low-voltage electric fields that image the fish's surroundings in darkness (e.g., Engelmann et al., 2008) and allow these animals to communicate over short distances in support of sexually-selected behaviors serving courtship, male competition, and territorial defense (e.g., Henninger et al., 2018). The electric organ discharge (EOD) waveforms of many extant freshwater species have complex, polyphasic voltage waveforms (Hopkins and Heiligenberg, 1978; Hopkins, 1980). These waveforms appear to bear the signatures of historic selection for predator avoidance, mate attraction, and species isolation (Feulner et al., 2008, 2009; Arnegard et al., 2010; Crampton et al., 2011; Waddell et al., 2016). A cogent argument has been made that multiple signal phases reduced or eliminated the low-frequency power in the signals in response to selection by electroreceptive predators, providing the key substrates for subsequent evolution of sexual signaling and species isolation mechanisms (Stoddard, 1999, 2002a).

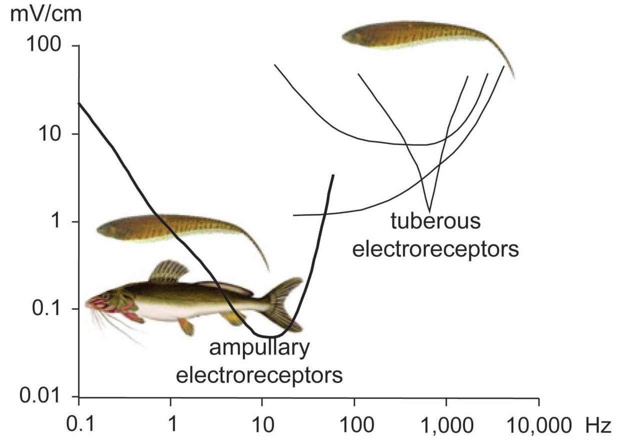

FIGURE 1 | Tuning curves of the two general types of electroreceptors. All electroreceptive fishes have some sort of ampullary electroreceptors, which are extremely sensitive to low-frequency electric fields. Gymnotiform and mormyrid electric fishes have also evolved tuberous electroreceptors which are less sensitive and tuned to higher frequencies to detect the fish's own electric field and electric fields of nearby conspecifics. The ampullary receptor curve was recorded from a *Gymnotus* sp. (Dunning, 1973), and the tuberous receptor curves were recorded from *Brachyhypopomus occidentalis* (Shumway and Zelick, 1988). Adapted from Stoddard (2002a) with permission of the publisher.

ELECTRORECEPTIVE PREDATORS

Although uncommon as a mode of communication, electric fields do not constitute a private channel. Catfishes (order Siluriformes) are the sister group to the gymnotiform electric fishes. Although few catfish produce electric fields, all share electroreceptors by descent, creating the potential (no pun intended) for hostile electroreceptive eavesdropping by the piscivorous catfish species (Kalmijn, 1974). Catfish have radiated widely in the Neotropics and Sub-Saharan Africa, sympatric with the radiations of gymnotiform and mormyroid lineages of weakly electric fishes, respectively (Sullivan et al., 2006; Armbruster, 2011; Day et al., 2013). Although the diets of catfish are diverse, the large piscivorous species are ideally poised to shape the signals of sympatric weakly electric fish (Merron, 1993; Duque and Winemiller, 2003; Petrere et al., 2004).

All electroreceptive fishes express some sort of cutaneous ampullary electroreceptor (Bennett, 1971b; Bullock, 1982; Zakon, 1986). Ampullary electroreceptors of freshwater teleosts are highly sensitive to low-frequency electric fields (rev. Finger, 1986; Peters et al., 2007) ranging from 0 Hz (DC) up to approximately 100 Hz (**Figure 1**; Peters and Buwalda, 1972; Dunning, 1973). These data are derived from temperate catfish

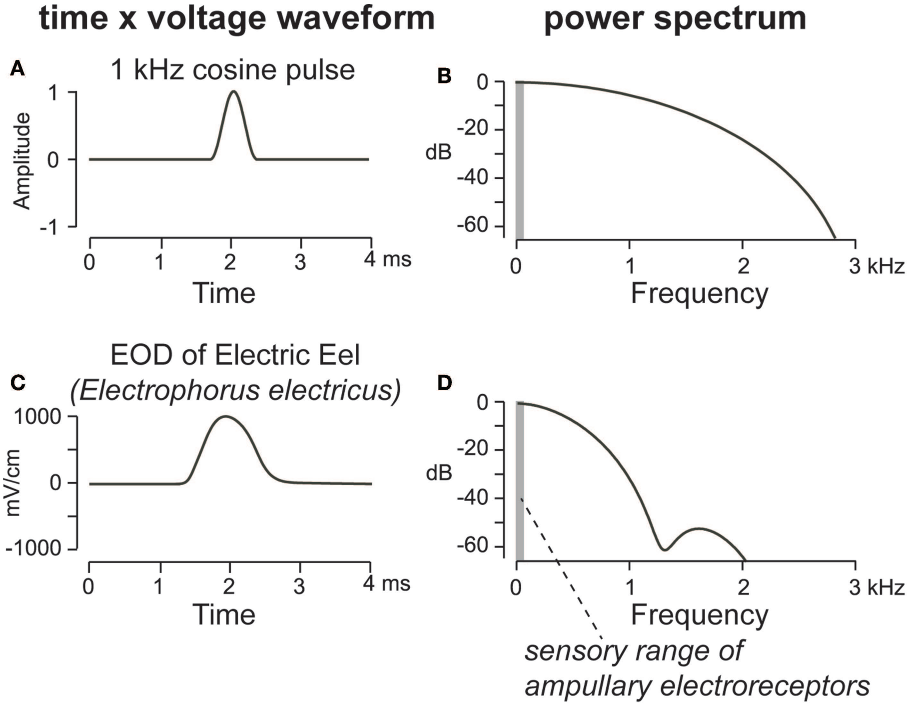

FIGURE 2 | Shown here is a single-period cosine wave **(A)**, its corresponding power spectrum **(B)**, and the monophasic pulse EOD of an Electric Eel **(C)**, the low-voltage signal it produces for electrolocation and communication, with its power spectrum **(D)**. The energy spectrum of a monophasic EOD pulse (**B** or **D**) is dominated by low frequencies in the sensory range of ampullary electroreceptors (vertical gray bar) which should make it readily detectable by electroreceptive predators, including catfish and Electric Eels. Adapted from Stoddard and Markham (2008) with permission of the publisher.

of the genus *Ictalurus,* and a gymnotiform electric fish of the genus *Gymnotus*, neither of which are predators of weakly electric fish. Similarity in the physiological response of their ampullary electroreceptors suggests a general vulnerability of EODs with low-frequency energy to piscivores with ampullary electroreceptors, but physiological studies should be conducted to confirm this assumption; limited anatomical data suggest that catfish that hunt weakly electric fish may have evolved higher frequency electroreception (Andres et al., 1988).

Weakly electric fish have evolved additional classes of tuberous electroreceptors, tuned to the fish's own EOD and used in active electroreception and communication (revs. Hopkins, 1981, 1995). Tuberous electroreceptors respond to higher frequencies than ampullary electroreceptors, albeit with less sensitivity (**Figure 1**; Bennett, 1971b).

The key electroreceptive predators of weakly electric fishes appear to be their sister group Siluriformes, the catfishes. Stomach content analyses reveal that piscivorous catfishes of the Neotropical family Pimelodidae regularly prey upon weakly electric gymnotiforms (Reid, 1983; Duque and Winemiller, 2003; Petrere et al., 2004). The African Sharptooth Catfish, *Clarias gariepinus* has been documented actively hunting mormyrid electric fish (Merron, 1993). The Electric Eel (*Electrophorus electricus*), a strongly electric gymnotiform species, has been observed stalking weakly electric gymnotiforms in the field (Westby, 1988). In the lab, both Sharptooth Catfish and Electric Eels spontaneously attack electrodes playing signals of weakly electric fish, favoring those EODs that contain energy in the spectral range of ampullary electroreceptors (Hanika and Kramer, 1999, 2000; Stoddard, 1999). Stomach contents of Electric Eels collected in the Mamiraua reserve of Brazil included weakly-electric gymnotiforms along with a wide variety of aquatic vertebrates and invertebrates, suggesting no particular specialization on gymnotiform prey (W. Crampton, pers. com.). We conclude that piscivorous catfish are likely the primary electroreceptive predators of weakly electric fish, and that Electric Eels are opportunistic predators.

EOD PROPERTIES AND DETECTABILITY BY PREDATORS

The waveform of the EOD determines its spectral energy content and thus its capacity to attract predators. The simplest EOD waveform is a monophasic pulse, resembling a single-period cosine rising off a zero-volt baseline. The energy spectrum of a single monophasic EOD pulse is dominated by low frequencies (**Figure 2**), which should make it particularly detectable by ampullary electroreceptors and thus attractive to electroreceptive predators. Monophasic pulsed EODs appear to be the ancestral condition in most or all electric fishes, both weak and strong

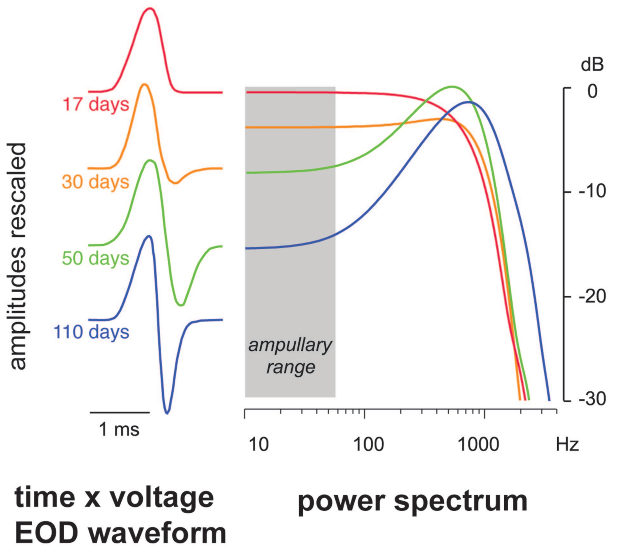

FIGURE 3 | EOD ontogeny of the gymnotiform electric fish *Brachyhypopomus gauderio* (Franchina, 1997). The larval fish's initial EOD is a simple monophasic pulse with abundant energy in the spectral range of the ampullary electroreceptors (gray bar). Over the next 2 months the EOD transforms into a symmetrical biphasic pulse that suppresses the low-frequency spectrum and reduces detectability by ampullary electroreceptors. This transformation should reduce risk of predation from electroreceptive predators. Adapted from Stoddard and Markham (2008) with permission of the publisher.

(Bass, 1986; Kirschbaum, 1995; Alves-Gomes, 2001). Electric signals that have emerged in disparate fish lineages including skates, stargazers, mormyroids, gymnotiforms, and even a few catfishes, first appeared as monophasic pulsed EODs, except for synodontid catfish which make EODs from a modified swim bladder (Bass, 1986; Hagedorn et al., 1990; Baron et al., 1994; Sullivan et al., 2000; Boyle et al., 2014). Larval gymnotiforms and mormyrids produce monophasic EODs, gradually replacing them with polyphasic pulses that shift the frequency upwards as their electric organs mature through development (**Figure 3**; Franchina, 1997; Kirschbaum and Schugardt, 2002; Stoddard, 2002a; Crampton et al., 2011). Monophasic pulsed EODs are rare within the gymnotiform and mormyrid lineages, likely because their low-frequency bias attracts predators. Where monophasic species do occur, monophasy appears to be derived rather than plesiomorphic (Alves-Gomes and Hopkins, 1997; Arnegard et al., 2010; Lovejoy et al., 2010; De Santana and Crampton, 2011; Alda et al., 2013; Crampton et al., 2013, 2016). Evolutionary reemergence of monophasy in weakly electric fish is surprising, given the conspicuousness of monophasic signals to electroreceptive predators. Several monophasic *Gymnotus* species reside in low-predation refugia, and another in anoxic floating meadows not easily penetrated by predatory catfish (Crampton et al., 2013). By contrast, a common monophasic species from the Amazon, *Brachyhypopomus bennetti,* is subject to heavy tail-grazing, but does not change its EOD shape when the tail is damaged, a possible advantage for species discrimination in mixed-species assemblages (Sullivan et al., 2013), a recognized force shaping evolution of signal forms in electric fish (Crampton et al., 2011). The Electric Eel, which may be basal to the gymnotiform clade (Tagliacollo et al., 2016), retains a monophasic pulsed EOD. It can signal in the low-frequency spectrum with impunity because it can also generate a separate high-voltage discharge strong enough to repel any predator that tries to eat it (Faraday, 1839; Catania, 2016).

To understand how weakly electric fish have shifted their signal frequencies away from the sensory range of predators, we first consider how electric field waveforms of different shapes distribute energy across the spectrum (**Figure 4**). The key feature is symmetry of the energy around the zero-volt baseline (Stoddard and Markham, 2008); any imbalance in the mean voltage will create a net-DC shift, which necessarily creates a low-frequency component that will stimulate ampullary electroreceptors of predators. A continuous sine wave, centered evenly around zero volts (**Figure 4A**), has energy at the fundamental frequency only, thus a 1,000 Hz sinewave has energy only at 1,000 Hz. As an electric field, this waveform would be imperceptible to ampullary electroreceptors of piscivorous predators, which are tuned much lower in frequency (**Figure 1**). However, if the same sine wave is offset up or down in amplitude from a center of zero volts (**Figure 4B**), a new spectral component emerges at 0 Hz that is readily detectable by ampullary electroreceptors. A single-period sinusoid centered around zero volts (**Figure 4D**) has a broader spectrum than the continuous sine wave, but little low-frequency energy, so a pulsed EOD with such a waveform would be undetectable by ampullary electroreceptors. As with the continuous sine wave, any DC asymmetry in the single-period sinusoid would likewise add energy to the low end of the spectrum, making the signal readily detectable by the ampullary system. The most extreme case of DC asymmetry is a monophasic EOD pulse (**Figures 2**, **4C**).

Actual EODs (**Figure 5**) distribute energy the same way as the canonical trigonometric waveforms. "Wave EODs" are strings of EOD pulses timed to produce a continuous sinusoid. The individual EODs making up a wave EOD can be sinusoidal pulses, as produced by the fish in the family Apteronotidae, or can be cosine-like pulses, offset by a DC current to balance symmetrically around 0 V, as produced by fish in the family Sternopygidae (**Figure 5A**). These DC-balanced wave EODs have no energy in the sensory range of ampullary electroreceptors and are expected to reduce predation by electroreceptive predators (Stoddard, 2002a), though nobody has tested electroreceptive predators for their ability to detect wave-type EODs.

"Pulse EODs" have a variable duty cycle, with inter-EOD intervals longer than the EOD pulses themselves. Pulse EODs of many species are simple, single-period sinusoids, but others are made up of 1–5 wavelets (Rodriguez-Cattaneo et al., 2008; Gallant et al., 2011). Such variety is even seen within a genus. During development, pulse-type EODs develop more phases and become DC-balanced (Franchina, 1997; Crampton et al., 2011) until they have little to no energy in the sensory range of ampullary electroreceptors (**Figure 3**). Captive playback studies have shown that DC-balanced pulse-type EODs are not attractive to electroreceptive predators, whereas those with DC-asymmetry are highly attractive to these predators, both catfish and Electric Eel (Hanika and

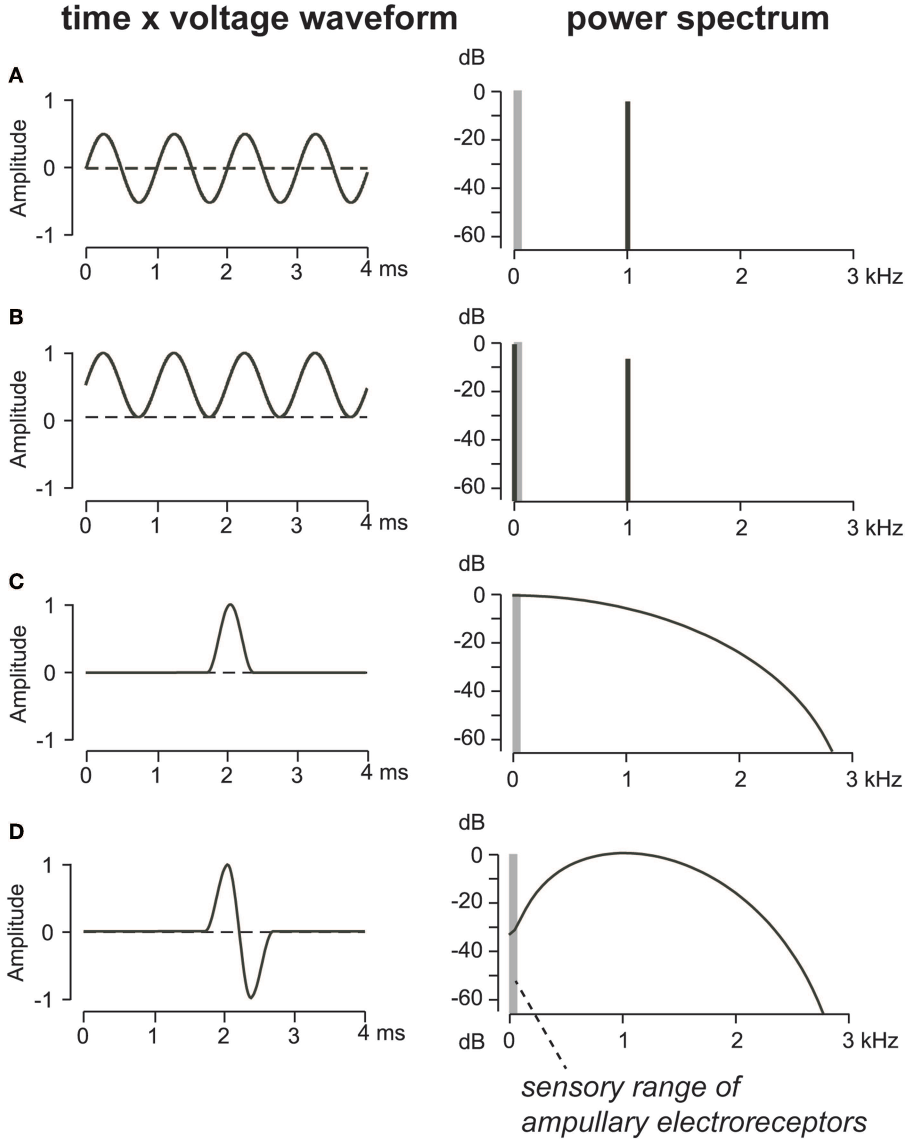

FIGURE 4 | (A) A pure 1,000 Hz sine wave centered symmetrically around zero Volt amplitude has no low-frequency energy in the range of ampullary electroreceptors (vertical gray bar). **(B)** That same sine wave with a DC-offset has signal energy in the low-frequency range of the ampullary system. **(C)** An offset cosine pulse, resembling a monophasic EOD, has abundant low-frequency energy in the spectral range of ampullary electroreceptors. **(D)** A single-pulse sinusoid with a 1,000 Hz fundamental frequency has a much broader spectrum than the continuous sine wave, but does show some suppression of low-frequency energy. Adapted from Stoddard and Markham (2008) with permission of the publisher.

Kramer, 1999, 2000; Stoddard, 1999). Field playbacks have been attempted by various researchers without success, probably because electroreceptive predators are sparse, and because EODs of most species are detectable only over short distances from the source fish (e.g., 1–1.5 m; Hopkins et al., 1990; Hanika and Kramer, 2000) compared to cues detected over longer distances such as odor plumes or turbulence wakes behind the prey (Pohlmann et al., 2001).

Both in gymnotiforms and mormyrids, breeding males of several genera produce pulse EODs that extend one EOD phase to create DC-asymmetry (e.g., Hopkins, 1999; Stoddard, 2002b), particularly at night when courtship and spawning occur. This DC-asymmetry destroys the electric crypsis of the multiphasic waveform by diverting significant energy to the spectrum detected by ampullary electroreceptors. The presence of breeding females elicits dynamic 2nd phase extension by male *Brachyhypopomus gauderio* (Gavassa et al., 2013) and a corresponding boost in low-frequency energy (**Figure 6**). This sexual dimorphism is further enhanced at night by a circadian rhythm in the hormones that regulate waveform shape (Stoddard et al., 2003, 2007; Markham and Stoddard, 2005; Markham et al., 2009a), in part through trafficking of ion channels (Markham

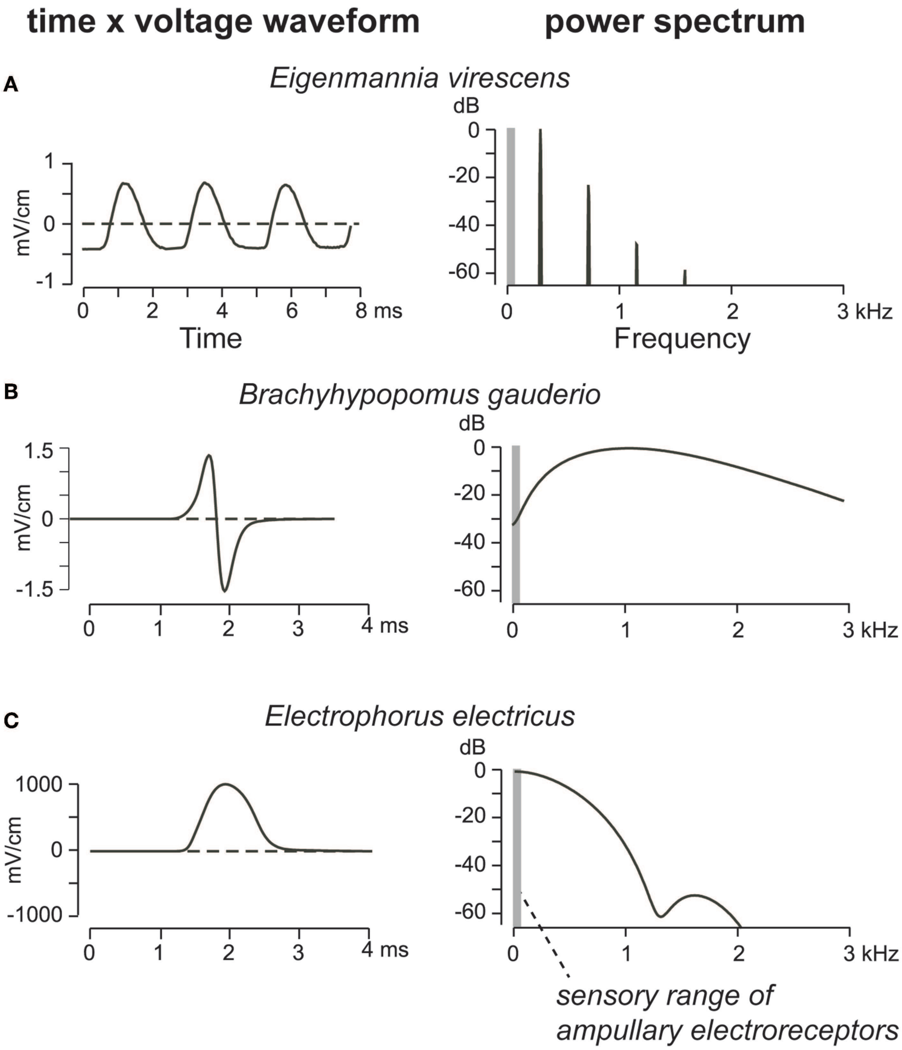

FIGURE 5 | EODs of three gymnotiform electric fish species and their corresponding power spectra. **(A)** Wave EOD of the Glass Knifefish, *Eigenmannia virescens* (Sternopygidae), is a continuous series of monophasic pulses, offset by a DC current to resemble a sine wave. The EOD is balanced around 0 Volts DC, and thus has no energy in the spectral range of ampullary electroreceptors. **(B)** The EOD of a female *Brachyhypopomus gauderio* (Hypopomidae) resembles a symmetric single-period sinusoid. Some low-frequency energy is present, but much less than **(C)** in the monophasic pulse EOD of the Electric Eel, *Electrophorus electricus* (Gymnotidae). Adapted from Stoddard and Markham (2008) with permission of the publisher.

et al., 2009b). The transiently DC-imbalanced EODs of these pulse-type male electric fish may thus bear an increased risk of detection by electroreceptive predators and could therefore serve as indicators of male quality, consistent with the handicap mechanism proposed by Zahavi (1975).

PREDATION DENSITY AND EOD PROPERTIES IN NATURAL POPULATIONS

If electroreceptive predators have a shaping effect on the EODs of weakly electric fish, one would predict differences in EOD waveform and power spectrum between populations exposed to strong versus weak predation pressure. Such evidence has recently been uncovered in a study of the pulse-type gymnotiform species *Brachyhypopomus occidentalis* in Panama. These electric fish are found in nearly all Atlantic- and Pacific-slope drainages of Panama (Picq et al., 2014). A comparison of the divergence pattern of the EODs of male *B. occidentalis* from different drainages with the divergence pattern of neutral genetic markers is consistent with a sizable effect of genetic drift on EOD evolution (Picq et al., 2016). Within-drainage variation in EOD properties suggested, however, that additional factors are likely shaping the waveform as well. Strong variation in the percentage of fish found with damaged and regenerating tails pointed at differences in predation pressure between streams within the same drainage. The amount of tail damage in each stream corresponded with stream

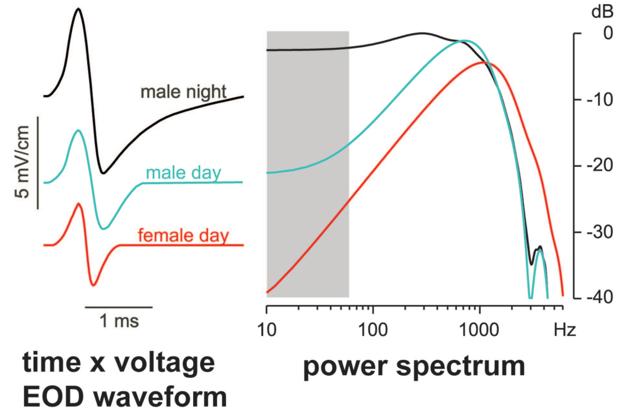

FIGURE 6 | Male *Brachyhypopomus gauderio* extend the second phase of the EOD, creating DC-asymmetry, which boosts energy in the frequency range of ampullary electroreceptors (gray bar). Accordingly, males have more low-frequency energy than females, and even more at night when they further enhance the signal. Adapted from Stoddard and Markham (2008) with permission of the publisher.

counts of a piscivorous pimelodid catfish, *Rhamdia quelen*, a potential electroreceptive predator of *B. occidentalis* (Tran, 2014). Further, *B. occidentalis* from streams with higher incidence of catfish produced a less-extended EOD second phase with upward shifted power spectrum compared to fish from streams within the same drainage that had fewer catfish (**Figure 7**). To compare susceptibility to detection by predators equipped with an ampullary electrosense, Tran (2014) measured the frequencies of peak power of the EOD for *B. occidentalis* from a low-predation and a high-predation stream in each of three drainages (data from males and females were pooled for each drainage, as their EODs did not differ significantly in peak frequency). Compared to the EOD of *B. occidentalis* from low-predation streams, the frequency of peak power was significantly reduced in animals from the high-predation streams (mean differences in peak frequency between fish from the high- and low-predation populations were between 130 and 320 Hz; ANCOVA, $p < 0.001$). The reduced low-frequency power of fish exposed to relatively high predation pressure is consistent with the hypothesis that electroreceptive predators have been shaping the EOD properties of weakly electric fishes in the direction of greater waveform symmetry. Whether the within-drainage differences in EOD properties found in Panamanian *B. occidentalis* are indeed heritable or result from individually plastic response to presence of predators or predation remains to be determined.

ENERGETIC COSTS OF PRODUCING DC-BALANCED EODS

Electric fish with DC-symmetrical EODs pay an energetic cost for the ionic mechanisms that reduce or eliminate the low-frequency energy in the signals. Species that make DC-symmetrical, pulsed EODs do so by adding phases to the initial monophasic EOD. Each phase would seem to add linearly to the cost of signal production, however, the action potentials underlying the additional phases temporally overlap one another within and between electrogenic cells (electrocytes) in the electric organs (Bennett, 1961, 1970, 1971a; Caputi et al., 1994; Stoddard et al., 1999). Temporal overlap results in cancellation of significant amounts of energy invested in electrogenesis (**Figure 8**) (Stoddard and Markham, 2008; Markham and Stoddard, 2013; Markham and Zakon, 2014). We postulate that reduction of predation pressure by balancing the DC energy in the EOD is worth the energetic expense of losing most of that energy to temporal overlap. Multiple EOD phases also allow for greater species specificity during mate selection, which appears to be another selective force shaping electric waveforms (Crampton et al., 2011).

PARALLELS TO OTHER SYSTEMS

Microgeographic patterns of electric signal crypsis among *B. occidentalis* in Panama parallel the predator-driven pattern seen in Trinidadian guppies (*Poecilia reticulata*). Male guppies have more conspicuous patterning than females, particularly so in streams, or even parts of streams, where predators are less frequent (Endler, 1991). Guppies translocated between high- and low-predation areas quickly evolved color patterns that balanced sexual attractiveness against the prevailing predation risk (Reznick et al., 1997). Female preferences for male EODs have not been explored yet in *B. occidentalis*. Gravid females of the related species, *B. gauderio*, preferred larger over smaller males, when given a choice (Curtis and Stoddard, 2003). The larger males had EOD pulses of larger amplitude and longer duration than smaller males, the latter feature being consistent with female preference for signals with more low-frequency power. Playback experiments with gravid females are needed to assess whether the females base their preference on EOD amplitude and/or duration or whether they evaluate male size independently of the EOD. Similar experiments with *B. occidentalis* may permit quantifying the trade-off between sexual and natural selection in a lower-dimensional system than the visual communication of guppies, where sexual selection appears to push male coloration in different directions depending not only on the specific habitat conditions but also the starting trait of the particular lineage under selection (Kemp et al., 2018).

Division of electric signal energy between the high-frequency band detected by tuberous electroreceptors and the low-frequency band detected by ampullary electroreceptors of conspecifics and predatory eavesdroppers alike, bears a parallel to mate attraction calls of the Túngara frog complex *Physalaemus* spp. of the Neotropics. Frogs have two auditory organs, the basilar papilla and amphibian papilla, with high and low frequency tuning, respectively (Zakon and Wilczynski, 1988). Male Túngara frogs produce a "whine" call for mate attraction. However, when competing with conspecific males, male Túngara frogs add lower-frequency "chuck" call components with energy focused in the frequency band of the basilar papilla, which makes them more attractive to conspecific females, but also to predatory

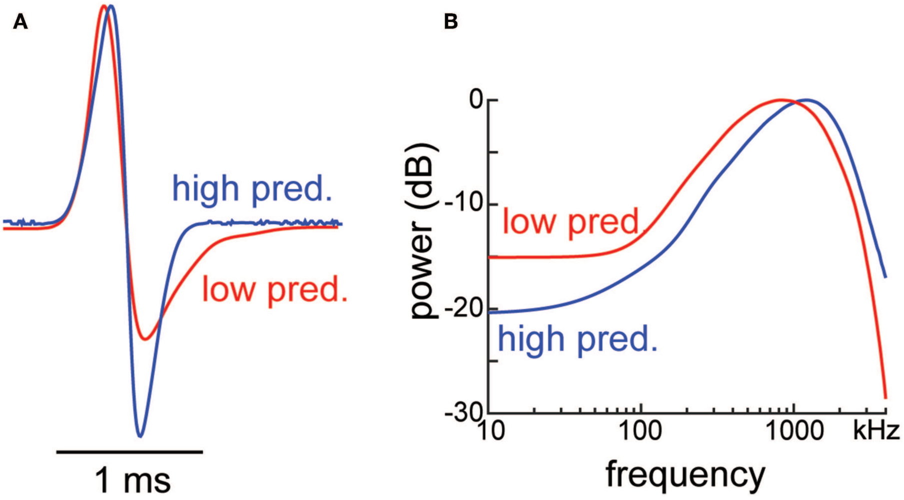

FIGURE 7 | (A) *B. occidentalis* from streams in Panama with lower incidence of piscivorous catfish (red line) produced EODs with a more-extended second phase than animals in streams with high incidence of catfish (blue line). **(B)** The power spectra of a typical EOD from a low-catfish stream (red line) has more energy in the spectral range of ampullary electroreceptors than the EOD of a male from a high catfish stream (blue line).

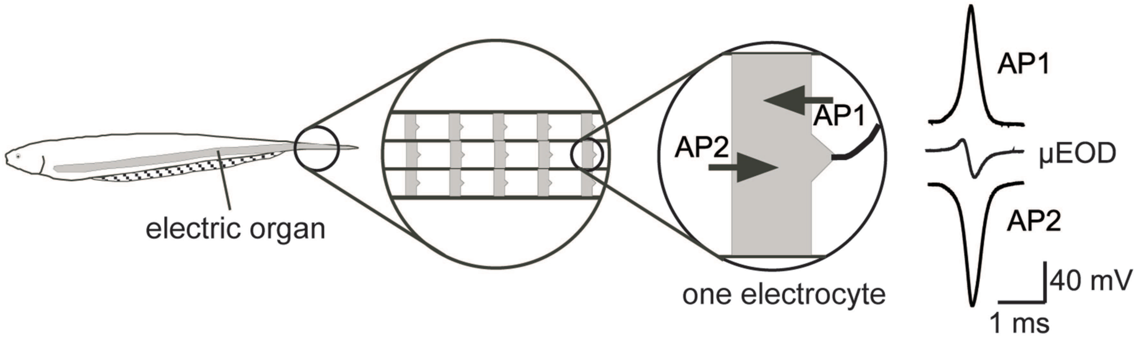

FIGURE 8 | The biphasic EODs of *B. gauderio* and others are produced at the level of the single electrocyte by a pair of action potentials (APs) driving sodium currents in opposite directions (AP1 headward, AP2 tailward). The action potentials are temporally offset, which produces a biphasic micro-EOD when the two currents sum outside the cell. The temporal offset is only partial, however, so the current from each action potential partially cancels out the other. Thus, the 2nd EOD phase that balances the EOD to reduce predation risk also wastes significant energy. Adapted from Stoddard (2002a), Markham and Stoddard (2005), and Stoddard and Markham (2008) with permission of the publisher.

bats and parasitic flies (Ryan et al., 1990; Ryan, 1992; Bernal et al., 2006; Page and Ryan, 2008). We see a similar pattern in males of the electric fish, *B. gauderio*, which enhance their low-frequency power output in the presence of either sex, but boost their signal amplitude only when competing males are present (Franchina et al., 2001; Gavassa et al., 2013). Increasing EOD amplitude is expected to increase predation risk by expanding the space over which predators can detect the emitter. A second effect of the boost in amplitude is the added energetic expense of producing larger currents flowing across the electrocyte membranes (Salazar and Stoddard, 2008; Markham et al., 2009b). Whereas the energetic cost of male Túngara frogs producing whines, and increasing the rate of whine production, was assessed many years ago (Bucher et al., 1982), the cost of adding chucks to whines has, to our knowledge, not been estimated.

FUTURE DIRECTIONS

Although predatory catfish are believed to shape the evolution of electric signals in the dominant groups of electric fish, tuning curves of ampullary receptors in the catfish, the presumed dominant predatory drivers, have been characterized only in temperate catfish of North America (Dijkgraa, 1968; Peters and Buwalda, 1972; Bullock, 1979; Finger, 1986; Peters et al., 1997; Eeuwes et al., 2001; Collin and Whitehead, 2004). A detailed study of sensory physiology and predation on electric fish by Neotropical pimelodid catfishes would be a useful addition to our understanding. Likewise, although we find strong signatures of sensory drive on electric signals by electroreceptive predators, the microgeographic differences in EOD spectrum seen in male electric fish in Panama (Tran, 2014) could result from either evolutionary or developmental response to predation. Resolution of this question could prove interesting. Finally, we have assumed that the dangerous low-frequency components of male electric courtship signals are attractive to conspecific females (Stoddard, 2002a,b), but no studies have tested this assumption directly. Such studies are tricky: female electric fish are finicky subjects for mate choice studies, and low-frequency, low-intensity electric fields require special care to measure and regulate.

AUTHOR CONTRIBUTIONS

PS and RK wrote the manuscript. AT and RK conducted the predation study in Panama.

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Loudness–Duration Tradeoff in Ultrasonic Courtship Songs of Moths

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Moths have evolved auditory channels under predation pressure from insectivorous bats that emit ultrasonic pulses for capturing prey, including moths. Tympanate moths perform evasive behavior in response to echolocation calls of bats, but they also utilize ultrasonic signals mostly generated by males close to an intended female mate in the context of courtship. Unlike calling songs used to advertise the presence and sexual attractiveness of the signaler, courtship songs need not always be acoustically conspicuous. Male courtship songs are predominantly soft but sufficient for detection by a nearby potential mate. Quiet courtship songs are thought to effectively avoid being eavesdropped by gleaning bats, acoustic parasitoids, and conspecific competitors, i.e., rival males. However, males of some moth species generate loud courtship songs. In the present study, the duration of courtship song, in addition to the sound level of the song was predicted to affect the likelihood of being perceived by eavesdroppers. Loud and lengthy courtship songs, which are easily exploited by eavesdroppers, would be expected to rarely evolve, because a female receiver close to a male emitting a conspicuous song would also be exposed to strong predation pressure. This study explored the relationship between the peak sound level and the duration of single song bouts in 26 moth species from the following families: Noctuidae, Erebidae, Crambidae, Pyralidae, and Geometridae. The softest and loudest songs with mean peak sound levels of 64 and 129 dB peSPL had mean durations of 1,900 and 312 ms, respectively, whereas the shortest and longest songs with mean durations of 110 and 8,839 ms had mean peak sound levels of 102 and 74 dB peSPL, respectively. The peak sound level and duration of courtship song exhibited a significant negative relationship across species. Although the energetic cost of producing song and the size of the sound-producing organ might also affect the relationship, the data support the conclusion that acoustic moths have adaptively evolved ultrasonic courtship songs with properties between "soft-and-long" and "loud-and-short" to avoid eavesdroppers.

Keywords: bat-predator, courtship song, eavesdropper, moth-prey, ultrasonic communication

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INTRODUCTION

Animals have evolved communication signals for mating. During a mating sequence involving emission of a signal to a focal receiver i.e., usually a female, an unintended receiver has a chance to exploit the signal to find, locate, and hunt or parasitize a conspicuous signaler (Zuk and Kolluru, 1998). In addition, conspecific competitors may steal a mating opportunity. Loud calling songs are widespread in acoustic animals because of their usefulness to advertise the presence of the caller and attract mating partners from a long distance, but conspicuous songs simultaneously convey information on the location of the caller to predators, including bats, birds, and reptiles (Tuttle and Ryan, 1981; Sakaluk and Belwood, 1984; Bell, 1985; Tuttle et al., 1985; Bailey and Haythornthwaite, 1998; Igaune et al., 2008; Jones et al., 2011); parasitoids and blood-sucking flies (Cade, 1975; Walker, 1993; Bernal et al., 2006; Bernal and de Silva, 2015); and rival males of the same species (Cade, 1980; Bailey and Field, 2000; Zuk et al., 2006; Bailey et al., 2010).

Calling songs of moths are also prey cues used by insectivorous bats (Alem et al., 2011). Males of the lesser wax moth *Achroia grisella* (Pyralidae) generate loud ultrasonic clicks to attract female receivers (Jang and Greenfield, 1996; Greenfield, 2014). Bat predators with gleaning strategies, such as the greater horseshoe bat, *Rhinolophus ferrumequinum*, can exploit a moth's ultrasonic calling songs as a landmark of their prey (Alem et al., 2011). As countertactics to avoid predation by eavesdropping bats, singing males of *Achroia grisella,* like crickets and katydids (Spangler, 1984; Nolen and Hoy, 1986; Libersat and Hoy, 1991; Faure and Hoy, 2000; Schulze and Schul, 2001), cease emission of their calling songs, and the females stop orientation toward calling males, when they detect ultrasonic echolocation calls of hunting bats (Spangler, 1984; Greenfield and Baker, 2003; Greig and Greenfield, 2004; Rodríguez and Greenfield, 2004; Cordes et al., 2014).

The use of calling songs by moths has been confirmed in only a few species (Conner, 1999; Greenfield, 2014), but it has been increasingly reported that moths communicate acoustically with male courtship songs (Nakano et al., 2015). Male moths produce courtship songs after they have approached close to (within a few centimeters of) a female that has released sex pheromones to attract males from a long distance. For the tiger moth and the lichen moth (Erebidae), it is implied that male courtship song serves as a signal for mate recognition (Conner, 1987; Nakano et al., 2013). However, some noctuid and crambid moths do not discriminate between courtship songs of conspecific male moths and echolocation calls of bat predators (Nakano et al., 2008, 2010a, 2013). Females of these moths show a freezing response in response to the male song as well as to bat cries, which enables the singing male to readily attempt copulation with the stationary female (Nakano et al., 2008, 2010b, 2013).

Males are vulnerable to predation during courtship (Endler, 1987; Alem et al., 2011). Excessive concentration of a male's attention on a female (and subsequent sperm transfer) could cause him to delay perception of the presence or approach of eavesdroppers, including predators. To survive while performing reproductive behavior, males and even females need to maintain multiple multimodal sensory systems to decide between defense and copulation. One solution for this tough choice is to mate "privately" to avoid eavesdropping (Dabelsteen et al., 1998; Dabelsteen, 2004). In singing animals, "soft" song with low-amplitude sound is one of the adaptive courtship behaviors associated with defensive responses to eavesdroppers (Nakano et al., 2009a; Balenger, 2015; Reichard and Anderson, 2015). Low-amplitude signals render a caller inconspicuous to eavesdropping enemies and competitors. Soft songs have the disadvantage of being effective only over a short distance, but the caller can overcome this disadvantage by generating the soft song in close proximity to the intended receiver. Soft courtship songs are found among moths of diverse taxonomic groups, including Noctuidae, Erebidae, Crambidae, Pyralidae, and Geometridae (Conner, 1999; Nakano et al., 2009a,b, 2015). However, courtship songs are not necessarily of low amplitude (e.g., Conner, 1987; Sanderford and Conner, 1995; Nakano et al., 2012a). In this study, we examined how the courtship songs of moths are adaptively balanced between conspicuous and inconspicuous characteristics to enable effective mating while avoiding eavesdroppers.

MATERIALS AND METHODS

Study Insects

We studied 26 moth species belonging to the Noctuoidea (five noctuid and three erebid species), Pyraloidea (14 crambid and three pyralid species), and Geometroidea (one geometrid species). In addition to 14 species previously reported (Nakano et al., 2006, 2009a,b, 2012a), male courtship songs were newly recorded for 12 species and analyzed by the procedure described below. Moths of all growth stages were maintained under a 16 h light:8 h dark photo-regime in experimental rooms at 20 ± 1°C for three Canadian species (three crambids: *Desmia maculalis*, *Desmia funeralis,* and *Nomophila nearctica*) and 24 ± 1°C for nine Japanese species [three noctuids (*Spodoptera picta*, *Spodoptera exigua*, and *Spodoptera pecten*), one erebid (*Lithosia quadra*), three crambids (*Ostrinia zealis*, *Ostrinia palustralis*, and *Ostrinia latipennis*), and two pyralids (*Paralipsa gularis* and *Endotricha icelusalis*)]. Larvae were reared on their host plants or an artificial diet (Silkmate-2M; Nosan Corp., Yokohama, Japan). To ensure the virginity of the moths until they were used, each newly emerged male or female adult moth, designated as 0 days old, was separately kept in a nylon mesh cage (30 × 30 × 30 cm) with water or 10% honey solution *ad libitum*. To minimize the colony artifact associated with inbreeding, we used the generation collected in the field and the next generation.

Sound Recording

We directly observed the mating behavior of 2–4 days old previously unmated moths confined in the cubical mesh cages, which were placed in a soundproof box (90 × 65 × 65 cm) with one side opened in the scotophase (dark phase) under a dim red light at 0.6 lux. Male courtship ultrasounds were individually recorded with a 1/4-inch condenser microphone (type 4939; Brüel and Kjær, Nærum, Denmark) connected to a preamplifier (type 2670; Brüel and Kjær) and a customized conditioning amplifier (Nexus type 2690, 0.02–140 kHz bandpass filter; Brüel and Kjær). The acoustic signals were digitized with an analog-to-digital converter, Wavebook 512A (12-bit; IOtech, OH, USA) or USB-1604HS (16-bit; Measurement Computing, MA, USA) at a sampling rate of 300 kHz. The microphone was hand-held and approximately kept 10 mm from the singing male, and the membrane was directed to the intended individual. The recorded courtship songs were stored as.wav format files.

Song Characteristics

To determine the relationships among loudness, duration, and peak frequency of male courtship ultrasounds, we extracted peak equivalent sound pressure levels (dB peSPL; re. 20 μPa), the longest duration of a single song bout, and dominant frequencies from the recorded sound files using the software BatSound 4.03 (Pettersson Elektronik, Uppsala, Sweden). The data were individually obtained from each singing male without replication. Sound pressure levels were calculated with reference to the known signal voltage of the sound calibrator (type 4231, 94 dB SPL, 1 kHz; Brüel and Kjær). Song duration was measured using both oscillogram and spectrogram. Because each recording was performed for a maximum of 10 s, the duration of a song that was continuously emitted over the length of the recording was recorded as 10 s for two of 20 songs of *Ostrinia furnacalis* (Crambidae), four of nine songs of *Ostrinia nubilalis* (Crambidae), one of seven songs of *Ostrinia scapulalis* (Crambidae), and four of seven songs of *Ostrinia zealis* (Crambidae). Dominant frequencies were determined by computing power spectra on a Hanning window with a fast Fourier transformation size of 1,024 points. These analyses were performed after high-pass filtering at 10 kHz to eliminate low-frequency background noise.

In statistical analyses of peak sound level, song duration and dominant frequency among species and families, we performed likelihood ratio (LR) test in generalized linear model (GLM) with Gamma error distribution. Additionally, we examined if significant relationships among the song characteristics were found within the species. Because of limited sample sizes ($n < 3$) for *Palpita nigropunctalis* (Crambidae) and *Herminia tarsicrinalis* (Noctuidae), we used 24 species out of 26 species for the within-species analysis. Relationships among the peak sound level, the song duration and the dominant frequency were analyzed by generalized additive model (GAM) (Wood, 2008). Coefficients in the relationships obtained from each species were used for the random effects meta-analyses using the restricted maximum likelihood (REML) estimation ("metafor" package; Viechtbauer, 2010) which tests the significance for 24 species. These analyses were done using R version 3.4.3 (R Core Team, 2017).

Construction of Phylogenetic Tree

For phylogenetic analysis of the 26 moth species, we used the nucleotide sequences deposited at GenBank® (http://www.ncbi.nlm.nih.gov). We tried to incorporate all the available nucleotide sequences of nuclear and mitochondria genes of the 26 species on the International Nucleotide Sequence Database into the construction of a phylogenetic tree. However, because only cytochrome oxidase subunit I (COI), cytochrome oxidase subunit II (COII), and NADH dehydrogenase subunit 5 (ND5) genes of mtDNA were listed for our moths, we searched the homologs of these three genes in the Nucleotide BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi) with the nucleotide sequences of COI, COII, and ND5 of *Ostrinia furnacalis* as the query (**Table S1**). The homologous sequences of *Hyphantria cunea* (Erebidae), *Paraona staudingeri* (Erebidae), *Nomophila noctuella* (Crambidae), *Palpita quadristigmalis* (Crambidae), *Corcyra cephalonica* (Pyralidae), *Endotricha consocia* (Pyralidae), and *Ectropis obliqua* (Geometridae) were substituted for those of *Spilosoma punctarium* (Erebidae), *Eilema japonica* (Erebidae), *Nomophila nearctica* (Crambidae), *Palpita nigropunctalis* (Crambidae), *Paralipsa gularis* (Pyralidae), *Endotricha icelusalis* (Pyralidae), and *Ascotis selenaria cretacea* (Geometridae), respectively, because these genes are not available in the present database (**Table S1**). Alignments were performed with the Clustal W program (Thompson et al., 1994) in MEGA7 (Kumar et al., 2016) with default values, and gap sequences were manually removed.

We estimated the phylogenetic relationships among the 26 species by four steps described below. In all steps, selection of the best-fit models of nucleotide substitutions was based on the Bayesian information criterion in MEGA7. The focal phylogenetic relationships, for which a geometrid moth *Ascotis selenaria cretacea* was treated as a root of the tree, were reconstructed by the maximum likelihood method. After bootstrap tests with 1,000 resamplings, we used branches with a bootstrap value of >60.

First, we drew an outline tree using 15 sequences of combinations of COI genes (1,514 bp) and ND5 genes (1,632 bp) for two noctuids (*Spodoptera litura* and *Spodoptera exigua*), two erebids [*Hyphantria cunea* (instead of *Spilosoma punctarium*) and *Paraona staudingeri* (instead of *Eilema japonica*)], seven crambids [*Ostrinia furnacalis*, *Ostrinia nubilalis*, *Glyphodes pyloalis*, *Spoladea recurvalis*, *Conogethes punctiferalis*, *Nomophila noctuella* (instead of *Nomophila nearctica*), and *Chilo suppressalis*], three pyralids [*Galleria mellonella* and *Corcyra cephalonica* (instead of *Paralipsa gularis*), and *Endotricha consocia* (instead of *Endotricha icelusalis*)], and a geometrid moth [*Ectropis obliqua* (instead of *Ascotis selenaria cretacea*)] based on the GTR+G model to estimate phylogenetic relationships at the interfamily level (**Figures S1A, S2A**).

Second, three intrafamily trees were constructed with six sequences of COI genes (1,423 bp) for five noctuids (*Spodoptera litura*, *Spodoptera picta*, *Spodoptera exigua*, *Spodoptera pecten*, and *Herminia tarsicrinalis*) and a geometrid moth [*Ectropis obliqua* (instead of *Ascotis selenaria cretacea*)] according to the GTR+G model (**Figures S1B, S2B**), with four sequences of COI genes (658 bp) for three erebids [*Hyphantria cunea* (instead of *Spilosoma punctarium*), *Paraona staudingeri* (instead of *Eilema japonica*), and *Lithosia quadra*] and a geometrid moth [*Ectropis obliqua* (instead of *Ascotis selenaria cretacea*)] according to the TN93+G model (**Figures S1C, S2C**), and with 12 sequences of COII genes (674 bp) for 12 crambids [*Ostrinia furnacalis*, *Ostrinia nubilalis*, *Ostrinia scapulalis*, *Ostrinia zealis*, *Ostrinia palustralis*, *Ostrinia latipennis*, *Glyphodes pyloalis*, *Spoladea recurvalis*, and *Palpita quadristigmalis* (instead of *Palpita nigropunctalis*), *Conogethes punctiferalis*, *Nomophila noctuella* (instead of *Nomophila nearctica*), and *Chilo suppressalis*] according to the TN93+G model (**Figures S1D, S2D**).

Third, the phylogenetic relationships among *Desmia maculalis*, *Desmia funeralis*, another five crambids [*Glyphodes pyloalis*, *Spoladea recurvalis*, *Palpita quadristigmalis*, *Conogethes punctiferalis*, and *Nomophila noctuella* (instead of *Nomophila nearctica*)] and a geometrid species [*Ectropis obliqua* (instead of *Ascotis selenaria cretacea*)] were estimated with the eight sequences of COI genes (657 bp) according to the GTR+G+I model (**Figures S1E, S2E**).

Fourth, the interfamily trees were combined with the outline tree.

Phylogenetic Comparative Analysis

To take account of species' non-independence due to phylogenetic relatedness (Felsenstein, 1985), we first estimated phylogenetic signals of Pagel's λ (Pagel, 1999) and Blomberg's K (Blomberg et al., 2003). We then applied the phylogenetic generalized least square (PGLS) models with the maximum likelihood method to analysis of relationships among the song characteristics (sound level, duration, and frequency) take into account of the reconstructed phylogenetic tree for our 26 moth species (Pagel, 1999). The PGLS approach includes a variance–covariance matrix with Pagel's λ correlation structure, which is derived from the Brownian motion model expecting a random walk, based on the phylogenetic relationships of species. We also fitted the Ornstein-Uhlenbeck process model expecting a random walk around a central tendency under stabilizing selection in PGLS (Martins and Hansen, 1997). Our data points in some cases seemed to better fit a nonlinear relationship. Therefore, in addition to PGLS models, we statistically analyzed relationships among the three parameters by generalized additive mixed models (GAMM) into which the taxonomic family was incorporated as a random effect (Bradshaw et al., 2008; Wood, 2008).

All analyses were done in R version 3.4.3. We calculated the phylogenetic signals and tested the null hypothesis of no phylogenetic signal using the "phytools" package (Revell, 2012). PGLS models and GAMMs were built with packages "nlme" (Pinheiro et al., 2019) and "gamm4" (Wood, 2008), respectively. A.nexus format file for phylogeny was read through the package "ape" (Paradis and Schliep, 2018). For GAMMs, we used gamma error distribution with log-link function to treat positive continuous variables showing the non-normal distribution and examined the significance of each explanatory variable by the LR test in the analysis of deviance.

RESULTS

The courtship songs of the male moths had highly diverse acoustic characteristics (**Figure 1**). Peak sound level, song duration, and frequency components varied among species even within the same family, Crambidae. Male songs of *Ostrinia palustralis* and *Ostrinia zealis* (**Figures 1A,B**) had lower amplitudes, longer durations, and lower frequency ranges than those of *Desmia funeralis*, *Palpita nigropunctalis,* and *Glyphodes pyloalis* (**Figures 1C–E**). The minimal sound units generated by one tentative cycle of the sound-producing movement were also different among species; some species generated consecutive pulses (bursts) and others generated several transient clicks. Details are given in subsection courtship song parameters.

Phylogenetic Relatedness

As in previous sophisticated molecular studies of Lepidoptera (Regier et al., 2013; Kawahara and Breinholt, 2014), superfamilies of Noctuoidea and Pyraloidea formed independent clades on a constructed phylogenetic tree (**Figure 2A**, **Table S1**). Five noctuid and three erebid species and 14 crambid and three pyralid species were classified into the monophyletic groups Noctuoidea and Pyraloidea, respectively. Thus, the 26 species belonging to five families (Noctuidae, Erebidae, Crambidae, Pyralidae, and Geometridae) formed five clusters of each taxonomic family on the phylogenetic tree. For the Noctuoidea, *Spodoptera* spp. (Noctuidae) and the two Lithosiini species (Erebidae) individually converged on single clades. For the Pyraloidea, the seven Spilomelinae, six Pyraustinae species (Crambidae), and two Galleriinae species (Pyralidae) each formed a single cluster.

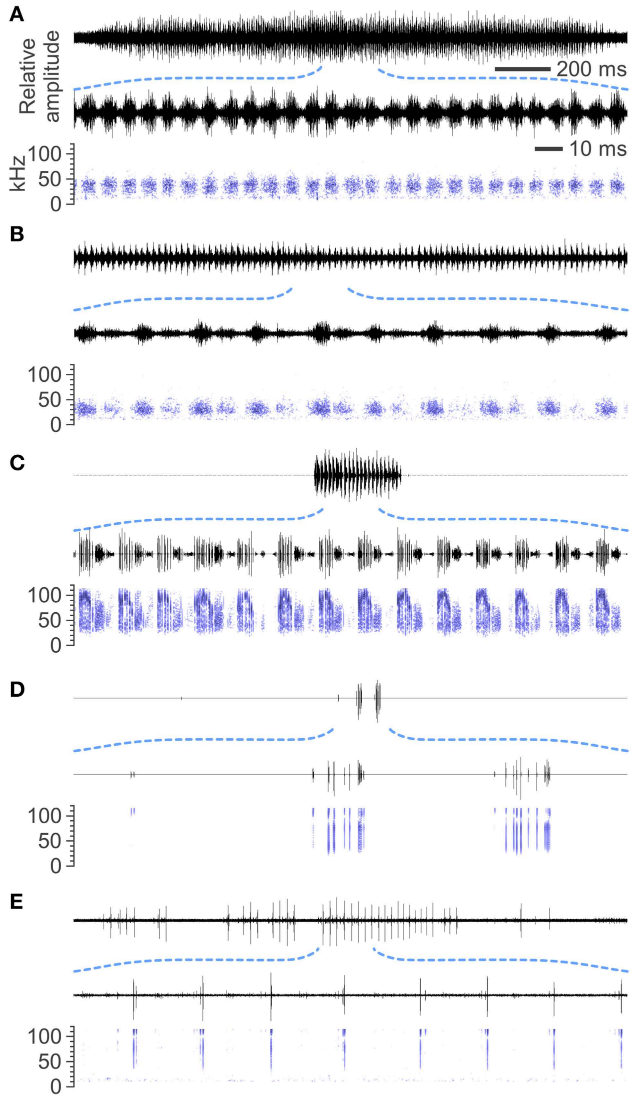

FIGURE 1 | Examples of male courtship songs in crambid moths. Representative oscillograms and spectrograms are shown. **(A)** *Ostrinia palustralis*, **(B)** *Ostrinia zealis*, **(C)** *Desmia funeralis*, **(D)** *Palpita nigropunctalis*, and **(E)** *Glyphodes pyloalis*.

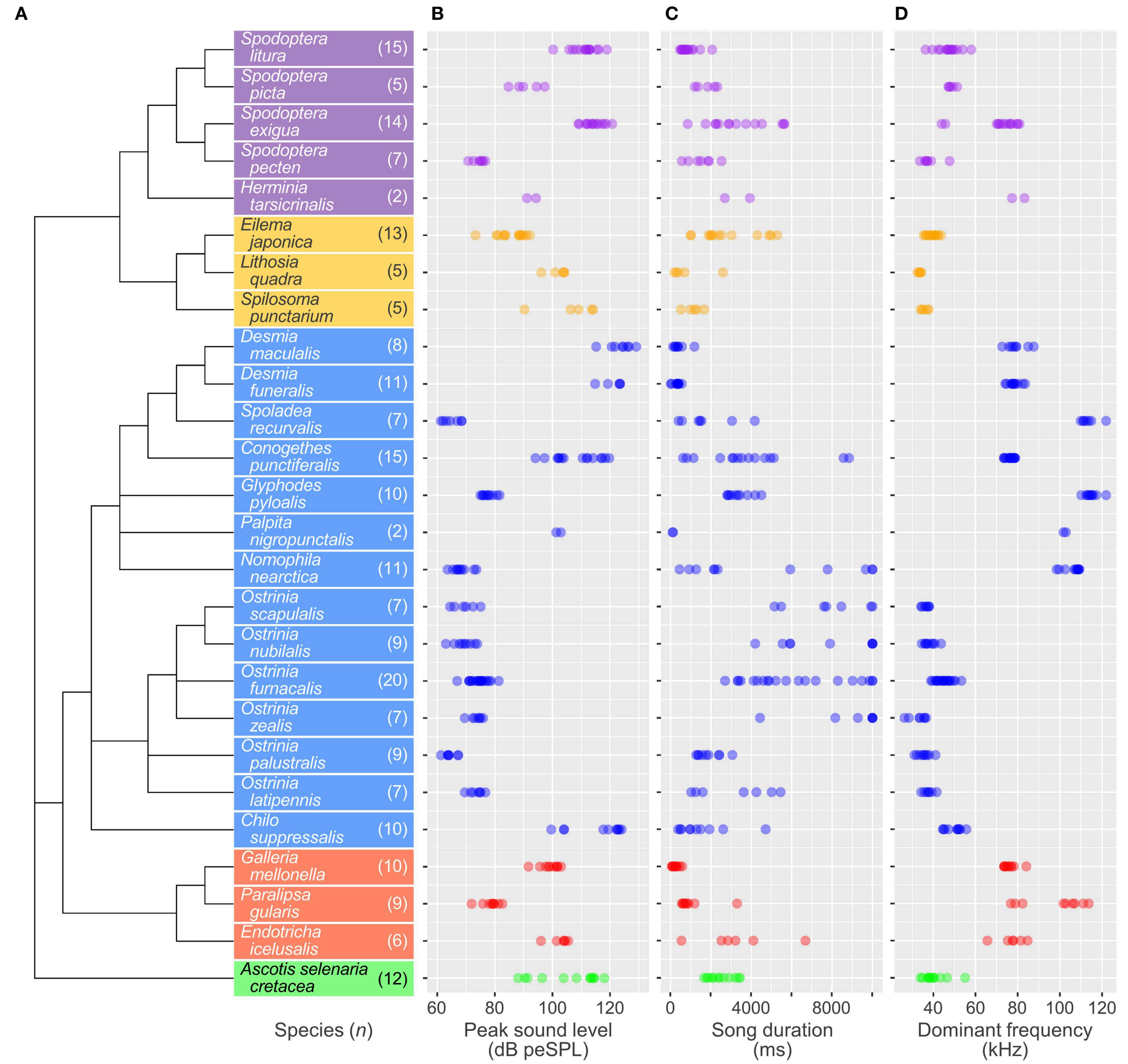

FIGURE 2 | Phylogenetic relationship of the 26 moth species and acoustic characteristics of male ultrasonic courtship songs in each species. **(A)** The phylogenetic tree was constructed by the maximum likelihood method. Colors indicate taxonomic families: purple, Noctuidae (Noctuoidea); orange, Erebidae (Noctuoidea); blue, Crambidae (Pyraloidea); red, Pyralidae (Pyraloidea); green, Geometridae (Geometroidea). The sample sizes used for acoustic analysis are shown in parentheses after the species names. Distribution of peak sound level **(B)**, song duration **(C)**, and dominant frequency **(D)** of male songs. Each circle denotes a value extracted from an individual singing male.

Courtship Song Parameters

At the species level, the mean peak sound levels ranged from 64 dB peSPL, emitted by *Ostrinia palustralis* (Crambidae; minimum–maximum, 59–67 dB peSPL; $n = 9$ males; **Figure 1A**), to 129 dB peSPL, emitted by *Desmia funeralis* (Crambidae; 115–134 dB peSPL, $n = 11$; **Figure 1C**). The sound level was significantly different among species (LR test in GLM with gamma error distribution; $\chi^2 = 11.30$; $p < 0.0001$; **Figure 2B**). The mean song duration ranged from 110 ms, emitted by *Palpita nigropunctalis* (Crambidae; 95–124 ms; $n = 2$; **Figure 1D**), to 8,839 ms, emitted by *Ostrinia zealis* (Crambidae; 4,430 to >10,000 ms; $n = 7$; **Figure 1B**). Song duration also significantly differed among species ($\chi^2 = 181.90$; $p < 0.0001$; **Figure 2C**). The mean dominant frequency ranged from 33 kHz, emitted by *Ostrinia zealis* (Crambidae; 26–37 kHz; $n = 7$; **Figure 1B**), to 115 kHz, emitted by *Glyphodes pyloalis* (Crambidae; 110–122 kHz; $n = 10$; **Figure 1E**). The peak frequency differed significantly among species ($\chi^2 = 39.16$; $p < 0.0001$; **Figure 2D**).

At the family level, the mean peak sound levels were 107 dB peSPL (Noctuidae, $n = 5$ species), 104 dB peSPL (Erebidae, $n = 3$), 112 dB peSPL (Crambidae, $n = 14$), 98 dB peSPL (Pyralidae, $n = 3$), and 110 dB peSPL (Geometridae, $n = 1$) (**Figure 3A**). The sound level did not significantly differ among families (LR test in GLM with gamma error distribution, $\chi^2 = 0.11$, $p = 0.75$). The mean song duration was 2,174 ms (Noctuidae, $n = 5$), 1,609 ms (Erebidae, $n = 3$), 3,736 ms (Crambidae, $n = 14$), 1,538 ms (Pyralidae, $n = 3$), and 2,484 ms (Geometridae, $n = 1$) (**Figure 3B**). Song duration did not significantly differ among families ($\chi^2 = 3.23$, $p = 0.24$). The mean dominant frequency was 57 kHz (Noctuidae, $n = 5$), 36 kHz (Erebidae, $n = 3$), 68 kHz (Crambidae, $n = 14$), 84 kHz (Pyralidae, $n = 3$), and 40 kHz (Geometridae, $n = 1$) (**Figure 3C**). The frequency did not significantly differ among families ($\chi^2 = 1.32$, $p = 0.079$).

Relationship Among Song Parameters

In the within-species analyses (**Table S2**), estimated mean of the coefficient in the relationship between the song duration and the peak sound level was −0.086 (95% CI: −0.20–0.027) with no significant difference from 0 ($z = -1.49$, $p = 0.14$). For the relationship between the duration and the dominant frequency, estimated mean was −0.0053 (95% CI: −0.094–0.083) and was not significantly different from 0 ($z = -0.12$, $p = 0.91$). Estimated mean of the coefficient between the frequency and the sound level was −0.0021 (95% CI: −0.013–0.0086) and was not significantly different from 0 ($z = -0.38$, $p = 0.70$).

For the peak sound level, phylogenetic signals of Pagel's λ and Blomberg's K were 0.76 ($p = 0.0038$) and 0.92 ($p = 0.0020$), respectively. For the dominant frequency, λ and K were 0.52 ($p = 0.15$) and 0.66 ($p = 0.062$), and those for the song duration were 0.76 ($p = 0.0047$) and 0.90 ($p = 0.0050$), respectively.

Considering phylogenetic relatedness (see Construction of phylogenetic tree and Phylogenetic comparative analysis), we found a significant negative linear relationship between song duration and peak sound level (Brownian motion model in PGLS, $t = -2.23$, $p = 0.035$, AIC = 474.49; Ornstein-Uhlenbeck model in PGLS, $t = -2.11$, $p = 0.045$, AIC = 474.92). The results of statistical analyses with GAMM also indicated that song duration was significantly associated with peak sound level (LR test in GAMM, $\chi^2 = 8.83$, $p = 0.012$; **Figure 4A**).

There was no significant relationship between song duration and dominant frequency (Brownian motion model in PGLS, $t = 1.04$, $p = 0.31$, AIC = 476.34; Ornstein-Uhlenbeck model in PGLS, $t = -0.21$, $p = 0.84$, AIC = 478.61). GAMM supported the results shown above. There was no significant relationship between song duration and dominant frequency ($\chi^2 = 1.49$, $p = 0.47$; **Figure 4B**).

No significant relationship was detected between peak sound level and dominant frequency (Brownian motion model in PGLS, $t = -1.29$, $p = 0.21$, AIC = 234.35; Ornstein-Uhlenbeck model in PGLS, $t = -0.80$, $p = 0.43$, AIC = 233.80). In contrast, GAMM indicated that peak sound level was significantly associated with dominant frequency ($\chi^2 = 14.77$, $p = 0.00062$; **Figure 4C**).

In the present study, we analyzed the greatest number of species of crambid moths among the five families. Male courtship song in crambids showed a high diversity (**Figure 1**), ranging from soft to loud songs (60–130 dB peSPL at 10 mm) and from short to long songs (20 to >10,000 ms) (**Figures 2B–D**).

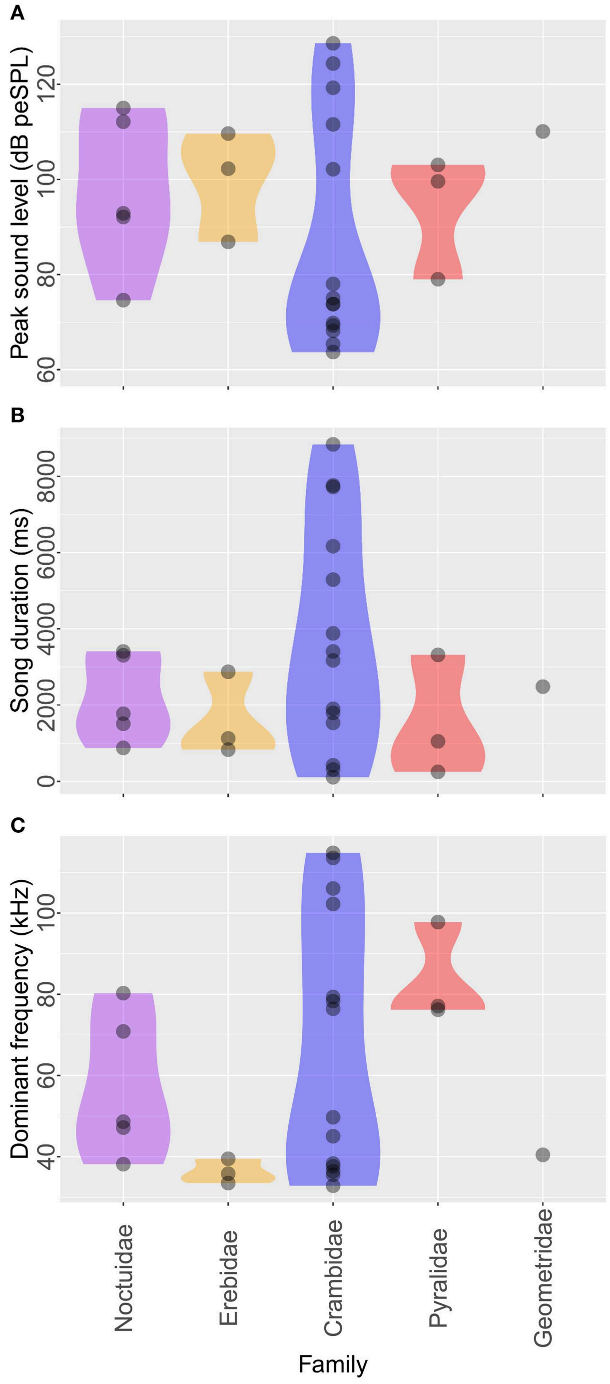

FIGURE 3 | Acoustic characteristics of male ultrasonic courtship songs in each moth family. Peak sound level **(A)** and song duration **(B)** do not differ among the five moth families but dominant frequency **(C)** differs among them. In these violin plots, the upper and lower limits indicate the minimum-to-maximum range, and the width indicates the relative frequencies of the data points.

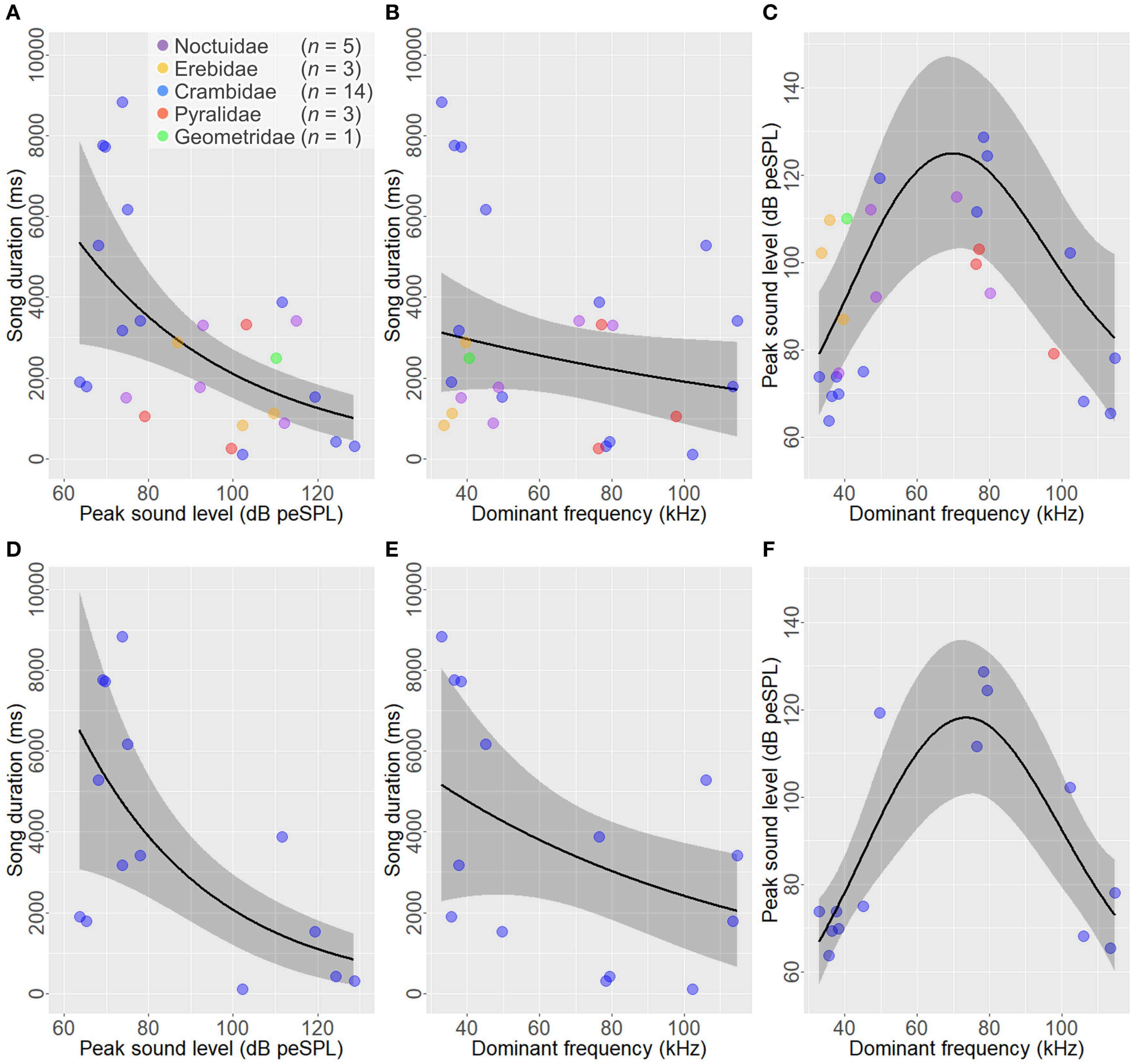

FIGURE 4 | Relationships among song duration, peak sound level, and dominant frequency in male ultrasonic courtship songs of moths. For the 26 moth species, there is a negative relationship between song duration and peak sound level **(A)**, whereas no relation is found between song duration and dominant frequency **(B)**. A significant nonlinear relationship is found between peak sound level and dominant frequency **(C)**. When considering only the 14 crambid moths, a negative relationship between song duration and peak sound level is prominent **(D)**, there is no relation between song duration and dominant frequency **(E)**, and a nonlinear relationship is significant between peak sound level and dominant frequency **(F)**. Black lines and gray bands are means and 95% confidence intervals estimated by GAMM. Colored circles are means for each species; purple, Noctuidae (Noctuoidea); orange, Erebidae (Noctuoidea); blue, Crambidae (Pyraloidea); red, Pyralidae (Pyraloidea); green, Geometridae (Geometroidea).

Even when focusing on the single taxonomic family Crambidae, we again corroborated the negative relationship between song duration and peak sound level (LR test in GAMM, $\chi^2 = 5.32$, $p = 0.0025$; **Figure 4D**), the absence of a significant relationship between song duration and dominant frequency ($\chi^2 = 3.06$, $p = 0.058$; **Figure 4E**), and the negative relationship between peak sound level and dominant frequency ($\chi^2 = 0.73$, $p < 0.0001$; **Figure 4F**).

DISCUSSION

We have shown that a negative relationship between loudness and duration exists in the ultrasonic courtship songs of male moths. Because loud-and-long songs are conspicuous to unintended receivers as well as to potential mating partners, we propose that the acoustical tradeoff in moth song is a consequence of evolutionary adaptation relevant to avoidance of location by eavesdroppers. Males of some field crickets are known to generate "soft" courtship songs after attracting a female by calling songs (Alexander, 1961; Balenger, 2015). The courtship songs of the field crickets last only a few seconds, suggesting that the softness and the shortness of the songs evolved for the avoidance of eavesdropping by predators and parasites. Successful copulation (genital coupling) in insects generally requires the absence of interference from other males. Courtship songs are likely to evolve to be soft and short to reduce the opportunity for a rival male to interrupt the courtship behavior of a singing male and, in some cases, to steal an intended mate (Balsby and Dabelsteen, 2005; Balenger, 2015; Reichard and Anderson, 2015).

In moths, multiple males may gather around a single female that is releasing a sex pheromone in advance of a mating bout (Baker, 1983; Schlaepfer and McNeil, 2000; Nakano et al., 2014). Hence, singing males would gain the benefit of avoidance of eavesdropping by emitting low-amplitude courtship songs that can be detected only by a female in close proximity to the singer. Lengthy courtship songs, such as those of *Ostrinia* lasting for >10 s, might be perceived by predacious gleaning bats, which can even perceive the rustling sounds of small moving insects (Fuzessery et al., 1993; Goerlitz et al., 2008; Jones et al., 2011; Siemers et al., 2012). However, the longer the duration of a moth song, the lower is the peak sound level. Taking account of atmospheric attenuation of high-frequency ultrasonic courtship songs, the opportunity for eavesdropping long-and-soft songs of moths would be limited for bats as well as for male moth competitors. In this study, we focused on comparison of peak sound level and duration of courtship song among various species that emit ultrasounds ranging from transient clicks to consecutive bursts (**Figure 1**). It is hard to perform a direct comparison of total acoustic power, consisting of sound amplitude and song duration, among the 26 species we studied, but the energetic cost of production of courtship song also could contribute to the negative relationship between peak sound level and song duration (**Figures 4A,D**) (Hoback and Wagner, 1997; Reinhold et al., 1998; Oberweger and Goller, 2001; Clark, 2012). In terms of explaining the obtained results of the acoustical tradeoff, hypotheses of physical constraints on the energetic cost and the sound-producing mechanism are not mutually exclusive to our hypothesis that moths evolved hidden courtship songs for avoiding eavesdroppers. The within-species analyses, however, supported no significant relationships among the song characteristics, implying that the energetic constraint may not affect the acoustical tradeoff in the courtship songs of each moth species. To corroborate the adaptive function of the countertactic courtship song, we need to confirm that insectivorous bats more often (1) approach louder-and-longer courtship songs and (2) attack male moths singing louder-and-longer songs in a future study. For the significant nonlinear relationship between peak sound level and dominant frequency (**Figures 4C,F**), we speculate that the mechanical constraint in the ultrasound production influences this relationship. It is generally because the stridulation and percussion organs do not generate extremely high-frequency ultrasounds, whereas ultrasonic songs produced by the tymbal organs include high-frequency components of >50 kHz (Nakano et al., 2015). Taking the damping of high-frequency ultrasounds in the air into consideration, the dominant frequency of courtship songs might be related to the eavesdropping; however, the hypothesis that courtship songs with higher frequency have higher sound levels is not supported by our data.

For the peak sound level and the song duration, phylogenetic signals (Pagel's λ and Blomberg's K) which significantly differed from no signal indicated that the two traits were not independent of the species relatedness, but more divergent than expected under the Brownian motion models of evolution (random drift). By contrast, the phylogenetic signals of the dominant frequency of song supported the independence of the phylogeny, and less similar than expected under random drift. PGLS and GAMM approaches suggest that the correlation between sound level and duration evolved under a random walk and the negative relationship was affected by directional selection (**Figure 4**). Moderately strong phylogenetic relatedness in the peak sound level and song duration supports the conserved ultrasound-producing mechanisms in erebid and pyralid moths and the recent independent evolution of diverse ultrasound-producing mechanisms in noctuid and crambid moths (Conner, 1999; Nakano et al., 2015). In the family Erebidae, tiger and lichen moths have similar organs on the lateral side of the metathorax (Conner, 1987, 1999; Nakano et al., 2013), and in the family Pyralidae, Galleriinae moths have corrugated tymbals on the tegulae covering the base of the forewings (Spangler, 1986; Conner, 1999; Kindl et al., 2011). In the family Noctuidae, *Spodoptera* moths have tymbal membranes on the ventral side of the metathorax (Nakano et al., 2009b, 2010a), *Hecatesia* moths have alar castanets on the forewings (Bailey, 1978), and *Rileyana fovea* has stridulation organs on the hindwings and hind legs (Surlykke and Gogala, 1986). In the family Crambidae, *Conogethes punctiferalis* has smooth tymbal organs on the lateral side of the mesothorax (Nakano et al., 2012b), and *Ostrinia* moths have specific stridulation scales on the mesothorax and forewings (Nakano et al., 2008). While the ultrasound-producing mechanisms for courtship songs vary among genera (or families for Erebidae and Pyralidae), the peak sound level and duration of moth courtship songs showed a significant negative relationship among the 26 species for five moth families that we used. The negative relationship, therefore, has possibly originated from selective forces from eavesdroppers and female receivers.

Females may evolve a preference for acoustically conspicuous courtship songs, similar to the calling songs generated by high-quality or good-condition males (Jang and Greenfield, 1996; Simmons et al., 2013; Cordes et al., 2014; Balenger et al., 2016). Among acoustic moths in which the function and detailed acoustic characteristics of the songs have been analyzed to date, courtship songs relevant to mate recognition or mate preference are found only in the erebid *Eilema japonica* (Nakano et al., 2013), the crambid *Conogethes punctiferalis* (Nakano et al., 2012a, 2014), and the pyralid *Galleria mellonella* (Spangler, 1985, 1986). Males of these species emit courtship songs at average peak sound levels of 87, 112, and 100 dB peSPL and average durations of 2,872, 3,880, and 249 ms, respectively, indicating that they do not produce loud-and-long courtship songs. This finding suggests that the preference of female receivers for male courtship song is also affected by negative selection pressures. A female close to a male that is emitting exaggerated loud-and-long songs would be exposed to predation from eavesdropping bats that are hunting singing males (Pocklington and Dill, 1995; Candolin, 1997; Alem et al., 2011). In moth species, in which the males use "deceptive" courtship songs toward females, i.e., *Spodoptera litura* and *Ostrinia* spp. (Nakano et al., 2008, 2010a,b), such a risk of predation on silent females by eavesdropping bats would increase if these males generated conspicuous lengthy songs in close proximity to focal females. We suggest that both avoiding eavesdroppers and being detected by intended receivers drive the current tradeoff between loudness and duration of male courtship song. A similar relationship in song characteristics may be found in other singing animals as well.

AUTHOR CONTRIBUTIONS

RN conceptualized the study, performed acoustic recordings and measurements, performed statistical analyses, and wrote the original draft. KN carried out and wrote the phylogenetic analyses.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00244/full#supplementary-material

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From Understory to Canopy: *In situ* Behavior of Neotropical Forest Katydids in Response to Bat Echolocation Calls

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Predator-prey interactions take place in complex environments, and research on the sensory ecology of predator-detection relies on understanding when, where, and how prey experience and respond to predator cues. Bats are significant nocturnal predators, and insects have evolved diverse strategies for avoiding predation by bats. While it is well-known that insects exhibit anti-bat strategies, from avoidance flight to reduced acoustic signaling, the specific conditions that elicit some of these behaviors are less well-known. To illuminate how insects respond to bats in nature, we studied how calling behavior changed when katydids experienced echolocation calls in a Neotropical forest. The diverse Neotropical bat community includes species that eavesdrop on prey sounds, such as the songs produced by male katydids. Previous research has shown that some katydid species respond to echolocation calls by reducing acoustic signaling. To capture the interactions of bats and katydids, we placed acoustic monitors at heights of 8, 16, and 24 meters above ground in 10 locations in the forest on Barro Colorado Island, Panama and recorded continuously for 24 h at each location. We randomly selected 250 recordings with echolocation calls and compared the acoustic spectrum of the forest before a bat arrived, when a bat was present, and after the bat was no longer detectable. We tested whether the response to bat calls changes with height, the family of bat producing the calls, the duration of the echolocation sequence, call amplitude, and call peak frequency. Bats appeared on ~50% of nighttime recordings, but echolocation calls that could have been produced by eavesdropping bats were rare (<4% of calls). Insect response to bats was nuanced and context-dependent. Despite the rarity of truly dangerous predator cues, echolocation decreased insect sound at several frequencies and heights. Insect response was not uniform, and in many cases echolocation calls had little effect on insect activity, perhaps reflecting the fact that echolocation calls were an inconsistent cue for the presence of eavesdropping bats. These nuanced responses raise interesting questions about predator detection in noise and provide valuable context for laboratory investigations on the sensory ecology of how individual prey species respond to predator cues.

Keywords: canopy, predator-prey interaction, eavesdropping, gleaning bats, Tettigoniidae, sensory ecology

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INTRODUCTION

Detecting and avoiding predators is a fundamental selective pressure on sensory systems and behavior (Endler and Basolo, 1998; Fullard, 1998; Lacalli, 2001), but predator detection and avoidance is often studied in laboratory contexts that cannot capture the full complexity of natural environments (Calisi and Bentley, 2009). Therefore, to understand the evolution and maintenance of anti-predator behaviors, it is important to investigate prey responses both in the lab and the field. Quantifying how prey detect and respond to predators in natural environments is often logistically challenging because these interactions occur in habitats that are structurally complex and contain many interacting species (Belwood and Morris, 1987; Williams et al., 2004; Staller et al., 2005). In addition, the behavior, physiology and responses of organisms are affected by variables such as weather, light level, and reproductive stage (Thompson, 1978; Christian and Tracy, 1981; Berger, 1991; Culler et al., 2015). Without information on the natural range of behaviors and responses, scenarios used in laboratory investigations might represent atypical cases or extreme conditions. Understanding the range of natural predator stimuli and prey responses is foundational to choosing appropriate experimental stimuli and testing paradigms for more controlled studies of behavior, physiology, and sensory system evolution.

Bat-insect interactions provide an excellent opportunity for studying predator-prey interactions due to the almost exclusive use of sound for both predator and prey detection (Conner and Corcoran, 2012; Yager, 2012; ter Hofstede and Ratcliffe, 2016). Bats produce high-frequency echolocation calls to orient in their environment and locate insect prey while in flight. The intense predation pressure exerted on insects by bats (Kalka et al., 2008; Williams-Guillén et al., 2008; Boyles et al., 2011) has selected for the evolution of ultrasound sensitive ears and ultrasound-triggered defensive behavior in at least six orders of insects (Yack and Dawson, 2008). The combination of lab and field studies on insect ultrasonic hearing (Roeder and Treat, 1957; Yager and Spangler, 1995; Schul and Sheridan, 2006; Yager and Svenson, 2008), anti-bat behavior (Rydell et al., 1997; Yager et al., 2000; Rosen et al., 2009; Römer et al., 2010; Barber and Kawahara, 2013) and predator-prey interactions (Miller and Olesen, 1979; Ghose et al., 2009; Corcoran and Conner, 2012) have revealed enormous variation in insect defenses against bats. This variation suggests multiple outcomes of arms races between bats and insects depending on the natural history of the predator and prey species involved.

Orthopterans, the insect group that includes crickets and katydids, are especially well-suited for studying predator-prey dynamics because both bats and prey produce and respond to acoustic signals (Nolen and Hoy, 1986; Faure and Hoy, 2000; ter Hofstede and Fullard, 2008; Jones et al., 2011). Male crickets and katydids produce songs to attract females. Bats prey on orthopterans in many environments, but in Neotropical forests, bat predation is particularly intense, especially for insects that produce sound (Belwood and Morris, 1987; Belwood, 1988a,b; ter Hofstede et al., 2017). The Neotropical bat community is one of the most diverse in the world, with species feeding on everything from fruit and nectar, to insects, vertebrates and even blood (Kalko et al., 1996; Bernard, 2002). The majority of insectivorous bat species in Neotropical communities are aerial insectivores, catching insect prey in flight (Denzinger et al., 2018). However, there are also a number of bat species in the family Phyllostomidae that eavesdrop on the communication signals and incidental sounds produced by insects to detect and locate prey and then glean them off vegetation (Tuttle et al., 1985; Belwood, 1988a,b; Falk et al., 2015). These gleaning bats present a particularly serious threat for orthopterans that attract mates using acoustic signals.

Orthopterans, however, are not defenseless. Many can hear bats and modify their behavior in response (Moiseff et al., 1978; ter Hofstede and Fullard, 2008). Crickets and katydids in flight will veer away from the echolocation calls of a bat (Moiseff et al., 1978; Nolen and Hoy, 1984; Libersat and Hoy, 1991; Schulze and Schul, 2001). In Neotropical forest katydids, many species have very low signal repetition rates and produce very little total sound (<5 s/night in some species) (Belwood, 1988a, 1990; Symes et al., 2016). Calling cessation provides a particularly useful lens for assessing prey responses to predator cues because the reaction of the insect and the dynamics of the predator-prey interaction can be captured using acoustic recording alone. Laboratory investigations of Neotropical katydid responses to the echolocation calls of gleaning bats have yielded mixed results, with some katydid species reducing call production while others persist (ter Hofstede et al., 2010). The variable laboratory results suggest that responses in the field may vary also, potentially in ways that shed light on why individual katydid species respond in the way that they do.

By placing acoustic monitors in a Neotropical forest, we used the passage of bats as a natural experiment to test whether katydid call cessation is a common response to predator cues in nature, and to assess the conditions under which it occurs. This *in situ* design allows us to infer how insects respond when they are experiencing a natural rate and pattern of bat exposure. In addition, recording in the forest captures the behavior of insects when they have a natural range of hiding locations, vegetation density, exposure to conspecific and heterospecifics cues, and spatial information provided by bat echolocation calls. To test how katydids respond to predator cues, we quantified the acoustic profile of the forest before, during and after bat echolocation sequences recorded on acoustic monitors.

In addition to the overall response of katydids to bat calls, we investigated specific parameters that might influence whether katydids respond to bat calls. First, we tested whether katydid responses to bat echolocation calls differ by height in the forest. For example, katydids might show greater responses to bat calls at intermediate heights where vegetation is expected to be less dense than in the understory and canopy (Marten and Marler, 1977). Second, we tested whether katydid responses differ depending on the family of bat or the peak frequency of the echolocation calls. Some bat species produce quasi-constant frequency calls (e.g., Emballonuridae) whereas others use downward frequency modulated sweeps (Phyllostomidae, Vespertilionidae). The peak frequency of echolocation calls varies across species in taxa that produce each type of echolocation call (Fenton et al., 1999;

Jung et al., 2007; Surlykke and Kalko, 2008; Zamora-Gutierrez et al., 2016). If katydids are capable of differentiating among bat calls, the strongest insect response is predicted to occur in response to echolocation calls of the Phyllostomidae, the bat family that is known to contain eavesdropping predators. Because phyllostomids produce relatively high frequency calls, katydids might also be more responsive to higher than lower frequency calls. Third, we considered two parameters that provide information about the risk of an individual bat: amplitude, which provides information about proximity of the predator, and the duration of the detected bat pass, which might indicate a bat hunting in the area.

MATERIALS AND METHODS

Study Site

To quantify the acoustic interactions of Neotropical bats and katydids, we generated audio recordings on Barro Colorado Island, Panama (BCI). The forest on BCI is primarily secondary growth tropical lowland rainforest (Ziegler and Leigh, 2002). We selected 10 sites that represent the mix of closed canopy and small gaps present on BCI and placed audio recorders at three heights in each of these sites.

Recording Insect and Bat Activity in the Forest

We used two towers and eight canopy emergent trees as recording sites (**Figure S1**). At each site, to sample as much of the height distribution as possible, we placed recording equipment at three heights (8, 16, and 24 m ± ca. 1 m) relative to the base of the tree or tower. In towers, the equipment was secured directly to the structure with the microphones pointed horizontally away from the tower. In trees, we climbed the tree, placed a pulley on a branch above 24 m in height and used a distance-calibrated rope to raise and lower recording equipment in protective cases that held the microphone in a horizontal position. At each site, we recorded continuously for 24 h. Recordings were made using acoustic monitors with ultrasound sensitive microphones (D500X, Pettersson Elektronik AB, Sweden). The trigger sensitivity was set very low so that the recorders were triggered continuously. The recorder created a file each time it was done saving the previous file, generating approximately one 20 s.wav file per minute for 24 h. After each of the 10 sites had been sampled, we repeated the sampling, resulting in a second 24-h recording from each site approximately 2 weeks after the first.

Measuring Frequency Structure of Katydid Community

To characterize the signals of the BCI katydid community, we captured male katydids, identified them, and recorded the sounds they produced. Katydids were collected by searching vegetation in the forest and catching individuals that flew to lights. Katydids were identified to species using several published resources (Nickle, 1992; Naskrecki, 2000; Cigliano et al., 2018). Male katydids were recorded in buildings on BCI with large screen windows so that they experienced ambient temperature, humidity, light and sounds of the forest but were protected from rain and predation during recording.

Male katydids were placed individually in cylindrical mesh cages that do not interfere with sound transmission across the frequencies of interest. A microphone (CM16, Avisoft Bioacoustics) responsive to frequencies between 3 and 100 kHz was positioned 30 cm from and pointing at the cage. Microphones were connected to a high-speed data acquisition board (UltraSoundGate 416, Avisoft Bioacoustics), which was connected by USB to a laptop computer running RECORDER software (Avisoft Bioacoustics). Recordings were triggered by the sound produced by katydids, with a pre-trigger time of at least 1 s to record the entire call.

To determine the typical frequencies produced by katydids on BCI, we analyzed one call per individual for three individuals per species for 34 katydid species (see **Table S1** for species). High quality recordings were filtered with the inverse of the microphone frequency response to obtain natural relative amplitudes for each frequency. These recordings were high pass filtered at 7 kHz, a frequency that was lower than the lowest frequency in any of the calls. We then used the *spec* function of the R *seewave* package to extract the spectral distribution for each recording (Sueur et al., 2008) and took the median of these spectral distributions to represent the frequency distribution of the community.

Quantifying Bat Presence

To determine how often katydids are exposed to bat echolocation calls, we randomly selected five recordings from each site from each height and each sampling event. The recordings were randomly selected during the nighttime hours of 18:00 to 06:00 with an equal number of recordings drawn from each site and height. This selection process resulted in a sample of 300 recordings that were then scored for whether bat echolocation calls were present or absent. Sound files were opened in SASLab Pro sound analysis software (Avisoft Bioacoustics, Germany) and spectrograms were visually screened at 1 s durations. To identify echolocation signals, we searched the literature for publications describing echolocation signals for the 76 bat species documented on BCI (Denzinger et al., 2018). Signals in recordings that matched the shapes, durations, repetition rates and frequency ranges of documented bat calls were classified as bat echolocation calls. Signals that fell outside the range of one of these parameters were not classified as bat echolocation calls.

Quantifying Katydid Responses to Bat Passes

Our goal was to test whether katydid calling patterns change when bats are present. The katydid chorus consists of a few calls of individuals near the microphone that can be identified to species as well as the calls of more distant individuals that cannot be identified to species because the calls are quieter and are degraded by passage through, and reflection by, the vegetation. Therefore, instead of testing whether individual katydids stopped singing when bats were present, we tested whether the acoustic profile of the forest was changed by the passage of bats, and specifically whether the range of frequencies typical for katydid acoustic signals decreased in amplitude, reflecting calling cessation by some individuals. To our knowledge, this is a novel analysis approach and one that may be broadly applicable in a variety of organisms.

We identified focal recordings that contained echolocation calls indicating a bat pass. We obtained five focal recordings from each height at each site for each sampling interval for a total of 300 possible recordings (5 focal recordings × 3 heights × 10 sites × 2 sampling intervals). Each recording was obtained by first selecting a random number, finding the corresponding recording, and then progressing through the recordings in sequence until we arrived at a recording that contained echolocation calls. Because power to one recorder failed in the middle of recording and some sites did not have enough recordings with sufficient time before the first bat call to collect a complete set of 5 recordings, the extracted sample was 250 recordings that contained echolocation calls. For each focal recording, we identified bats to family, genus or species and obtained the time for the first and last detectable echolocation call on the spectrogram as well as the time, amplitude, and dominant frequency of the highest amplitude echolocation call. We used a similar screening process to select control recordings that did not contain bat calls, allowing us to conduct parallel analyses on these recordings.

To assess changes in acoustic profile, we compared the energy spectrum before the arrival of the bat against the energy spectrum when the bat was present (**Figure 1**). From each focal recording, we compared two windows of time, a "before bat" window and a "during bat" window, each lasting 3 s. The before bat window spanned from 5 to 2 s before the first detectible echolocation call on the recording. The during bat window centered on the loudest echolocation call and included a window of 1.5 s on either side of this time. These same time windows were applied to the control recordings to assess whether amplitude differed between two time points when bats were not present. To determine how quickly the insect community recovered, we identified a third window of 3 s that spanned from 2 to 5 s after the last detectible echolocation call. Using the R packages *seewave* and *tuneR*, we extracted these windows of time from the full recording and used the *meanspec* function to find the mean spectral energy present in each frequency bin from 0 to 150 kHz (256 bins, each 0.59 kHz) (Sueur et al., 2008; Ligges et al., 2018).

Sound amplitude is typically reported using the decibel scale, which reflects the logarithmic nature of amplitude perception in humans and at least some other animals (Brumm, 2013). On the decibel scale, the amount of sound energy that is needed to increase amplitude by 6 dB is not equal to the amount by which sound energy must decrease to result in a 6 dB amplitude decrease. The nature of this measurement makes numeric means and standard deviations an inaccurate representation of amplitude. Consequently, statistics on decibel level were performed using non-parametric tests.

To analyze spectral changes associated with bat passes, we used paired Wilcoxon rank sum tests, a non-parametric analog of a paired *t*-test. We tested for significant changes at 5 kHz intervals from 10 to 30 kHz, frequencies representative of katydid calls. Analyzing calls at 5 kHz intervals allowed us to test whether insects that called with high peak frequencies had a different response to echolocation calls than insects that called with a lower peak frequency. The use of 5 kHz bins also allowed us to isolate the bin that contained the low harmonic of emballonurid bat echolocation calls. Analyzing the data by frequency increased the number of tests that we performed, increasing the probability of finding significant differences, but also decreased the power of the tests, which decreased the probability of detecting differences. Wilcoxon rank sum tests were used to compare the two time samples within a recording for the following comparisons: before vs. during bat, before vs. after bat, and the control analysis that compared two times in recordings that did not contain bat echolocation calls. Non-parametric Spearman's rank correlations were used to test for correlations between the strength of insect response to bats and three acoustic characteristics of the echolocation calls: duration of the bat pass (time from the

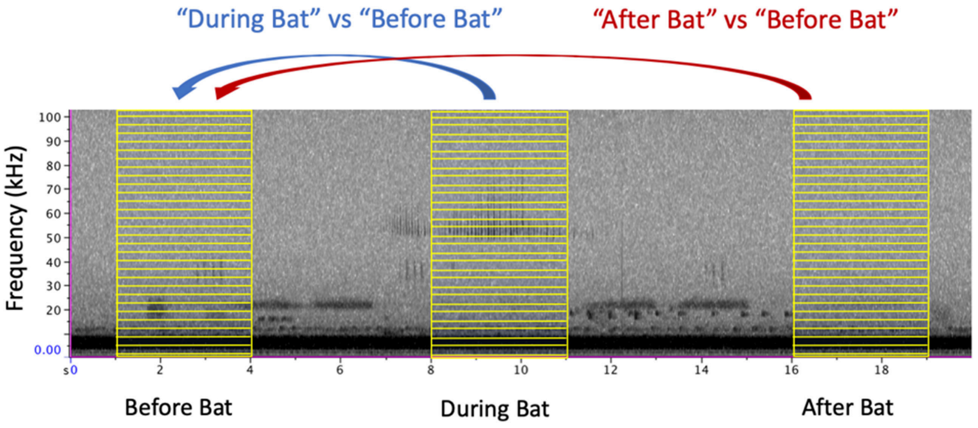

FIGURE 1 | Sample windows were comprised of a 3 s window of sound. The "Before Bat" window ended 3 s before the first detectible echolocation call and the "After Bat" window began 3 s after the last detectible echolocation call. The "During Bat" window was centered on the highest amplitude echolocation call. For clarity of illustration, only a subset of the frequency bins are shown (yellow boxes).

first to the last call detectable on the spectrogram), amplitude (measured as peak-to-peak voltage from the oscillogram), and peak frequency (frequency with the most energy, as measured from the power spectrum).

Due to the combination of tests that include both independent and partial overlap of samples and also recordings that presumably include both katydid species that produce narrowband calls at specific frequencies and those that produce broadband calls across all frequencies, we do not use corrected alpha values for multiple tests. We report p-values and interpret these values using an alpha value of 0.05, but note that readers should consider the possibility of non-independence between tests at adjacent frequencies and pooled samples compared to tests by height and bat family.

RESULTS

Frequency Structure of the Katydid Community

The katydid community of Barro Colorado Island produces calls that occupy a range of frequencies (**Figure 2**). Most of the sound energy occurs between 10 and 30 kHz, although some species produce frequencies of up to 80 kHz (ter Hofstede et al., 2010; Montealegre, 2012).

Presence of Bats

In ambient recordings, bats were pervasive, appearing in 46% of randomly selected recordings between 18:00 and 06:00 (51% of recordings at 8 m, 45% at 16 m, and 43% at 24 m). The probability of bats appearing on the recording did not differ by height ($\chi^2_2 = 1.39$, $p = 0.50$).

Of the 250 recordings used to measure changes in frequencies typical of katydid calls, we were able to assign approximately 92% of echolocation recordings to bat family (**Figure 3**). In order of abundance, families included Emballonuridae ($N = 130$), Vespertilionidae ($N = 70$), Mormoopidae ($N = 37$), Phyllostomidae ($N = 7$), and Molossidae ($N = 1$). Within Vespertilionidae, we were able to identify all 70 recordings as belonging to bats in the genera *Myotis* or *Rhogeesa*. Within Emballonuridae, we identified calls of *Saccopteryx bilineata* ($N = 53$), *Saccopteryx leptura* ($N = 16$), *Centronycteris centralis* ($N = 36$), *Cyttarops alecto* ($N = 16$), and *Peropteryx macrotis* ($N = 1$). Within Mormoopidae, we were also able to identify calls of three bat species: *Pteronotus gymnonotus* ($N = 22$), *Pteronotus parnellii* ($N = 14$), and *Pteronotus personatus* ($N = 1$). Peak frequency of the bat echolocation calls ranged from 19.7 to 78.1 kHz, with a median of 46.6 kHz (25th/75th quantile spread: 42.9–53.5 kHz).

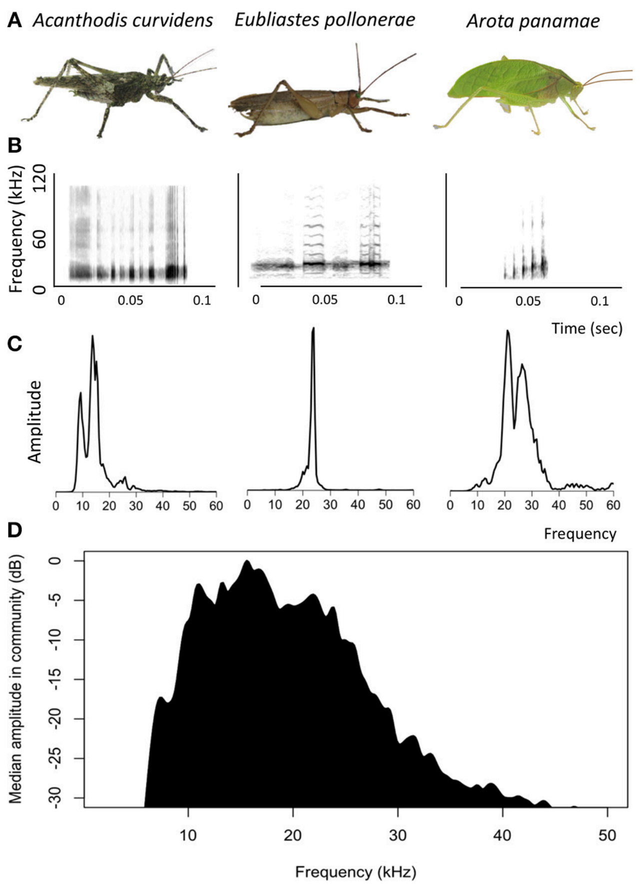

FIGURE 2 | Acoustic signals of katydids recorded on Barro Colorado Island, Panama. **(A)** Photographs of three katydid species. **(B)** Spectrograms of the calls of three katydid species. **(C)** Power spectra of the calls of three katydid species. **(D)** Median power spectrum of 34 katydid species common on Barro Colorado Island, Panama (three individuals per species).

Change in Frequency Structure When Bats Pass

To test whether there is a change in acoustic activity when echolocation calls appear on recordings, we compared the amount of energy at focal frequencies for: (1) two time bins of 3 s in a recording that did not contain a bat pass, (2) the time bin before and the time bin during a bat pass, and (3) the time bin before and the time bin after a bat pass. In randomly selected recordings that do not contain bat echolocation calls, there were no significant differences in the amount of energy at frequencies between 10 and 30 kHz for the two time selections (Wilcoxon paired rank sum tests, $p > 0.05$; **Figure 4A**). In recordings with bat echolocation calls, sound levels decrease in a subset of the frequency bands produced by katydids during the bat pass (**Figure 4B**). The decrease was significant at 10 kHz ($V = 18{,}309$, $p = 0.011$) and 30 kHz ($V = 18{,}128$, $p = 0.017$). The increase in amplitude at ~20 kHz is due to the lower harmonic of bat echolocation calls, primarily those produced by the Emballonuridae, which were abundant in our sample. For comparisons of time bins before and after bat echolocation calls, there was a significant decrease in energy at 30 kHz ($V = 13{,}213$, $p = 0.008$) and a trend toward decreasing amplitude at 10 kHz ($V = 12391$, $p = 0.068$).

The strength of the acoustic response to bats also differed with the height of the recorder in the forest and the family of bat (**Figures 5**, **6**). We tested for significant decreases in energy at 10, 15, 20, 25, and 30 kHz at each of the three heights of the

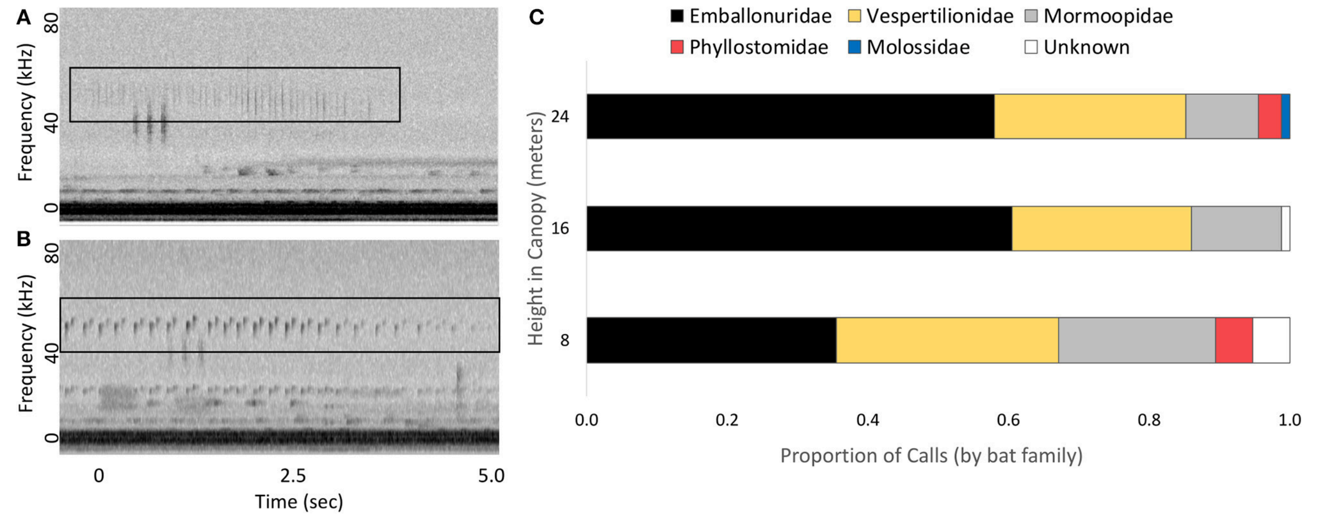

FIGURE 3 | Echolocation calls of bats recorded on Barro Colorado Island, Panama. Example echolocation calls from two bat families (**A**: Phyllostomidae, **B**: Emballonuridae, echolocation calls indicated with black boxes) and the proportion of echolocation calls at each height produced by each family of bats **(C)**.

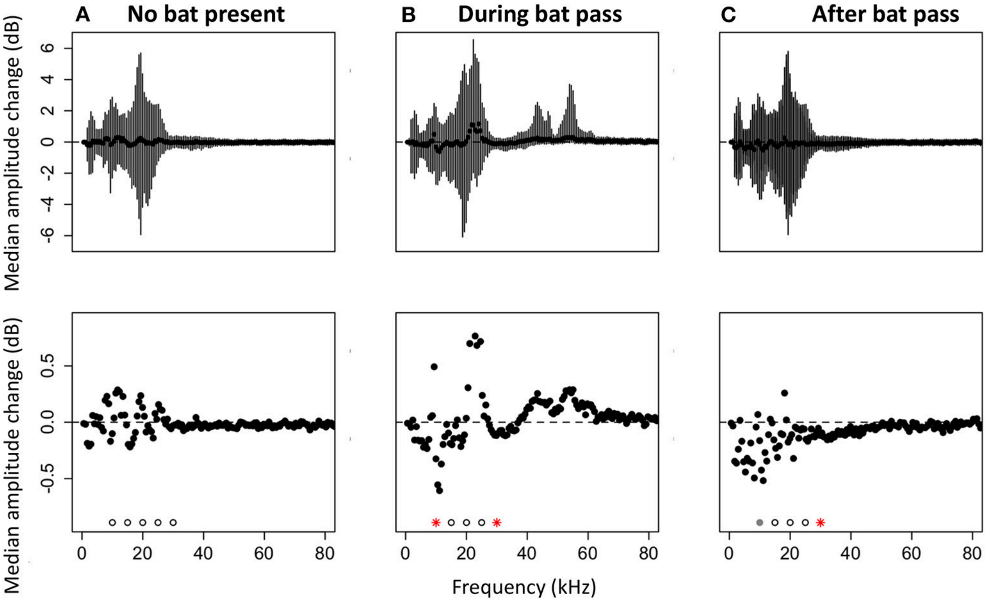

FIGURE 4 | Median changes in amplitude by frequency. Negative values indicate less energy in the second time bin. **(A)** Median amplitude change between two time bins in a recording without echolocation calls ($N = 246$ recordings). **(B)** Median amplitude change comparing time bins before and during an echolocation sequence of a bat ($N = 250$ recordings). **(C)** Median amplitude change comparing time bins before and after an echolocation sequence of a bat ($N = 210$ recordings). Top panels: medians with error bars representing the 25th to the 75th percentile. Bottom panels: same data as top panels, but scaled in to show just the median values. Significance was tested at 5 kHz intervals from 10 to 30 kHz. Significant differences are shown with red asterisks (Wilcoxon paired ranks sums tests, $p < 0.05$), marginally significant differences are shown with gray circles ($0.05 < p < 0.1$), and tests that were not significant are shown with open circles.

recorders. When comparing time windows before and during bat echolocation calls, there was a significant decrease in amplitude at 30 kHz at 24 m in the canopy ($V = 2{,}478$, $p = 0.015$, $N = 88$), there were no significant changes in amplitude at any frequency at an intermediate height of 16 m ($N = 86$), and there was a significant decrease in energy at 10 kHz at 8 m ($V = 1858$, $p = 0.021$, $N = 76$; **Figure 5**). When comparing time bins before and after a bat pass, there were significant decreases in energy at all frequencies except 15 kHz at a height of 24 m (10 kHz: $V = 1{,}757$, $p = 0.040$; 20 kHz: $V = 1{,}747$, $p = 0.045$; 25 kHz: $V = 1{,}859$, $p = 0.011$; 30 kHz: $V = 1{,}815$, $p = 0.020$; $N = 75$), there were no significant changes in amplitude at any frequency at an intermediate height of 16 m ($N = 67$), and there were significant decreases in amplitude at 8 m for 25 kHz ($V = 1{,}419$,

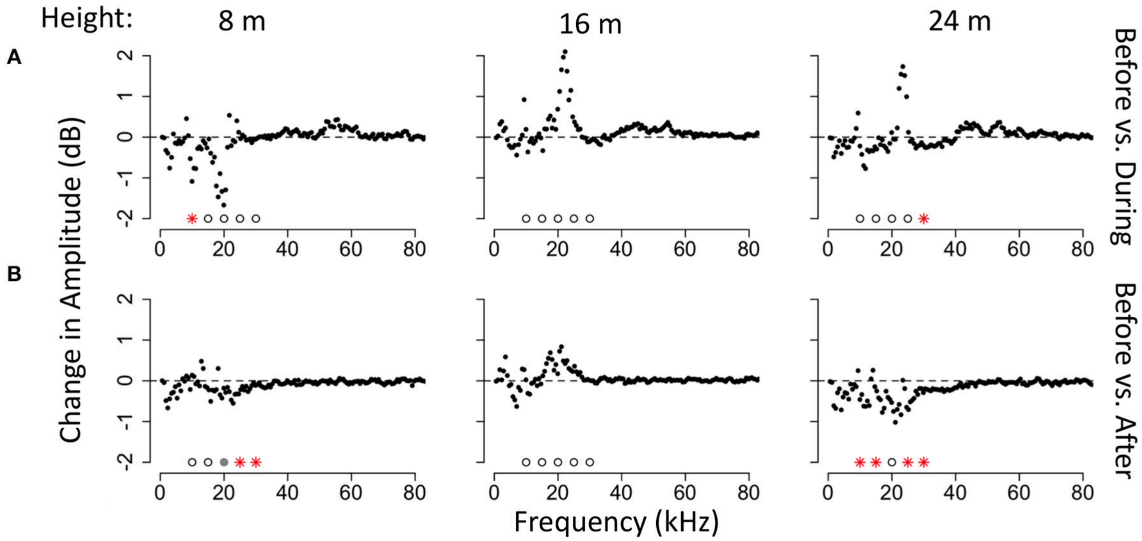

FIGURE 5 | Median changes in amplitude by frequency and height of the recorder. **(A)** Median amplitude change comparing time bins before and during a bat echolocation sequence. **(B)** Median amplitude change comparing time bins before and after a bat echolocation sequence. Significance was tested at 5 kHz intervals from 10 to 30 kHz. Significant differences are shown with red asterisks (Wilcoxon paired ranks sums tests, $p < 0.05$), marginally significant differences are shown with gray circles ($0.05 < p < 0.1$), and tests that were not significant are shown with open circles.

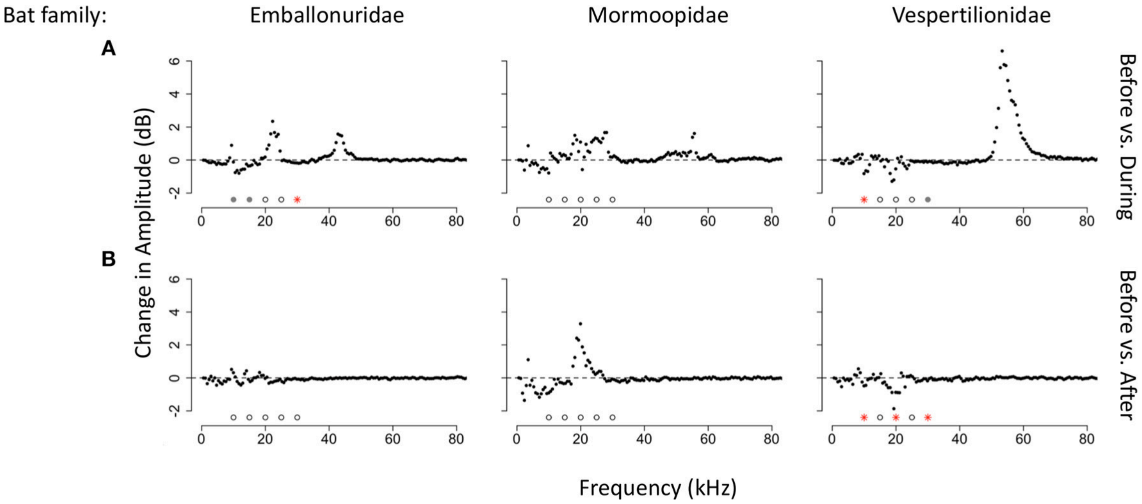

FIGURE 6 | Median changes in amplitude by frequency and bat family. **(A)** Median amplitude change comparing time bins before and during a bat echolocation sequence. **(B)** Median amplitude change comparing time bins before and after a bat echolocation sequence. Significance was tested at 5 kHz intervals from 10 to 30 kHz. Significant differences are shown with red asterisks (Wilcoxon paired ranks sums tests, $p < 0.05$), marginally significant differences are shown with gray circles ($0.05 < p < 0.1$), and tests that were not significant are shown with open circles.

$p = 0.040$) and 30 kHz ($V = 1,464$, $p = 0.021$) and a trend toward decreasing amplitude at 20 kHz ($V = 1,419$, $p = 0.095$).

We also tested for changes in amplitude for the three families of bats with the largest sample sizes in our recordings. When comparing time windows before and during bat echolocation calls, calls of bats from the family Emballonuridae significantly decreased the amplitude of the 30 kHz band ($V = 5,747$, $p < 0.001$, $N = 130$; **Figure 6A**) with a trend toward reducing insect sound at 10 kHz ($V = 4924$, $p = 0.061$) and 15 kHz ($V = 4,941$, $p = 0.056$), whereas there were no significant differences at any frequency when comparing time bins before and after emballonurid bat passes. Calls of bats in the family Mormoopidae did not result in detectible decreases in amplitude at any frequency either during ($N = 37$; **Figure 6B**) or after echolocation sequences ($N = 33$). Calls produced by bats of the family Vespertilionidae resulted in a significant decrease at 10 kHz ($V = 1,566$, $p = 0.016$, $N = 69$; **Figure 6C**) and showed a trend toward reducing sound at 30 kHz ($V = 1,460$,

$p = 0.066$) during bat passes, and caused significant decreases in amplitude at 10 kHz ($V = 1{,}226$, $p = 0.011$), 20 kHz ($V = 1{,}147$, $p = 0.044$) and 30 kHz ($V = 1161$, $p = 0.035$) after bat passes.

Amplitude of the echolocation calls and duration of the bat pass both affected the strength of insect response at some frequencies (**Table 1**). Louder echolocation calls led to a greater amplitude decrease at 10, 20, and 25 kHz, whereas longer echolocation call sequences led to a greater decrease in amplitude at 20 kHz. When the peak frequency of echolocation calls was higher, there was a greater response at 25 kHz.

DISCUSSION

Bats are common and diverse in Neotropical forests (Denzinger et al., 2018) and the insect response to bat echolocation calls is variable and context-dependent (**Figures 4–6**). While it is tempting to infer that katydids consistently stop calling when they hear bats, the observed behavior is far more nuanced. A striking feature of the acoustic environment is the sheer prevalence of echolocation calls. Between 18:00 and 06:00, nearly half of the 20 s recordings contained bat echolocation calls, meaning that insects are exposed to this cue repeatedly throughout the night. Of these echolocation calls, less than 4% are produced by bats in the family Phyllostomidae, the family that is known to contain eavesdropping bats that hunt katydids by the sounds that they make (Jones et al., 2014; Falk et al., 2015). Even within the phyllostomids, many species are not known to engage in eavesdropping behavior and instead feed on fruit or flying insects (Fleming, 1991; Teixeira et al., 2009; Weinbeer et al., 2013). Consequently, extremely few of the echolocation calls that are experienced by katydids come from predators that are a threat to these insects when they are singing. The variable results observed in this study might be a reflection of the rare enemy effect, where the strength of selection for defensive adaptations is weak due to the rarity of the predator (Dawkins and Krebs, 1979). In addition, the modest response of insects may reflect reliance on a passive defense (low baseline calling or calling from dense vegetation) rather than an active defense (reduced calling in response to echolocation calls) (Belwood and Morris, 1987). Many of the insect species that produce many calls are relatively small in size, while larger insects that may be more desirable prey for bats produce fewer calls (Symes et al. in prep).

If most of the echolocation calls heard in the forest are not a threat, it raises the question of why any katydid would reduce signaling in response to echolocation calls, potentially reducing its opportunity to attract mates (Sih et al., 1990; Magnhagen, 1991; Candolin, 1998). Phyllostomid bats produce highly directional calls with relatively low amplitude (Brinkløv et al., 2011; Surlykke et al., 2013). Consequently, although phyllostomid echolocation calls are infrequently detected on recorders, it does not necessarily mean that eavesdropping predators are rare in the environment. Using mist nets baited with singing katydids, Belwood captured an average of 1.85 eavesdropping bats per hour (Belwood, 1988a). Many eavesdropping bats will perch and produce low amplitude echolocation while waiting for prey sounds (Surlykke et al., 2013), meaning that even if eavesdropping species are relatively rare on passive recordings, insects that produce sound may attract these predators and experience dangerous echolocation calls more often, driving the evolution of behavioral responses to echolocation calls even when they are produced by other types of bats. A second, non-mutually exclusive, possibility is that even if echolocation calls are an inconsistent indication of risk, the cost of calling reduction is low enough to make call cessation either a favorable behavior or nearly cost-neutral (Wolf et al., 2007). If insects are long-lived and not highly mobile, this lost window of mate signaling may have negligible effects on mate attraction relative to the potential cost of predation. Many Neotropical katydids also tremulate, producing vibrational signals in the substrate to attract females and they might adjust their reliance on acoustic or vibrational signaling depending on predation risk (Römer et al., 2010).

There were differences in the response of the katydid community to bat echolocation calls by height in the forest. Echolocation calls decreased insect sound at 10 kHz low in the canopy (8 m) and at 30 kHz high in the canopy (24 m), but there were no differences in amplitude at the intermediate height (16 m). This result goes against our predictions based on the idea that katydids would be at greater risk of gleaning bats in areas of the forest with less dense vegetation. We do not, however, know the absolute amplitudes of sounds at the different heights in the canopy, and it is possible that the difference in

TABLE 1 | The relationship between acoustic characteristics of bat echolocation calls and the change in amplitude of ambient sound by frequency (Spearman rank correlation coefficients and *p*-values).

		Amplitude of frequency (kHz)				
		10	**15**	**20**	**25**	**30**
Duration of bat pass	Rho	−0.045	−0.109	−0.146	−0.036	0.021
	P	0.476	0.085	**0.021***	0.571	0.737
Maximum amplitude of echolocation calls	Rho	−0.156	−0.115	−0.143	−0.153	0.039
	P	**0.014***	0.069	**0.024***	**0.015***	0.536
Peak frequency of echolocation calls	Rho	−0.074	−0.121	−0.051	−0.146	−0.082
	P	0.243	0.056	0.427	**0.021***	0.197

The bold values indicate cases where the p-value is < 0.05.

insect response by frequency and height might reflect where different insect calls are more prevalent or which bat species are hunting in a given habitat. If the amplitude of the insects does not change, this could mean that insects do not respond, or that no insects with that frequency are present at that height. Although we had only a few recordings of phyllostomid bat calls and therefore we cannot quantify vertical distribution of this family, it is interesting to note that these bats were only recorded by the lowest and highest recorder, but not by the intermediate height recorder, in our random sample. Within eavesdropping bats, different bat species are known to target different acoustic characteristics of prey calls (Falk et al., 2015), and different bat species are found at different heights in the forest (Bonaccorso, 1979; Bernard, 2001) suggesting that the risk of different call types may co-vary with where particular species of bats hunt.

There were also differences in the response of the katydid community by bat family. We recorded too few echolocation sequences of phyllostomid bats to assess changes in amplitude to this group. Bats in the family Vespertilionidae triggered more significant decreases in insect sound than bats in the families Emballonuridae and Mormoopidae. Vespertilionids are aerial insectivores, but they produce downward frequency-modulated sweeps similar to phyllostomids. The acoustic similarity between the calls of phyllostomids and vespertilionids might be one reason why they elicit greater amplitude reductions in sound than quasi-constant frequency calls typical of the emballonurids. Some of the insect responses to emballonurids, however, might also be masked by the presence of lower frequency harmonics (∼20 kHz) in the echolocation calls of these bats. Insect response at these frequencies is particularly apparent when examining the acoustic profile of the forest 3 s after the bat has left the area. In this before and after comparison, it is possible to see that sound is reduced at 20–25 kHz after the bat calls are no longer detected, suggesting that insect response at these frequencies is masked by the harmonic of the bat echolocation call during the bat pass.

The acoustic characteristics of the echolocation calls had strong effects on the responses of insects. Specifically, higher amplitude echolocation calls were associated with stronger insect response across a range of frequencies (**Table 1**), suggesting that cues related to predator proximity, more than predator species, drive insect responses to bat cues. TN-1, or the T-cell, is a well-studied auditory interneuron in katydids that is broadly tuned to high frequency sound and is thought to function in bat detection in certain contexts (Faure and Hoy, 2000; Schul and Schulze, 2001). It adapts (i.e., stops responding to stimuli) in response to highly repetitive or continuous acoustic stimuli (Schul and Sheridan, 2006; Abernethy et al., 2008; Schul et al., 2012), like the backdrop of crickets in the forest. In the adapted state, however, it will respond to rarer stimuli that differ in frequency from the repetitive stimulus (Schul and Sheridan, 2006; Schul et al., 2012). In this way, it can encode the occasional high-frequency calls of echolocating bats in noisy environments (Römer et al., 2008). A single neuron cannot provide information about changes in the frequencies of the echolocation call it is encoding, which would be necessary for katydids to distinguish between types of bat echolocation calls. TN-1, however, is not the only auditory interneuron providing information to the brain in katydids. Numerous ascending auditory interneurons with varying frequency tuning have been identified in katydids, although these neurons have only been studied in a few katydid species (Stumpner and Nowotny, 2014). Therefore, there is the potential for katydids to gain information about frequency modulation in bat calls and use this information to assess risk of predation by gleaning bats.

It is often difficult to observe how prey respond to predator cues in natural contexts, but it is critical to understand the context in which interactions take place (Apfelbach et al., 2005; Calisi and Bentley, 2009). It has been known for many years that katydids respond to echolocation calls but examining the dynamics in the natural habitat and partitioning responses by height in the forest and bat family provides a more detailed look at the complex interactions in this system. The acoustic characteristics of the call produced by an insect species may interact strongly with how that species responds to bats. Future research that tests for linkages between call characteristics and response to echolocation calls will provide insight about strategies for avoiding and mitigating predation. Additional insight will come from examining how individual insect species respond to playbacks of bats to understand how insect behavior differs with body size, mating strategy, and position in the canopy.

One of the most notable findings in this research is the prevalence of echolocation calls in the nighttime soundscape. Nearly 50% of nighttime recordings contain bat echolocation calls, most produced by bat species that do not eavesdrop on the sounds produced by insects. While detecting and responding to echolocation calls could help insects increase survival, interrupting calling in response to a false danger cue could also reduce opportunities to attract mates and compete with rivals, reducing fitness. The unreliability of echolocation calls as an indicator of predator presence raises important questions about the evolution of anti-predator strategies in noisy environments, particularly when different predator and prey species arrive at diverse solutions (McElreath and Strimling, 2006).

DATA AVAILABILITY STATEMENT

Sound files and extracted data will be archived on Dryad after acceptance.

AUTHOR CONTRIBUTIONS

HtH and LS conceived and designed the study. L-OH selected the trees and LS and SM climbed them. LS and SM organized the database and L-OH and HtH selected and screened the recordings. LS wrote the analysis code and HtH identified the bats and verified the code. LS wrote the framework of the manuscript with substantial text contributed by HtH and RP. All authors read, revised, and approved the manuscript before submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2018.00227/full#supplementary-material

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The Influence of Signaling Conspecific and Heterospecific Neighbors on Eavesdropper Pressure

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The study of tradeoffs between the attraction of mates and the attraction of eavesdropping predators and parasites has generally focused on a single species of prey, signaling in isolation. In nature, however, animals often signal from mixed-species aggregations, where interactions with heterospecific group members may be an important mechanism modulating tradeoffs between sexual and natural selection, and thus driving signal evolution. Although studies have shown that conspecific signalers can influence eavesdropper pressure on mating signals, the effects of signaling heterospecifics on eavesdropper pressure, and on the balance between natural and sexual selection, are likely to be different. Here, we review the role of neighboring signalers in mediating changes in eavesdropper pressure, and present a simple model that explores how selection imposed by eavesdropping enemies varies as a function of a signaling aggregation's species composition, the attractiveness of aggregation members to eavesdroppers, and the eavesdroppers' preferences for different member types. This approach can be used to model mixed-species signaling aggregations, as well as same-species aggregations, including those with non-signaling individuals, such as satellites or females. We discuss the implications of our model for the evolution of signal structure, signaling behavior, mixed-species aggregations, and community dynamics.

Keywords: mixed-species aggregations, eavesdroppers, mating signals, collateral damage, heterospecific neighbors, predation, parasitism

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INTRODUCTION

While the use of conspicuous sexual signals to attract mates is pervasive across animal taxa, these signals come with a cost (Olson and Owens, 1998; Andersson et al., 2002; Andersson and Simmons, 2006; Bradbury and Vehrencamp, 2011). In addition to attracting females, conspicuous signals are used by eavesdropping predators and parasites to home in on their prey (Cade, 1975; Soper et al., 1976; Endler, 1980; Ryan et al., 1982; Slagsvold et al., 1995; Zuk and Kolluru, 1998; Haynes and Yeargan, 1999; Bernal et al., 2006; Siemers et al., 2012; Steinberg et al., 2014). For sexual displays that attract females and eavesdroppers, the interaction between these two selective forces is profoundly important in shaping the evolution of signal structure and of signaling behavior (Endler, 1983; Zuk and Kolluru, 1998; Kotiaho, 2001). Moreover, the influence of female choice on signal evolution (typically for more conspicuous signaling) will often be at odds with that of pressures resulting from the attraction of eavesdroppers (typically for less conspicuous signaling; Endler, 1980; Goodale et al., 2019). In such cases, the locally adapted signal is the result of a balance between sexual selection imposed by females and natural selection imposed by eavesdropping enemies (Tuttle and Ryan, 1981; Endler, 1983, 1995a; Beckers and Wagner, 2012; Trillo et al., 2013).

Changes in eavesdropper pressure can significantly shift the balance between sexual and natural selection, and thus drive signal evolution. A common response to increased eavesdropper pressure is a plastic or evolutionary decrease in signal conspicuousness (Endler, 1980, 1983; Tuttle and Ryan, 1981; Ryan et al., 1982; Ruell et al., 2013; but see Beckers and Wagner, 2012). Decreased conspicuousness can be achieved through multiple means. Signalers can, for example, change their signaling behavior by timing their displays to moments of low eavesdropper abundance or activity (Endler, 1987; Gerhardt, 1994; Bertram et al., 2004; Velez and Brockmann, 2006), by reducing signaling activity (Tuttle et al., 1982; Cade and Wyatt, 1984; Cade, 1991; Jennions and Backwell, 1992; Gerhardt, 1994), or by switching to an alternative sensory modality (Morris, 1980; Morris and Beier, 1982; Belwood and Morris, 1987). They can also alter the signal itself by decreasing signal rate or duty cycle (Morris and Beier, 1982; Belwood and Morris, 1987; Halfwerk et al., 2018), by adding signal components (Stoddard, 1999), by subtracting signal components (Endler, 1980; Ryan et al., 1982; Trillo et al., 2013), or by ceasing to signal altogether (Zuk et al., 2006). In contrast, reduced eavesdropper pressure is expected to result in increasingly conspicuous and attractive signaling systems. A decrease in eavesdropper pressure due to urbanization, for example, significantly increased call complexity and calling rate in the Túngara frog, *Physalaemus pustulosus* (Halfwerk et al., 2018). Finally, the eavesdroppers' ability to shift the cost-benefit tradeoffs in mating signals can have longstanding consequences for lineage diversification if geographic variation in eavesdropper pressure influences signal divergence (Verrel, 1991; Hoskin and Higgie, 2010; Trillo et al., 2013).

Several factors can alter the pressures posed by eavesdroppers. Here we focus on nearby signalers as a key source of variation. While the effect that signaling conspecifics have on an individuals' eavesdropper risk has been well-studied (Cade, 1979; Ryan et al., 1981; Jennions and Backwell, 1992; Bernal et al., 2007; Alem et al., 2011), less is known about the role of signaling heterospecifics in modulating eavesdropper pressure, and thereby affecting the balance between natural and sexual selection (Trillo et al., 2016). Signaling aggregations in nature, however, are rarely homogeneous, and animals often signal from mixed-species groups (Morse, 1970; Kacelnik and Krebs, 1983; Sueur, 2002; Stensland et al., 2003; Phelps et al., 2006; Wells, 2010; Römer, 2013). Our aim in this article is to explore how signaling heterospecifics influence eavesdropper pressure in mixed-species mating aggregations. We first review studies that look at the influence of signaling conspecific and heterospecific neighbors on the risks posed by eavesdropping enemies. Next, we present a model that can be used to predict how changes in an individual's predation and parasitism risks depend on the relative attractiveness, identity, and density of its neighbors. In the final section, we discuss the influence of heterospecific signalers on the evolution of signal structure, signaling behavior, mixed-species aggregations, and community dynamics.

THE INFLUENCE OF SIGNALING NEIGHBORS ON EAVESDROPPER PRESSURE

Conspecific Neighbors

Proximity to conspecifics can alter the selective pressures acting on a signaling individual (Jennions and Backwell, 1992; Bernal et al., 2007). On one hand, the presence of signaling conspecifics can enhance eavesdropper attraction if they increase encounter rates (Shelly, 2018). On the other hand, the presence of signaling conspecifics can reduce predation or parasitism risk and alleviate eavesdropper pressure via increased detection abilities (Pulliam, 1973; Van Schaik et al., 1983; Dehn, 1990), the dilution effect (Hamilton, 1971; Williams et al., 1993), the confusion effect (Landeau and Terborgh, 1986; Goodale et al., 2019), or any combination of these mechanisms. Studies on chorusing frogs and lekking moths, found that while an increase in group size did not change the number of eavesdroppers attracted to an aggregation, it did decrease *per capita* predation risk. In these cases, group size also influences male mating probability because females are disproportionally more attracted to larger groups (i.e., female-to-male ratio increases; Ryan et al., 1981; Alem et al., 2011). Thus, both studies argue that decreased predation costs paired with increased mating benefits might explain the evolution of communal displays in frogs and insects.

Heterospecific Neighbors

Prey foraging in mixed-species groups have been widely documented to enjoy reductions in predation risk (Grand and Dill, 1999; Stensland et al., 2003; Sridhar et al., 2009), but less is known about how inter-species dynamics influence risks to prey in signaling aggregations. In fact, until recently, studies of eavesdropping enemies and their effects on mating signals, have focused on single species of prey, signaling in isolation (Trillo et al., 2016). In nature, however, males advertising for mates often signal from mixed-species aggregations. Such aggregations are common in birds, frogs, and insects (Sueur, 2002; Marler and Slabbekoorn, 2004; Phelps et al., 2006; Wells, 2010; Römer, 2013). Mixed signaling aggregations may occur as a byproduct of habitat heterogeneity, if signaling species share similar requirements for mating and larval habitats and these habitats are patchily distributed (Downes, 1969; Davies, 1977; Macedo and DuVal, 2018). Additionally, selection pressure from eavesdropping enemies might also promote the evolution of mixed-species signaling aggregations in the same way that it promotes the evolution of single-species aggregations (Goodale et al., 2019).

The roles of eavesdroppers in modulating trade-offs between sexual and natural selection are likely to be amplified in mixed-species aggregations. Females are under strong selection to detect and choose males of their own species, and pairings with heterospecific males are likely to be restricted to discrimination or localization errors (Pfennig, 2000; Bonachea and Ryan, 2011).

Eavesdroppers, however, are usually not as restrictive in their prey selection, and can often benefit from attacking a broad range of prey. As a result, predator and parasite attention attracted by a given signal can spill over to neighboring prey irrespective of species. Through this mechanism, predation and parasitism risks associated with eavesdropping are especially likely to transfer between neighbors in mixed-species aggregations, shifting the balance between natural and sexual selection.

Asymmetric Attraction and Preference on the Part of Eavesdroppers

While some eavesdroppers can be relatively permissive with their choice of prey, it is important to note that not all individuals within an aggregation are necessarily equal in the eyes, or ears, of predators and parasites homing in on their signals. We consider asymmetries in neighbor-mediated eavesdropper risk at two levels. First, eavesdroppers searching for an aggregation may be more or less attracted to different kinds of signaling prey. Then, after an eavesdropper arrives at an aggregation, it may preferentially attack one prey species over another. We label these two phases of choice as "attraction" and "preference," respectively. Both definitions are sufficiently broad to include not only cognitive decisions, but also other components of choice such as the localizability of signals. Variation in the relative attractiveness of prey types may result in changes to the overall number of eavesdroppers attracted to the aggregation. Moreover, when eavesdropper preferences are asymmetrical, there may be a net transfer of eavesdropper attention between adjacent signalers. While these inequalities in attractiveness and preference can occur in conspecific aggregations, they are likely to be more important in mixed-species groups, where signals will differ substantially between prey species (Sueur, 2002; Schmidt et al., 2013; but see Tobias et al., 2014).

Signalers in an aggregation can alter eavesdropper risks faced by their neighbors in one of two ways. Signaling neighbors can increase the predator or parasitism risks of a focal individual, thus conferring "collateral damage" upon the focal. Alternatively, signaling neighbors can decrease the risks for a focal individual, thus providing a "shadow of safety" (Trillo et al., 2016). These terms have previously been applied to situations in which both the focal individual and the neighbor are signaling, and those in which the neighbor is substantially more attractive to eavesdroppers. For the purpose of this paper, we will consider the definitions of "collateral damage" and "shadow of safety" as sufficiently broad to also encompass situations in which the neighbor is not signaling, and in which the neighbor is less attractive to, or less preferred by, eavesdroppers than is the focal individual. In a study of *P. pustulosus* (túngara frogs) and *Dendropsophus ebraccatus* (hourglass treefrogs), Trillo et al. (2016) found a three-fold increase in the number of blood-sucking midges attracted to playbacks of hourglass treefrog calls when these calls were played near those of túngara frogs, demonstrating that proximity to heterospecific signalers can drastically alter the risks of signaling (in this case, through collateral damage). Similarly, Segami et al. (2016) found an increase in predation risk to cryptic female strawberry poison frogs that associated with conspicuous, aposematically colored males.

Given that mixed-species aggregations are common, we expect the previously described risk transfer mechanisms to be prevalent, and to thus be an important source of variation in the balance between natural and sexual selection acting on mating signals. Below, we describe a model that predicts the eavesdropper pressures faced by a focal signaler in an aggregation consisting of two types of prey. The model permits variation in the number of signalers of each prey type, the attractiveness of each type to mutual enemies, and the enemies' relative preference for the two types of signalers.

DESCRIPTION OF THE MODEL

Our simple mathematical model estimates the number of enemies that are expected to attack a focal individual in an aggregation that contains two types of signalers: type 1 and type 2 (**Table 1**). We model the number of enemies that attack an individual of type 1 (E_F) as the product of the total number of enemies that are attracted to the aggregation (E_C) and the proportion of those enemies that attack the focal individual (P_F, Equation 1). This can be considered an extension of earlier attempts to model conspecific aggregations by breaking down the costs and benefits of group living into the product of the rate of enemy encounters with an aggregation and the dilution of the resulting risk amongst group members (Wrona and Dixon, 1991). As with earlier efforts, the number of attacks on a focal signaler described in our model will be strongly influenced by the number of eavesdroppers attracted to an aggregation, and the dilution of risks they pose to prey. Our model also enables users to examine the effects of asymmetries on the attractiveness of, and eavesdropper preferences for, neighboring signalers.

$$E_f = E_c P_f \tag{1}$$

TABLE 1 | Model terminology and description.

Term	Class	Description
E_F	Prediction	The number of enemies that attack a focal individual of type 1
E_C	Prediction	The total number of enemies attracted to the aggregation
P_F	Prediction	The proportion of enemies at the aggregation that attack a focal individual of type 1
N_1	Variable	The number of type 1 individuals at the aggregation
N_2	Variable	The number of type 2 individuals at the aggregation
Q	Constant	The number of enemies attracted to an individual of type 1 signaling alone
R	Constant	Scales type 2's attractiveness to enemies relative to type 1's attractiveness
S	Constant	Relates the scaled number of signalers to the number of enemies attracted to the aggregation
P_1	Constant	The enemy's relative preference for type 1 signalers. $P_1 < 1$ when enemies prefer type 2, and $P_1 > 1$ when enemies prefer type 1.

We model the number of eavesdropping enemies attracted to the aggregation (E_C) as a function of the number of prey individuals of each type in the aggregation (N_1 and N_2), their attractiveness to distant eavesdroppers (Q and R), and the relationship (S) between the weighted number of prey individuals and the number of attracted eavesdroppers (Equation 2). The term "R" scales type 2's attractiveness relative to type 1's. For example, $R = 2$ if one individual of type 2 attracts twice as many eavesdroppers as does one individual of type 1. Then "Q", which is the number of enemies attracted to a single type 1 individual, scales the attractiveness of both types, weighted by R. For example, Q might be <1 when modeling the attraction of a rare enemy (e.g., a predatory mammal), because the probability of even a single attack is low. By contrast, when modeling the attraction of a common enemy (e.g., a blood-sucking parasite), Q would be high, because an individual prey can expect multiple attacks. The exponent "S" is discussed in more detail below (see section "Assumptions").

$$E_c = Q\,(N_1 + RN_2)^s \tag{2}$$

We estimate the proportion of eavesdropping enemies at the aggregation that attack an individual of type 1 (P_F) as a function of the number of type 1 and type 2 individuals and the enemies' relative preference for prey of type 1 vs. type 2 (Equation 3). The term "P_1" describes eavesdroppers' expressed preference for type 1 relative to type 2 prey (see section "Assumptions").

$$P_F = \frac{1}{N_1}\left(\frac{P_1 N_1}{P_1 N_1 + N_2}\right) \tag{3}$$

Which reduces to the following:

$$P_F = \left(N_1 + \frac{N_2}{P_1}\right)^{-1}$$

We substitute Equations (2, 3) into Equation (1) to arrive at the full model (Equation 4).

$$E_F = Q\,(N_1 + RN_2)^s\,\frac{1}{N_1}\left(\frac{P_1 N_1}{P_1 N_1 + N_2}\right) \tag{4}$$

Which reduces to the following:

$$E_F = Q\frac{(N_1 + RN_2)^s}{\left(N_1 + \frac{N_2}{P_1}\right)}$$

ASSUMPTIONS AND LIMITATIONS OF THE MODEL

For this model, we assume that each eavesdropper attracted to the aggregation attacks exactly one group member. Alternatively, we can consider the attraction phase to apply only to those enemies that eventually attack, as long as no enemies attack more than one prey. This assumption is likely to be valid for parasites, including parasitoids, and smaller predators that only consume one prey before moving on. The model would need to be modified to accommodate larger predators that consume more than one prey at a time, or to include multiple attacks by a single eavesdropper resulting from failure to capture prey on the first attack. One way to do this is to conceptualize E_C as the number of "attacks" attracted to the aggregation and E_F as the number of attacks per individual.

We also assume that eavesdropping enemy attraction follows an exponential function, permitting a range of response curves from flat ($S = 0$), through positive decelerating ($0 < S < 1$), linear ($S = 1$), and positive accelerating ($S > 1$). Values of $S < 1$ may be used, for example, to indicate environmental constraints on the numbers of eavesdropping enemies that can be attracted to the aggregation of signaling prey. In this case, the number of eavesdroppers attracted to the signaling aggregation increases with the size of the aggregation, but the marginal increase in the number of eavesdroppers attracted diminishes as the pool of potential enemies is exhausted. Attraction curves that cannot be represented by an exponential function, such as asymptotic or sigmoidal curves, could be accommodated with a slight modification to the model.

Importantly, our model assumes that both types of signalers have similarly-shaped enemy attraction functions that can be combined into a single function. This assumption does not hold in cases where signals produced by one species may directly interfere with eavesdropper perception of a second species (Simmons et al., 1971), or where the signaling behavior of one species may be influenced by that of another (Schwartz and Wells, 1984). The complexities of these interactions are beyond the scope of our simple model. Finally, we assume that the probability of attacking any one signaler is random, implying that signalers of types 1 and 2 are homogenously mixed in space. This assumption, of course, is often violated in nature (e.g., Given, 1990). This model considers only one kind of enemy at a time. However, multiple models could be used to assess multiple enemies.

It is important to note that although P_1 is defined as a preference, it encompasses the overall relative probability of an eavesdropper attacking a type 1 individual vs. a type 2 individual. This is because P_1 is not simply equivalent to the eavesdropping enemy's performance in an unconstrained two-choice test. P_1 is also influenced by any constraints on the enemy's ability to attack one or both types of prey. For example, an enemy may "prefer" type 1 in a two-choice test, but if type 1 individuals are difficult to locate or difficult to attack because of their microhabitat, P_1 could be < 1, indicating a higher probability of attacking type 2 than type 1.

APPLYING THE MODEL

Baseline Model

Our model can be used to make predictions about E_F, the number of attacks on an individual of type 1. We summarize the main results of the model in **Table 2**. Here and in the following sections, we set $Q = 1$. Q is useful for scaling real data, but it does not affect the relationships between the variables and predictions (this can be inferred from Equation 4). We begin by letting $R = 1$, so that type 1 and type 2 prey are equally attractive, $P_1 = 1$, so that they are equally preferred, and $S = 1$,

TABLE 2 | Summary of major predictions of the model.

Parameters	Effect of N_1 and N_2 on E_F
Base model ($R = S = P_1 = 1$)	No effect
Type 2 is less attractive than type 1 ($S = P_1 = 1$; $0 \leq R < 1$)	E_F increases with N_1, marginal effect decreases. E_F decreases with N_2 (shadow of safety)
Type 2 is more attractive than type 1 ($S = P_1 = 1$; $R > 1$)	E_F decreases with N_1, marginal effect decreases. E_F increases with N_2 (collateral damage)
Enemies prefer type 1 ($S = R = 1$; $P_1 > 1$)	E_F is higher than when $P_1 = 1$. E_F decreases with N_1 and increases with N_2 (collateral damage)
Enemies prefer type 2 ($S = R = 1$; $P_1 < 1$)	E_F is lower than when $P_1 = 1$. E_F increases with N_1 and decreases with N_2 (shadow of safety)
Positive decelerating or flat response curve ($R = P_1 = 1$; $S < 1$)	Dilution effect: E_F decreases with increases to N_1 or N_2
Accelerating response curve ($R = P_1 = 1$; $S > 1$)	E_F increases with both N_1 and N_2, marginal effect depends on magnitude of S.

$Q = 1$ for all comparisons.

so that enemies scale linearly with the number of prey in the aggregation. With these parameters, E_F is independent of N_1 and N_2 (Equation 4), meaning that attacks on an individual of type 1 are independent of the numbers of type 1 and type 2 individuals. If we substitute $S = 0.5$ (or any non-negative value < 1), so that marginal attraction decreases with the number of chorus members, E_F becomes negatively related to both N_1 and N_2, demonstrating a dilution effect on eavesdropper pressure (**Figure 1A**; Hamilton, 1971). In this scenario, which assumes equal attraction and preference between prey types, the presence of other signalers, regardless of type, confers a shadow of safety effect on type 1 signalers.

The Effect of *R*

When we allow R, the relative attractiveness of types 1 and 2, to differ and set all other constants to one, the relationships between the variables N_1 and N_2, and the prediction E_F can be interpreted as the consequences of variation in the *per capita* attractiveness of the chorus. We begin by simulating a situation in which type 2 is less attractive to enemies than type 1 by lowering R to 0.5, while the other constants are 1. Under these conditions, the model predicts a positive, decelerating relationship between N_1 and E_F, because the *per capita* attractiveness of the chorus increases with N_1 (**Figure 1B**). The relationship between N_2 and E_F is negative because increasing numbers of type 2 individuals decreases the *per capita* attractiveness of the chorus. Thus, lowering the attractiveness of type 2 prey promotes a shadow of safety effect: Type 1 prey that associate with type 2 prey can expect fewer attacks than those that associate with an equal number of type 1s or display alone. If we set $R = 2$, type 2 prey are more attractive than type 1 prey, and the opposite pattern emerges: E_F decreases to an asymptote with increasing N_1, and increases to an asymptote with increasing N_2, tracking the *per capita* attractiveness of the chorus, such that the presence of type 2 prey promotes collateral damage on type 1 prey (not shown). Holding Q and S constant, the overall magnitude of E_F tracks R (compare **Figures 1B,C**). In real-world applications Q could be used to correctly scale eavesdropper attraction.

Taking a more extreme approach, we can set $R = 0$, to simulate a system in which type 2 individuals do not attract enemies to the aggregation but may still be attacked. Parameterizing the model this way estimates risks to a signaling individual in an aggregation that includes non-signaling "satellite" males (Rowell and Cade, 1993), females (Segami et al., 2016), or callers of a second species whose calls do not attract eavesdroppers at a distance (e.g., because they are imperceptible to the eavesdroppers). The predictions are similar, but more extreme than the $R = 0.5$ example described above: a steeply positive, decelerating relationship between N_1 and E_F, and a steeply negative, decelerating relationship between N_2 and E_F (**Figure 1C**). In this scenario, type 2 prey cast a powerful shadow of safety on type 1 prey, because they do not attract additional enemies, but they absorb some of the attacks from enemies attracted by type 1 prey.

The Effect of P_1

Setting P_1, the eavesdropper's expressed preference to attack individuals of type 1 vs. 2, to values less than one promotes a shadow of safety effect on type 1, whereas $P_1 > 1$ promotes collateral damage to prey of type 1 if type 2 signalers also attract eavesdroppers. We begin with all constants set to one, except for P_1, which we set to 2 to represent a system in which predators' preference for type 1 individuals is double their preference for type 2s (**Figure 1D**). For any given combination of N_1, N_2, and R, E_F is higher than in the condition $P_1 = 1$, because enemies attracted to the chorus preferentially attack type 1 individuals. In this case we see that E_F decreases with N_1 and increases with N_2, meaning that type 2s inflict collateral damage on type 1s, by attracting eavesdroppers that disproportionally attack type 1s. If we instead decrease P_1 to 0.5, we simulate eavesdroppers that prefer to attack type 2s, and observe the opposite patterns: E_F increases with N_1 and decreases with N_2, because the shadow of safety effect on type 1 increases with the proportional representation of type 2 individuals (figure not shown).

The Effect of *S*

Altering S changes the relationship between the scaled number of members in the aggregation, and the enemies attracted to the aggregation. Lower values of S tend to favor shadow of safety effects on type 1 prey. Setting $S = 0$ results in flat relationships between the number of enemies attracted to the chorus (E_C) and the variables N_1 and N_2, simulating a system in which the number of signalers does not influence the number of enemies attracted to the chorus. This configuration could represent situations where eavesdropping enemies are territorial, are limited by an external ecological factor, or follow a fixed foraging route. When we set $S = 0$ and all other constants to one, we find negative decelerating relationships between E_F and both variables N_1 and N_2 (**Figure 1E**). Under these

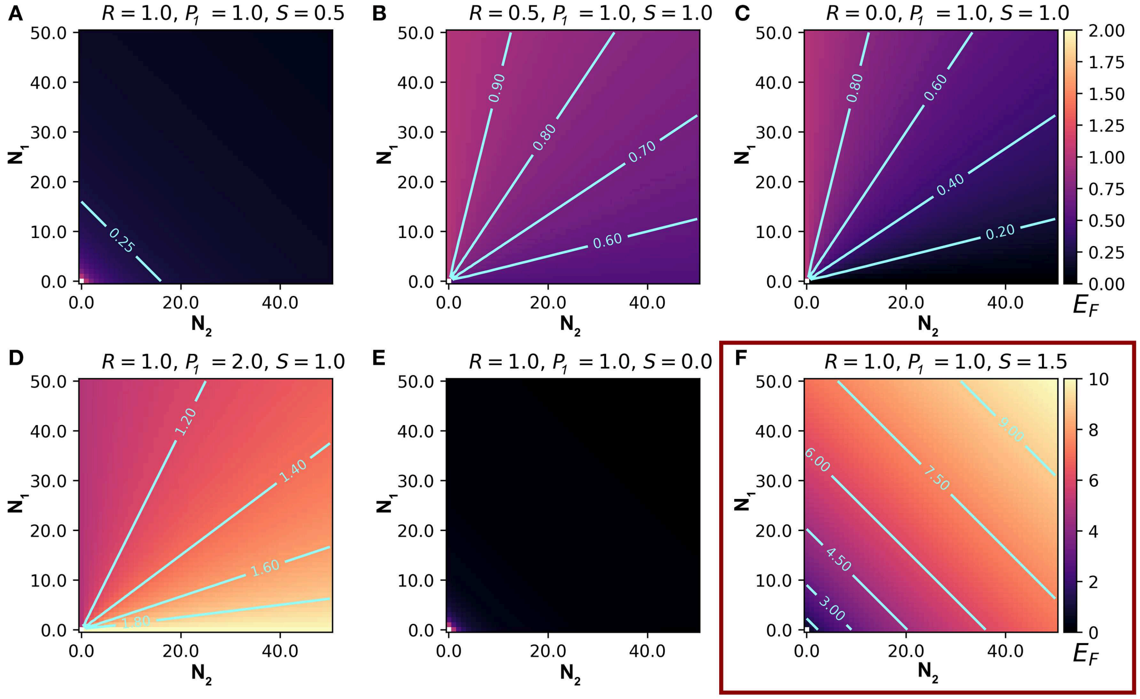

FIGURE 1 | Representative output from a model that predicts the number of eavesdroppers that will attack a focal individual (E_F) of prey type 1, in an aggregation containing varying numbers of type 1 and type 2 signaling prey. Each frame presents predictions based on different values of the relative attractiveness of the two prey types (*R*), the eavesdroppers' expressed preference for type 1 prey (P_1), and the relationship between the weighted number of prey and the number of eavesdroppers attracted to the aggregation (*S*). **(A–E)** represent E_F on a scale from 0 to 2 (scale bar on upper right), and **(F)** represents E_F on a scale from 0 to 10 (scale bar on lower right). See text for details.

conditions, a fixed number of enemies attend the aggregation, so type 1 prey benefit from the dilution effect generated by adding group members of either type. Similarly, values of S between zero and one result in negative decelerating relationships between E_F and both N_1 and N_2, because each additional chorus member results in diminishing marginal gains of enemies (E_C is positive decelerating; **Figure 1A**). Setting $S > 1$ results in positive relationships between E_F and N_1 and N_2 (**Figure 1F**). The shape of these relationships depend on the magnitude of S: positive decelerating when $1 < S < 2$, positive linear when $S = 2$, and positive accelerating when $S > 2$.

Visualizing Effects Over a Range of Parameter Values

In the previous section, we manipulated one parameter at a time to show that type 2 prey tend to cast a shadow of safety on type 1 prey when R, P_1, and S are low. Here, we use the model to visualize how variation in R and P_1 affect the consequences of signaling near one other individual (for this example $Q = 1$ and $S = 1$). We begin with a focal type 1 individual signaling alone, and examine the fitness consequences to that individual of adding one type 2 signaler. This can be achieved by calculating the difference in E_F for $N_1 = 1$ and $N_2 = 0$ vs. $N_1 = 1$ and $N_2 = 1$, and plotting that difference (ΔE_F) over the parameters R and P_1 (**Figure 2**). Compared to signaling alone, signaling near a heterospecific can confer either a shadow of safety or collateral damage, depending both on the difference in attractiveness between the two species (R) and the difference in the enemies' expressed preferences once they arrive at the aggregation (P_1).

DISCUSSION

Animals displaying to attract mates commonly seek out or find themselves in aggregations with other signalers. In many cases, these displays also attract enemies in the forms of predators or parasites, and the evolution of signal structure and signaling behavior will be shaped by the balance between attraction of mates and these dangerous eavesdroppers. Here, we have provided a framework for understanding how differences between neighboring signalers can alter eavesdropper risks faced by signalers of a given type. Our model breaks eavesdropper pressure down into two components: the attraction of enemies to an aggregation, and the preferences of enemies for certain prey within that aggregation. We show that, although they have rarely been considered, asymmetries within these attraction and preference phases are vital for understanding the risks faced by prey signaling in mixed-species groups.

When members of a signaling aggregation are similarly attractive to eavesdroppers, and these eavesdroppers show no preference to attack one prey type over another, increasing group size will equally affect the risks faced by all group members. Thus, when the per capita number of eavesdroppers attracted scales negatively with group size (e.g., when $S < 1$), all group members will enjoy an equal reduction in eavesdropper risk

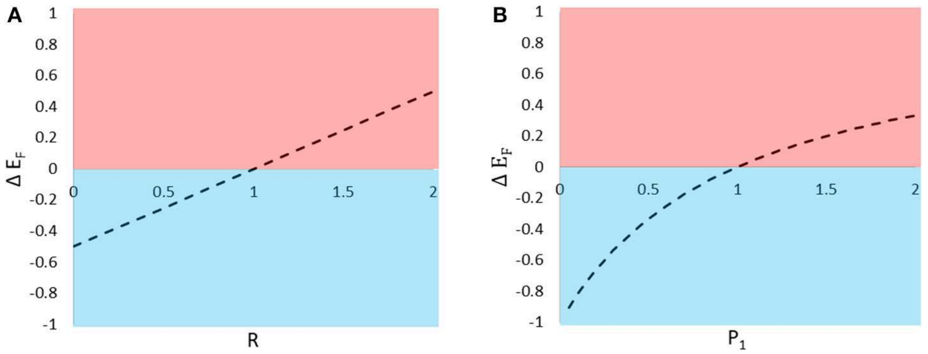

FIGURE 2 | The predicted change in eavesdropper pressure (ΔE_F) on an individual signaler resulting from the introduction of a neighboring individual. The change in eavesdropper pressure is predicted to vary with **(A)** the relative attractiveness of the two types of prey to distant enemies and **(B)** the enemy's relative preference for the two types of prey. Values of $\Delta E_F > 0$ indicate that the presence of the neighbor inflicts collateral damage on the focal individual (pink shading), and $\Delta E_F < 0$ indicate that the neighbor casts a shadow of safety on the focal signaler (blue shading).

due to dilution. When, instead, the per capita number of eavesdroppers attracted scales positively with group size (e.g., when $S > 1$), for example when large groups lead to higher encounter rates with eavesdroppers, all group members will suffer an equal increase in risk. In nature, however, group members might not be equally attractive to, or equally preferred by, eavesdroppers. In these cases, when prey attractiveness or preference are asymmetrical, individual prey may experience additional reductions or increases in eavesdropper pressure (shadow of safety or collateral damage, respectively) that can counteract or overwhelm group-wide dilution and encounter rate effects (**Figure 2**).

Collateral damage and shadow of safety effects resulting from asymmetries in eavesdropper attraction and preference have the potential to shape the evolution of signaling species in several interrelated ways. These include the emergence and composition of mixed-species signaling aggregations, the spatial distribution of signalers within an aggregation, the timing of signaling activity relative to neighbors, the structure of signals themselves, and even the geographic ranges of signaling species.

Neighbor-Mediated Asymmetries and the Evolution of Mixed-Species Signaling Aggregations

Each of the well-established adaptive explanations for the origin and maintenance of animal aggregations are also likely relevant to mixed-species groups of signalers. Larger, more complex groups may reduce risk faced by their members through predator dilution, enhanced detection abilities, and the confusion effect (Hamilton, 1971; Pulliam, 1973; Landeau and Terborgh, 1986; Gibson et al., 2002; Goodale et al., 2019). Our model suggests, however, that in order to understand eavesdropper risk faced by an individual in such an aggregation, asymmetries in the attraction to, and preference for, prey signals must also be considered.

Shadow of safety benefits resulting from asymmetries in eavesdropper attention (attraction and preference) are likely to combine with those due to dilution effects, and influence some prey to seek out aggregations with other species. In many cases, signalers displaying in proximity to relatively unattractive or highly preferred heterospecific neighbors will enjoy reduced eavesdropper pressure (**Figures 2A,B**). Thus, associations with unattractive or highly preferred heterospecific neighbors should encourage the evolution of mixed-species signaling groups. It should be noted, however, that the formation of such aggregations may not be evolutionarily stable if the shadow of safety benefits enjoyed by signalers of one species result in significant collateral damage to individuals of the other species.

Similarly, asymmetries in eavesdropper attraction and preferences are likely to modulate the benefits resulting from the confusion effect. Often considered for visually-oriented predators, the confusion effect describes situations in which the perceptual challenges faced by predators select for larger groups of prey (Pavlov and Kasumyan, 2000; Goodale et al., 2019). In many ways analogous to the "cocktail party" problem discussed for receivers in conspecific signaling contexts (Bee and Micheyl, 2008), these challenges are likely to be increased when additional signals produced by heterospecifics are added to the foraging tasks confronting eavesdroppers (see Goodale et al., 2019 for a review of this). This should result in reduced risks faced by prey, on average, within a group. However, as eavesdroppers attempt to integrate information from a wider range of sources in order to mitigate perceptual challenges (Schmidt et al., 2010), they are more likely to attend to characteristic differences between prey types. Túngara frogs, for example pair calls with conspicuous alternating inflations of their vocal sacs and flanks, while simultaneously producing ripples at the surface of the puddles from which they signal. Bat predators of these frogs are known to increasingly rely on echolocation cues rather than passive eavesdropping in contexts of high heterospecific chorus noise (Rhebergen et al., 2015). In this context, we might expect exaggerated preferences on the part of eavesdropping enemies for túngara frogs over heterospecific neighbors who produce more subtle modulations of their vocal sacs. Any apparent confusion benefits resulting from signaling within a mixed group, should thus, be weighed against collateral damage suffered by more conspicuous prey.

Influences on Signal Structure and Signaling Behavior

From the perspective of an individual deciding when and where to display within a mixed-species aggregation, neighbor-mediated eavesdropper risks are an important consideration. Whether it is more adaptive to signal in close proximity to, or distant from a heterospecific signaler will depend, in part, on whether eavesdropper risks will be transferred on net to (shadow of safety) or from (collateral damage) this potential neighbor. Similarly, neighbor-mediated eavesdropper risk may refine the timing of signaling behavior relative to that of signaling neighbors.

Signalers have been shown to adjust the timing or structure of their displays in response to those of heterospecific neighbors, but the role of eavesdroppers in the evolution of these aspects of signaling has generally not been addressed. Hourglass treefrogs (*D. ebraccatus*), for example, call less frequently and with fewer notes when neighboring small-headed treefrogs (*D. microcephalus*) are chorusing loudly (Schwartz and Wells, 1983). Modulations of signal structure and signaling behavior such as this are undoubtedly influenced by competition among males to maximally attract females. That said, this type of modulation is also consistent with the responses to changing neighbor-mediated eavesdropper pressures.

While the literature addressing eavesdropper effects on the structure of sexual signals is growing steadily, the role of signaling neighbors in shaping the evolution of signal structure is relatively unexplored. When focal signalers experience collateral damage, we can expect the balance between mate-choice and eavesdropper selection to shift in the direction of less conspicuous or less localizable signals. We expect the opposite shift when signalers experience shadow of safety benefits.

In some cases, collateral damage induced by the presence of nearby signalers may affect a species' geographic distribution. If one species of prey attracts sufficient numbers of enemies to an area, it may lead to reductions in the abundance or even extirpation of other, more vulnerable, species. This possibility is well-explored in the apparent competition literature (Holt, 1984; Holt and Bonsall, 2017). Our model suggests that asymmetries in the vulnerabilities of prey to eavesdroppers, specifically resulting from their proximity at signaling aggregations could function as one important mechanism by which apparent competition influences the composition of prey communities. While there already exists empirical support for the idea that geographic heterogeneity in eavesdropper risk can shape the distribution of species or promote signal divergence (Endler, 1995b; Trillo et al., 2013), the possibility that heterospecific neighbors mediate these effects remains unexplored.

The Congruence of Asymmetries in Attraction and Preference

Signalers that attract greater numbers of eavesdroppers to an aggregation may also be preferred by enemies choosing among prey/hosts within that aggregation. The contrasting situation, in which one type of signaler is more attractive to eavesdroppers at a distance but the other type is preferred at closer range is also plausible. The active spaces of signals produced by prey species may differ, and eavesdroppers attracted to a widely broadcast signal may prefer another signal with a more restricted active space once in range to assess both. Marbled newts (*Triturus marmoratus)* eavesdrop on the calls of natterjack toads (*Epidalea calamita*) to locate breeding sites, but short-range visual, and likely chemical, signals are used by the newts during courtship (Diego-Rasilla and Luengo, 2004). Moreover, some predators and parasites also switch to alternative sensory modalities when assessing signalers at close distance (Hendrichs et al., 1994; Page et al., 2012). Frog-eating bats (*Trachops cirrhosus*) use passive auditory cues at relatively long distances, but may switch to echolocation cues at intermediate distances, and ultimately base prey acceptance or rejection decisions on chemical cues (Page and Jones, 2016). As these bats can also switch their foraging decisions to nearby prey in fractions of a second before an attack (MSC, in prep), it seems plausible to conclude that, for this species, long distance attraction and short distance preferences may not always be in line with each other.

Extensions of the Model—The Influence of Signaling and Silent Conspecific Neighbors

The focus of our analysis has been on eavesdropper-mediated relationships between heterospecific signalers, but the general framework we set out can be readily extended to conspecifics displaying with differing signal variants, or to non-signaling conspecifics, such as females or satellite males. Individuals of types 1 and 2 in our model can represent distinct conspecific signal variants within an aggregation without any changes to the model parameters. Eavesdropper risks suffered by these signal variants can then be understood not only in the isolated two-choice contexts under which they are often studied (Ryan et al., 1982; Bernal et al., 2006; Trillo et al., 2013), but as interacting elements within a greater landscape of risk.

Our model also predicts the effects that non-signaling individuals have on the risks faced by signalers. The relative attractiveness of these individuals (R) is likely to be close to zero, but eavesdropper risk may still spill over to them at close ranges (i.e., $P_1 \neq \infty$). Risk to non-callers is expected to be greatest when enemies switch to alternative sensory modalities for close-range prey detection. Overall, satellite males and females are likely to result in some degree of shadow of safety for signaling males, as they do not attract additional enemies to the aggregations, and therefore reduce eavesdropper risks through dilution. We expect this shadow of safety to be augmented under conditions in which enemies face substantial perceptual challenges, such as loud chorus noise, and therefore suffer from reduced localization acuity (Caldwell and Bee, 2014; Rhebergen et al., 2015).

Extensions of the Model—The Influence of Neighbors on Mate Choice

Although we have limited our discussion to one side of the trade-off between mate-choice and eavesdropper pressure, the model we present here should be equally adept at predicting the effects of neighboring heterospecific and conspecific signalers on female attention garnered by a focal signaler. Just like predators and parasites, females must first navigate to a signaling aggregation, and then choose between individuals at that aggregation. While the terms "collateral damage" and "shadow of safety" may not seem as relevant to a mate-choice context, the concepts are equally applicable. When signaling next to an attractive neighbor who is not highly preferred, a focal signaler can expect to receive "collateral damage" in the form of an increased number of female encounters. This appears to be the case for some frogs. Male *Rhacophorus prasinatus* associate with highly attractive males while signaling, presumably to benefit from "collateral damage" resulting from the increased local attraction of females (Chang et al., 2018). Ultimately, one could simultaneously model both female choice and eavesdropper risk, given asymmetries in attraction and preference for signalers within an aggregation.

Extensions of the Model—Increased Model Complexity

We have chosen to keep our model somewhat simple to highlight its key aspects—namely that the number of eavesdroppers drawn to an aggregation will vary with the composition of the aggregation, that eavesdroppers attracted to an individual signaler may ultimately attack nearby guild members, and that eavesdropper risks faced by individual signalers are a function of both of these. There are many ways in which the model could be elaborated to more closely match the complexities of communication in nature. One such elaboration would be to include probabilities of prey capture success. While E_f predicts the number of eavesdropper attacks on a focal signaler, not all of these attacks will result in predation or parasitism (or copulation if modeling mate-choice). Furthermore, due to physical, chemical, or behavioral defenses, prey will differ in their ability to evade attacks. The dynamic behavior of both signalers and eavesdroppers could also be fruitful to model. For some species, signaling behavior is likely not independent of group size or composition. Túngara frogs, for example, are known to modify their call structure depending on the abundance of conspecifics, and alter their calling behavior depending on the signaling activity of heterospecifics (Phelps et al., 2006). Finally, we model fixed attractiveness of, and eavesdropper preferences for each type of prey. Eavesdropper behavior may change, however, with the absolute or relative abundances of signalers. Depletion of prey within an aggregation and prey switching, for example, may strongly affect the nature of predator-mediated intraspecific interactions (Holt and Kotler, 1987).

A Broader Theoretical Context

Collateral damage and shadow of safety effects predicted by our model can be viewed as mechanisms resulting in the widely modeled phenomena of "apparent competition" and "apparent mutualism" (Holt, 1977; Holt and Bonsall, 2017). These broader concepts include nearly any interactions between species mediated by a common predator. While the literature on apparent competition has focused on instances where the presence of one species negatively affects the abundance of the other by increasing predation on the second species (Holt and Bonsall, 2017), apparent competition theory itself is sufficiently broad to include positive interactions between guild members and alterations in predation risk, rather than changes in prey abundance (Holt and Kotler, 1987; Holt and Bonsall, 2017). Some places where our model extends beyond the traditional bounds of apparent competition theory are in the cases of eavesdropper-mediated interactions between conspecifics, and in the attraction of females, rather than predators.

CONCLUSIONS

We have presented a framework and a simple model for understanding how asymmetries in the attraction of eavesdroppers to an aggregation, and in their preferences for certain signalers within this aggregation can result in either heightened or relaxed risks for signalers. We expect the resulting collateral damage and shadow of safety effects to influence the evolution of signal structure, the spatial and temporal distributions of species within signaling aggregations, the species composition of such aggregations, and potentially the geographic distributions of signaling species.

Moving forward, several exciting paths for future research appear particularly promising. First, thus far, there are few empirical demonstrations of collateral damage or shadow of safety effects stemming from asymmetries in predator responses to prey (Segami et al., 2016; Trillo et al., 2016). Considering the near ubiquity of mixed-species aggregations and of eavesdropping enemies, these phenomena could be explored for much a wider range of taxa. Furthermore, while our model was conceived as a conceptual exploration of eavesdropper risks mediated by heterospecific signalers, its predictive power can be tested with natural populations. Importantly, we designed the parameters to be either directly measurable or their calculation to be straightforward, facilitating quantitative predictions. Finally, the model can be applied to examine the influence of neighboring signalers on female mate choice or extended to simultaneously include both females and eavesdroppers.

AUTHOR CONTRIBUTIONS

PT contributed the original concept. DL developed the initial mathematical model. PT, CB, MC, and DL further revised and troubleshot the mathematical model. PT, CB, MC, TL, OP, and DL contributed sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Predator Eavesdropping in a Mixed-Species Environment: How Prey Species May Use Grouping, Confusion, and the Cocktail Party Effect to Reduce Predator Detection

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The field of predator eavesdropping concentrates on the detection by a predator or parasite of signals that prey direct at conspecifics, and the subsequent evolution by prey to avoid or lessen such detection. Here, we first point out that signaling prey species are often found in mixed-species moving groups or stationary aggregations, and ask the question of how simultaneous signaling, by members of one species or more, might affect predator eavesdropping behavior and the composition of the groups themselves. The detection risk of prey species will be affected by the other species they associate with, and prey should generally avoid joining a group with more detectable species. Yet prey may select to join other species that are preferred by predators, diluting their own risk of attack, as long as that does not lead to substantially greater detection and thereby increased predation. We next review the evidence that prey grouping and collective responses when attacked can confuse predators, leading to lower capture rates. Evidence for this confusion effect mostly involves visually orienting predators. We then ask if a similar phenomenon could occur when animals in a group simultaneously produce acoustic signals and find relevant evidence for predator confusion under such situations in the literature associated with the "cocktail party effect." As confusion is heightened by similarities among mixed-species group members, this provides a force at ecological or evolutionary timescales to make species that associate in groups, and their signals, more similar to each other. However, heterogeneous mixed-species groups may be favored if species are differentially preferred as prey. We suggest experiments to examine whether the success rates of acoustically orienting predators depend on the group size of their mixed-species prey. More observations on the relative positions of conspecifics and heterospecifics in space, and the temporal association of their signals, will also increase our understanding of the relationship between mixed-species grouping and predator eavesdropping.

Keywords: animal sociality, cocktail party problem, communication networks, confusion effect, group living, mixed-species animal groups, mixed-species choruses, predator eavesdropping

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INTRODUCTION

The field of predator eavesdropping investigates the signaling behavior of prey animals in relation to their predator(s), with an emphasis on the co-evolutionary arms race between these two kinds of actors (Zuk and Kolluru, 1998). Studies to date have typically focused on isolated predator-prey pairs, and more rarely on situations with more than one predator or parasite, such as túngara frogs (*Engystomops pustulosus*) preyed upon by bats and also attacked by midges (Page et al., 2013). Yet, interactions between predators and prey occur in complex prey communities, in which several prey species are often signaling at the same time and may be grouped together in space. In the túngara frog case, for example, the frogs listen to the calls and silence of other frog species in their vicinity (Phelps et al., 2007). At the same time, other frogs are affected by them—when hourglass frogs (*Dendropsophus ebraccatus*) call close to túngara frogs, the hourglass frogs attract more midges (Trillo et al., 2016). Prey species are also tied together because eavesdropping predators are often capable of preying on a wide variety of species (Page et al., 2013). This leads to the question of how considering the wider social environment surrounding prey, i.e. the communication network (McGregor and Peake, 2000), might affect our understanding of predator eavesdropping.

Our aim in this article is to explore how the presence of multiple, potentially interacting prey species might affect predator eavesdropping, and conversely how the sensory and cognitive behavior of predators may shape mixed-species groups and aggregations of prey. In the first section, we review common situations in which mixed-species signaling takes place. In the second section, we concentrate on how grouping affects predation. We focus particularly on the "confusion effect," in which the presence of a large number of prey reduces the ability of the predator to capture a single prey individual (Neill and Cullen, 1974; Krakauer, 1995). The confusion effect has primarily been studied for visually orienting predators (Jeschke and Tollrian, 2007) and not usually in relation to prey signaling. In the third section, therefore, we ask whether the confusion effect might also apply to situations in which multiple species use acoustic signals, a situation referred to as the "cocktail party effect" (Bee and Micheyl, 2008). Overall, our aim is to show how various aspects of grouping can affect and potentially reduce predator eavesdropping, analogous to the way in which prey species develop "private channels" with conspecifics that avoid such detection (Cummings et al., 2003; Nakano et al., 2008). Further, we hope to encourage more studies of predator eavesdropping in mixed-species groups and aggregations.

SIGNALING IN MIXED-SPECIES GROUPS AND AGGREGATIONS

Animals often signal when in mixed-species groups of different types and at a variety of scales. Here we will distinguish between moving mixed-species groups, whose existence is entirely due to attraction between species, and stationary mixed-species aggregations, which form in a resource patch or enemy-free space (Powell, 1985; Goodale et al., 2017; Boulay et al., 2019), although interspecific attraction might also play a role (e.g., Ward and Zahavi, 1973; Gu et al., 2017). Aggregations and moving groups also differ in their prevalence across taxa: aggregations, although found in all taxa, are especially common in invertebrates, reptiles, and amphibians, whereas moving groups are predominantly found in fish, mammals, and birds (Goodale et al., 2017; Boulay et al., 2019). Finally, there is a difference in the spacing of individuals between these two kinds of groups. Individuals in moving groups are typically close to each other as they move in the same direction, but aggregations can range greatly in their scale, from groups of carrion insects clustered together on a decaying corpse (Boulay et al., 2019) to groups of seabirds spread over hundreds of square kilometers of ocean (Hunt et al., 1988).

Despite these differences, the benefits of mixed-species groups and aggregations can be quite similar, although the relative proximity of individuals is critical, and benefits will decline as proximity decreases. Benefits of grouping together frequently include increased foraging success and, more rarely, increased resistance to harsh environmental conditions or increased access to conspecific mating partners (Goodale et al., 2017; Boulay et al., 2019). Due to our focus on predator eavesdropping, however, we will primarily focus on benefits related to predation. These include the following: (1) encounter-dilution, a decrease in the probability of being attacked in larger groups; (2) vigilance, the increased detection of predators in larger and/or more diverse groups; (3) confusion, a disruption of the predator's ability to capture prey when many prey flee at the same time (see section Grouping and the Confusion Effect for a detailed discussion of this effect and its interaction with oddity); and (4) defense, the ability for a group of individuals to physically stand up to predators (Beauchamp, 2014; Goodale et al., 2017). These benefits are similar to those that can be found in single-species groups. However, mixed-species groups may be preferred to single-species groups in some situations. For example, competition could be lower, intraspecific social forces (e.g., aggression) could be diminished in mixed-species groups, or a heterospecific could bring a special quality that a conspecific does not have (e.g., it is particularly vigilant or good at finding resources; Sridhar and Guttal, 2018).

How do mixed-species moving groups and stationary aggregations relate to predator eavesdropping? Most studies on this topic focus on sexual signals, which are fundamental to animal fitness, and thus are strongly selected to persist even in the face of predation. Sexual advertisement is not usually a key feature of moving mixed-species groups, perhaps because of the risk of hybridization (e.g., Herzing and Elliser, 2013). However, moving groups tend to be constantly noisy, and hence conspicuous to predators, because of the need for group members to keep in contact as they move (Goodale and Beauchamp, 2010; Pagani-Núñez et al., 2018). Group members are also constantly exchanging information, including about predation via alarm calls (Goodale et al., 2010; Magrath et al., 2015). For this reason, we will return to discussing moving groups in sections Grouping and the Confusion Effect and The Cocktail Party Effect: Is There an Auditory Analog of the Confusion Effect?, where we investigate whether predators can be confused when facing large groups and, possibly, by multiple individuals simultaneously signaling within them.

In mixed-species aggregations, in contrast, sexual advertisement is common. In a few cases, mixed-species leks have been described (e.g., Gibson et al., 2002, in birds; and Srygley and Penz, 1999, in butterflies), whose main function appears to be sexual attraction. More frequently, different species at resource-based aggregations sexually advertise at the same time, forming what is known as a "mixed-species chorus" (Phelps et al., 2007; Nityananda and Bee, 2011). Indeed, the term "mixed-species chorus" can be used to describe simultaneous signaling of many animals in any habitat patch, such as crickets in a grassland (Schmidt et al., 2013) or birds in a forest singing at dawn (Luther, 2009). Because the audience for a sexual signal includes only conspecifics, heterospecific signals are simply considered noise and interference in such contexts. Hence, studies on these phenomena often focus on how species avoid overlapping (and hence competition) in time or acoustic characteristics (Cody and Brown, 1969; Hödl, 1977; Chek et al., 2003; Schmidt et al., 2013), although some recent work has shown that the expected partitioning may not always occur (Tobias et al., 2014).

Yet it is important to remember that despite some interference costs, animals may also gain from grouping with heterospecifics if they are sufficiently close to each other to accrue dilution, vigilance, confusion, or defensive benefits. For example, *Rana* frog species can aggregate together (at a scale of usually more than 1 but <10 meters apart; Given, 1990). Although this is not a tight group, individuals might benefit from dilution if predators search over wide areas (tens of meters or greater). For example, frogs could monitor each other's vocalizations to assess predation risk (Phelps et al., 2007) and perhaps benefit from some acoustic confusion of the predator (see section The Cocktail Party Effect: Is There an Auditory Analog of the Confusion Effect?). It is indeed possible that some aggregating animals may prefer to be closest to heterospecifics. Conspecifics may tend to be widely dispersed due to the requirements of territoriality, whereas heterospecifics could be closer without creating mating competition. However, a potential cost of having heterospecifics as the closest neighbors could be a risk of hybridization, at least in cases where the neighbor is from a closely related species with incomplete reproductive barriers. For these reasons, future work should give more attention to the relative distances between signaling and non-signaling animals of the same and different species (**Table 1**, point 1).

The benefits and costs of grouping need not be symmetric between two or more interacting species. As mentioned above, Trillo et al. (2016) recently studied the hourglass frog, which calls in mixed-species choruses with túngara frogs. They found that hourglass frogs closely associated with calling túngara frogs were approached by more parasitic midges. In contrast, the association affected neither the detection of frogs by predatory bats, nor the approach by midges to túngara frogs. One possible explanation for this result is that midges are especially good at detecting túngara frog calls (Bernal et al., 2006). The presence of a highly detectable species could thus increase detection risk for the whole aggregation, and future work should test for such "collateral damage" (*sensu* Trillo et al., 2016) in other systems. A related hypothesis, which also invites future investigations, is that less detectable species should avoid grouping with more easily detected ones (**Table 1**, point 2).

Another kind of asymmetry between prey species occurs if one species is preferred by predators because it is easier to attack and consume or because it provides more nutritional reward. Other prey species might prefer to associate with it, because once a predator finds the group, it will attack its preferred prey first, thus lowering the risk for other members (although prey species should not join such a group if the lowered risk of attack is outweighed by a greater risk of detection). Indeed, some species in mixed-species moving groups have been shown to prefer to associate with vulnerable prey species (in ungulates: Fitzgibbon, 1990; in fish: Mathis and Chivers, 2003). Again, evidence for such a "shadow of safety" (*sensu* Trillo et al., 2016) effect should be looked for in different systems and in both mixed-species moving groups and aggregations (**Table 1**, point 3). Paula A. Trillo and colleagues are currently developing a mathematical model describing how predators attack mixed-species groups, which incorporates this kind of asymmetry between prey species (i.e in predators' preferences), as well as asymmetries in detectability, discussed above.

A final (admittedly hypothetical) scenario is also possible: a prey species that is more easily detected or preferred by predators might try to hide in a group of less preferred prey (**Table 1**, point 4). Here, the prey might lower its own risk of predation by masking its detection or diluting its risk of attack, as long as it remains sufficiently rare in the group to avoid attracting additional predators. This behavior would work best if the prey species looked similar to the other group members. Otherwise, it could not hide well and might be preferentially targeted by the predator due to an "oddity effect" (see section Grouping and the Confusion Effect).

We also want to emphasize that in all the various scenarios discussed above, the question of whether the group persists (i.e., whether the other species move away) may be influenced by traits of the species other than their detectability or attraction to predators. For example, a species' mobility will determine if it can move away from other species without being followed, and its relative dominance (often correlated with size) will determine whether it can put an end to groups that are not beneficial to it, or stay in groups that are not beneficial to other group members. The idea of escaping from a group is similar to the phenomenon in which some host fish can "punish" cheating cleaning fish by simply ending their association with them (Johnstone and Bshary, 2002). But escape may not always be possible for slow or subordinate species.

We conclude this section by emphasizing that conspicuous mixed-species moving groups are easy targets for predators that eavesdrop on the behavior of their prey. Also, sexual advertisements will often occur in aggregations of individuals of both the same and different species. Therefore, the evolutionary processes that reduce detection by predators will also be influenced by other species signaling in the same environment. To understand the relationships between prey species, we need to know whether they share predators and which species predators prefer in addition to their relative mobility and dominance.

TABLE 1 | Fruitful directions for future research on how the social environment of prey species influences predator eavesdropping.

1	Do chorusing taxa (such as frogs and insects) cluster together spatially with heterospecifics so that they (a) get less risk due to grouping, or (b) get less mating competition?
2	Do prey species avoid aggregating or moving in a group with species that are more detectable than they are, increasing the detection of the group?
3	Do prey species select to aggregate or join a moving group in which there is a prey species that is preferred by predators, diluting their own chance of being attacked, as long as the presence of the preferred species does not increase their own risk of detection and hence their overall predation risk?
4	Might prey species that are more easily detected or preferred by predators join aggregations or groups of other species, hiding from their predators, as long as they remain a minority in the group?
5	Does acoustic signaling from multiple individuals cause confusion in predators? Specifically, is the success of prey capture by predators affected by the number of signaling individuals and the spacing between them?
6	Are prey species better able to locate nearby conspecifics in a noisy arena than predators are (i.e., do prey species cope with the cocktail party effect more readily than do predators)?
7	Could there be confusion effects in sensory modalities other than the visual and acoustic ones (e.g., in olfactory signals)?

Further, it would seem important in the future to gather more data on not only the synchrony of species' signaling in mixed-species choruses (e.g., Tobias et al., 2014) but also on the spatial positioning of individuals of the same and different species. We hypothesize that (a) prey should avoid grouping with more detectable species; (b) they should prefer grouping with species that are more preferred by predators, as long as the presence of such species does not increase their own detection; and (c) the more detectable or preferred species might try to hide in a group of less vulnerable species.

GROUPING AND THE CONFUSION EFFECT

Having discussed the different situations in which heterospecifics may be signaling together, we now turn to how grouping itself can affect predator eavesdropping. Specifically, in this section we will look at the so-called "confusion effect" experienced by a predator that needs to select one individual to attack from a large group of prey, a process we will refer to as "prey targeting." In many ways, predator eavesdropping and prey targeting are quite distinct processes. The simplest kind of predator eavesdropping involves an isolated predator-prey dyad, with the predator, far away from the prey, using the prey's signaling to detect and then approach it (**Figure 1A**). In contrast, we will define prey targeting as occurring after the predator has detected a group of prey and is now close to it; here the escaping prey are usually not signaling (**Figure 1B**).

Yet despite the apparently strong distinction between predator eavesdropping and prey targeting, in some situations they can blend together. First, as argued in the last section, the prey may not be isolated and the eavesdropping predator may detect from afar some or all of the group members and subsequently approach (**Figure 1C**). In this situation, all group members may be signaling, or only some, and the signaling of one group member may lead the predator to discover other group members that it would have otherwise been less able to detect, as studied by Trillo et al. (2016) and discussed in the last section. We could call this situation "predator eavesdropping on a group." Second, there may be situations in which the predator has approached close to or within a group in which multiple individuals are signaling (**Figure 1D**). While the predator's proximity to the group as a whole might be reminiscent of prey targeting, the distances between group members may be large, so that the predator is still far from any one individual, as in predator eavesdropping. This might occur, for example, when a parasitic fly is inside a field with many calling crickets (Zuk et al., 2006), or when a hawk that has approached a bird group hears many alarm calls from different individuals around it (Perrins, 1968). We refer to this situation as "prey targeting within a signaling group," and there is the potential for the predator's attack behavior to be influenced by the signals. We will return to this idea in section The Cocktail Party Effect: Is There an Auditory Analog of the Confusion Effect?, where we ask whether the predator could be confused by multiple signals after first discussing the confusion effect in more simple situations.

The idea that predators might be confused by the rapid motion of their prey was discussed long ago (Grinnell, 1903; Miller, 1922), and a small literature has developed to address the issue experimentally (Milinski, 1977; Jeschke and Tollrian, 2007). Jeschke and Tollrian (2007) summarized 25 studies, with 16 of these positively demonstrating a confusion effect. All but three of these studies focused on visually orienting predators, with the few exceptions involving tactile orientation. These studies demonstrate that the magnitude of the confusion effect can be large. In a laboratory study on fish, for example, Landeau and Terborgh (1986) found that predators caught 100% of prey when the prey were solitary, but only 13% when the prey were in groups of 5. Other laboratory studies on fish have shown that this effect is a result of the predator being less able to target an individual prey item (Ioannou et al., 2008). Another set of studies have used neural network modeling and an experimental setup in which humans try to capture moving objects on a computer screen. Again, capture rate decreases as the number of potential targets increases. This effect can occur when prey move independently of each other (Ruxton et al., 2007), but may be even more prominent when prey coordinate their movement following an attack (Ioannou et al., 2012). Finally, recent work has focused on how the confusion effect can be enhanced by striping patterns on the prey (e.g., Hogan et al., 2016).

An important pattern found repeatedly in empirical and theoretical evaluations of the confusion effect is that it is lessened by differences among the group members. In other words, there is an "oddity effect" in which individuals that look different from the majority of the group are captured at a higher rate. This result

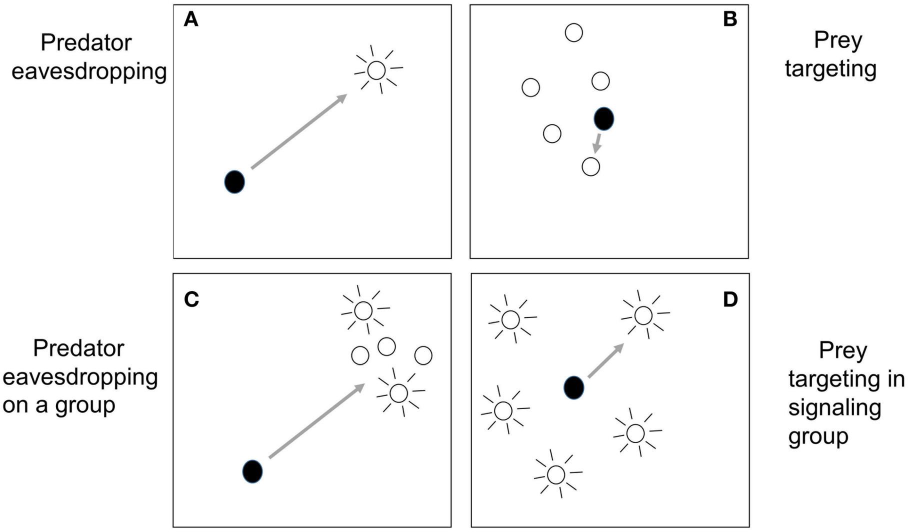

FIGURE 1 | How the simplest cases of predator eavesdropping **(A)** differ from prey targeting **(B)** is clear. In predator eavesdropping, a distant predator detects a signaling prey, and subsequently approaches, whereas in prey targeting, the predator has already detected a tight group of prey, is close to it, and now selects one individual to attack. However, other situations may be more of a blend of both processes. In **(C)**, predator eavesdropping on a group, a distant predator approaches a group as a whole after detecting the signaling of some of its members. Hence, the signaling of some group members influences the predation risk of others; see section Signaling in Mixed-Species Groups and Aggregations for a discussion of this situation. In **(D)**, prey targeting in a signaling group, the predator is close to or inside a group in which multiple individuals are signaling. In the widely dispersed group shown in this panel, the predator must travel a long distance to attack one prey, close to the distances traveled in predator eavesdropping. In section The Cocktail Party Effect: Is There an Auditory Analog of the Confusion Effect?, we ask if a situation such as **(D)** might result in a confusion effect, as occurs in the simpler case of prey targeting.

has been shown particularly in fish. In the experiment of Landeau and Terborgh (1986), an odd fish (one individual dyed blue out of eight normally silvered fish in total) was more often captured than when prey types were evenly distributed (four blue fish, four natural fish). Theodorakis (1989) showed similar results for body size; fish of a size class that constitutes a minority of the group were targeted more often. This phenomenon probably explains why fish with odd phenotypes leave schools when predation pressure increases (Wolf, 1985) and why rare fish appear to be captured more often in coral reefs (Almany et al., 2007). The same effect has been shown in experiments with humans analyzed through neural networks: the confusion effect is less pronounced in heterogeneous groups (Tosh et al., 2006; Ruxton et al., 2007).

The oddity effect may explain why different species in mixed-species groups often have similar phenotypes. Moynihan (1968) was among the first to notice similarities among the participants in avian mixed-species groups and argued that species might become morphologically and behaviorally similar to facilitate intra-group communication. Barnard (1979) viewed this idea as a group-selectionist argument and suggested that similarities were caused instead by the oddity effect. Lost in the ensuing discussion was the question of whether there really are similarities within mixed-species groups beyond what we would expect from shared ancestry or shared habitat. Beauchamp and Goodale (2011) reviewed cases of putative plumage mimicry in avian groups and found support for the idea: in 14/22 cases, two species in mixed-species groups were ranked by human observers as more alike than other species that are either closely related or live in similar habitats. Meta-analyses of mixed-species avian groups have also found that birds of similar sizes tend to associate together (Sridhar et al., 2012; Mammides et al., 2018), and similar patterns have been shown in the fish literature: fish groups are often strongly size-assorted (Krause et al., 1996), and schooling among fish with similar appearances has also been described (Pereira et al., 2011). In many cases such resemblances may be examples of ecological assortment, although some of the most striking examples suggest mimicry (Beauchamp and Goodale, 2011).

The oddity effect may be complicated by interactions with conspicuousness and size. Tosh et al. (2007) found through neural network analyses that cryptic prey were actually safer when rare in groups mostly composed of conspicuous prey. Rodgers et al. (2013) supported this result in lab studies with *Daphnia*. Later, Rodgers et al. (2015) found that larger *Daphnia* were always preferentially attacked, even when constituting the majority of a group, perhaps because they were more obvious and profitable. Here again asymmetries between species come into play. If one species is less preferred than another it may be selected to remain distinguishable from those more preferred.

To summarize this section, one benefit of grouping is that a large number of fleeing individuals can distract the predator from targeting a single prey. The confusion effect is lessened in groups that are more heterogeneous. Species that look alike may be selected to associate together, and there may be a force over evolutionary time toward phenotypic convergence. However, some heterogeneity in mixed-species groups can occur when a species joins others more preferred by shared predators.

THE COCKTAIL PARTY EFFECT: IS THERE AN AUDITORY ANALOG OF THE CONFUSION EFFECT?

In drawing a comparison between predator eavesdropping and prey targeting, as we did in section Grouping and the Confusion Effect on the confusion effect, one large difference still remains: predator eavesdropping implies that prey signaling increases predator detection, but prey targeting need not involve prey signaling at all. One can then ask whether there is any evidence that synchronous signaling by members of a group or aggregation (diagrammatized in **Figure 1D**) produces confusion (**Table 1**, point 5). This question leads us from the visual to the auditory modality, where signaling can more easily be turned on and off. More specifically, it leads to the phenomenon known as the cocktail party effect: how can people concentrate on one person's speech in a crowded room when everyone is talking at the same time (Bronkhorst, 2000)?

As the above definition of the cocktail party effect implies, much of the work in this field has concentrated on humans, and some reviews emphasize the uniqueness of speech and speech recognition (Bronkhorst, 2000). However, the universal qualities of the problem have been emphasized by Bee and Micheyl (2008) in their article "'The Cocktail party problem': What is it? How can it be solved? And why should animal behaviorists study it." They convincingly argued that many animals produce their signals under noisy conditions, and especially in environments with many other conspecific and/or heterospecific signalers. Bee and Micheyl (2008) and Hulse (2002) fit the cocktail party effect in the wider field of auditory scene analysis (Bregman, 1990), wherein animals take in sounds from a complex auditory environment and assign them to distinct sources.

The key to coping with the cocktail party effect, or performing auditory scene analysis, is finding similarities between sounds. Commonalties between sounds lead to their "integration" and assignment to one sound source, whereas differences among sounds lead to "segregation" (Bee and Micheyl, 2008). There are two components to auditory scene analysis: one is the parsing of sounds in a temporal sequence (sequential segregation), and the other is the parsing of sounds made at one time, but at different frequencies (i.e., perceived to be at different pitch, known as simultaneous segregation). Sequential segregation, of greater interest for this article, can be performed by looking at differences in frequency, in repetitive characteristics of the sound over time, in common modulation patterns over time, and in differences of spatial position (Bee and Micheyl, 2008; Farris and Ryan, 2011). A famous experimental paradigm known as "two-frequency spatial segregation tests" (see Figure 1 in Itatani and Klump, 2017) has been used to demonstrate sequential segregation by humans. If the frequency between two sounds presented from the same location is not very different, the human listener perceives one sound source, but if the frequency difference is greater, the listener perceives two sound sources. Ingenious experiments with animals have translated this paradigm to other species. For example, taking advantage of frog's phonotaxis to a speaker that broadcasts calls at a species-specific rate, or in a species-specific order, scientists can demonstrate that the frogs are able to segregate certain calls separated to a certain degree by frequency or spatial position, but not others separated by less than this threshold (Farris and Ryan, 2011; Nityananda and Bee, 2011).

These studies have shown that animals are able to cope with the cocktail party effect so that they can recognize and localize conspecific calls with high accuracy and little error. For example, some chorusing insects such as crickets have highly tuned frequency selectivity and "neuronal gain control" that provoke strong responses to conspecific calls (Schmidt and Römer, 2011). Tree frogs, a model taxon for the cocktail party effect, rely not only on such "matched frequency filtering" (Bee, 2015) but show many abilities to sequentially segregate sound based on spatial positioning (Bee and Riemersma, 2008) and amplitude modulation patterns (Lee et al., 2017). If prey species can deal with the cocktail party effect more effectively and quickly than predators, they could reach their mating targets while predators remain confused. Given that selection for the localization of a mate is very strong, it is likely the solution of a prey species might be better than a predator's, which usually needs to localize many different prey species. However, experiments are needed to further test this idea (**Table 1**, point 6).

The fact that similarities between signals impede the segregation of different sound sources makes it seem plausible that predators can be confused when multiple prey individuals are signaling simultaneously in a group. However, is there any evidence for this hypothesis? Echo-locating bats, which must hear sounds reflected off objects, struggle in cluttered arenas, and change their echolocation patterns in response, demonstrating that many sounds from different sources can be distracting (Moss and Surlykke, 2010). Similarly, a bat that hunts using auditory cues was shown to switch to echolocation in a noisy habitat, again indicating that multiple sources of noise can degrade the sensory pathway for prey detection (Gomes et al., 2016). Concurrent sources of noise can also interfere with the neuronal mapping of sound in the acoustically orienting barn owl, *Tyto alba* (Keller and Takahashi, 2005). However, more concrete evidence for a confusion effect due to group signaling is as yet missing. To test this hypothesis most directly, one should look at the effectiveness of predator attacks when prey groups contain different numbers of calling individuals. A confusion effect would be demonstrated if increased group sizes led to more targeting and localization errors.

Using the analogy to the confusion effect in the visual modality, the cocktail party effect might provide a selective force making the signals of heterospecifics that call together more similar. For example, researchers reported long ago similarities between the alarm calls of different bird species in mixed-species flocks (Marler, 1955; Jurisevic and Sanderson, 1994). This observation has been attributed to the different prey species all making signals that predatory hawks find hard to detect (Klump et al., 1986; Jones and Hill, 2001) and to similarities between species in their auditory physiology (Henry et al., 2016). However, it is also possible that alarm calls have been selected to be similar because similar sounds coming simultaneously from different places disrupt a predator's localization abilities (Grinnell, 1903; Perrins, 1968). Further, calls might sound similar at long distances from which they are heard by predators but still have subtle differences detectable at close range by other prey (Ruxton, 2009). Note that convergence seems particularly likely for alarm and contact calls in mixed-species moving groups since these types of signals should be under weaker divergent selection than sexual advertisement calls. Also, differences among prey in the degree to which they are preferred by predators may have similar effects as those discussed in section Grouping and the Confusion Effect. That is, in mixed-species aggregations or moving groups, if a predator prefers a certain prey species, other species might be selected to differentiate themselves, even if the overall attack rate on the group thereby increases due to a weakening of the confusion effect by an oddity effect.

In summary for this section, investigations of the cocktail party effect and ways of coping with it imply that predators can be confused by similar sounds coming from multiple locations. Hence, the cocktail party effect may cause an auditory confusion effect. If this is true, then prey may not need to make their calls less conspicuous. Generally, one way for prey to avoid predator eavesdropping is to group together and have a more effective solution to the cocktail party effect than the predator. However, direct tests of this hypothesis require data on capture rates in groups of different sizes for acoustically orienting predators. We note in closing that confusion effects may not be confined to visual or auditory domains but could also be found in other modalities (e.g., olfactory confusion?), although the lack of a large body of literature on how humans and non-human animals parse different sources of signals in such modalities makes the ideas more speculative (**Table 1**, point 7).

CONCLUSIONS

Ultimately, the field of predator eavesdropping aims to understand how prey can maximize communication with one another while minimizing detection by predators. In this contribution, we point out that prey are often associated with other prey species, and thus that their detection risk may be affected by how well the predator detects the other species. We expect prey to avoid grouping with more detectable species. Other expectations include that prey should select groupings with species that are more preferred by predators as long as this does not lead to them being more easily detected, and for more detectable or preferred prey to attempt to hide in groups that include larger numbers of other prey. We also discuss how prey detection can be disrupted when predators get confused, just as when they do not sense prey, and how this confusion effect is affected by group size and composition. Because similarity increases confusion, frequent participants in mixed-species groups might be selected to be more similar in their phenotypic attributes and signaling. At the same time, heterogeneity may still be favored in groups if predators prefer one prey species in the mix, making it beneficial for the other species to appear different. Other situations favoring heterogeneous mixed-species groups could arise if species are vigilant for predators that are dangerous for companion species although not for themselves (Rasa, 1983; Ridley et al., 2007), or if one species provides protection for the other (Quinn and Ueta, 2008).

Given the degree to which animal species participate in different kinds of groups or aggregations, we hope that the field of predator eavesdropping will continue to expand toward fully understanding the social environment in which signaling takes place. In section The Cocktail Party effect: Is There an Auditory Analog of the Confusion Effect?, we argue that it would be worthwhile to manipulate group size in chorusing animals and determine the success rate of acoustically orienting predators. But observational data can also be useful to determine inter-individual distances between conspecifics, at what scale conspecifics are grouped together, where heterospecifics are positioned relative to them, how often different species signal at the same time, the degree to which they share predators, and their relative dominance and mobility. We believe exploring this rich set of variables will uncover further complexity in how predators influence prey communication systems.

AUTHOR CONTRIBUTIONS

EG, GR, and GB conceived the article collectively. EG wrote the first draft, and then EG, GR, and GB worked together on subsequent revisions.

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REVIEW
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Unclear Intentions: Eavesdropping in Microbial and Plant Systems

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Eavesdropping, the interception of signals by unintended receivers, is an important component of the ecology and evolution of communication systems. Plants and microbes have complex communication systems with important consequences for agriculture, human health, and ecosystem functioning. Eavesdropping, however, has mostly been studied in animal systems. In this review, we argue that eavesdropping is an important force shaping the ecology and evolution of communication in these non-animal systems. To date, studying eavesdropping in plants and microbes has been limited by the fact that signaler "intention" is often unclear: distinguishing signals that evolved to convey information from unintended cues is particularly difficult in plants and microbes, and the fitness consequences of signaling are rarely measured. We describe some of the main examples of eavesdropping in plant and microbial communication and point out other murkier cases were the molecular and physiological basis of communication are well-understood, but the evolutionary implications have not been addressed. We argue that these systems provide experimental tractability to test some of the predicted ecological and evolutionary consequences of eavesdropping, and that the particularities of these systems can lead to an increased understanding of eavesdropping, and its importance in biological communication.

Keywords: eavesdropping, signal, cue, plant volatiles, quorum-sensing, cooperation, plant communication, microbial communication

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1. INTRODUCTION

Although the bright colors and conspicuous vocalizations of animal signals are most apparent to human observers, communication is fundamental to plant, fungal, and even microbial biology. The floral volatiles that plants produce to attract pollinators are one familiar example of communication in a non-animal system. Although plants and microbes differ from animals in the main sensory modalities they use to transmit and receive information, all signals are unified by a common theme: they evolved to convey information to an intended receiver, and are associated with a fitness benefit for the signaler (Laidre and Johnstone, 2013). And all signals, across the tree of life, are susceptible to a common threat: interception by unintended receivers known as "eavesdroppers."

The term "eavesdropping" evokes auditory communication, but eavesdroppers can exploit any sensory modality through which signals are conveyed. In addition to vocalizations, unintended receivers intercept visual (Earley and Dugatkin, 2002), olfactory (Nieh et al., 2004), vibrational (Laumann et al., 2007), electric (Stoddard, 1999), and chemical (Hsueh et al., 2013) signals. In animal communication, the evolutionary and ecological significance of eavesdropping has long been appreciated (Zuk and Kolluru, 1998; Searcy and Nowicki, 2005). By contrast, studies of eavesdropping in non-animal systems are much rarer. As a result, animal communication has disproportionately influenced our understanding of the ecological and evolutionary significance of eavesdropping. Moreover, our models of signal form and function in non-animal systems often overlook eavesdropping as a crucial evolutionary force.

Here, we argue that eavesdropping is a fundamental force shaping the ecology and evolution of communication in non-animal systems. We begin by reviewing evidence for eavesdropping in non-animal systems, primarily focusing on plants and microbes. We identify hypotheses in the animal eavesdropping literature that have yet to be rigorously evaluated in non-animal systems, and highlight how plants and microbes are poised to advance our understanding of eavesdropping. We conclude by outlining productive avenues for future research.

1.1. Eavesdroppers, Signals, and Cues

Eavesdropping implies a communication system with a signaler, a signal, and one or more intended receivers. The raison d'etre for a signal is information transfer (**Figure 1A**). Signals have evolved to elicit a response in an intended receiver (Maynard-Smith and Harper, 2004). Generally, the response a signal elicits benefits both the signaler and the intended receiver (**Figure 1A**). Eavesdropping does not necessarily have an effect on the fitness of the signaler (**Figure 1D**) but often it is costly (**Figure 1E**). Competitors, or even worse, predators and parasites can gain information through eavesdropping that results in damage to the signaler. Most eavesdropping literature—including this review—focuses primarily on eavesdropping that is costly for the signaler, like eavesdropping predators and parasites, because it imposes conflicting selection on the signaler: the signaler benefits from its signal reaching the intended receiver, but pays a fitness cost when the signal is intercepted by an eavesdropper.

Drawing from the animal communication literature, in this review we will distinguish between signals and cues. We use "cue" to refer to information produced inadvertently by a "signaler." Cues are any piece of information from the environment that organisms use to change their physiology or behavior (Laidre and Johnstone, 2013). Cues are distinct from signals in that they did not evolve to convey information; instead, cues are unintended byproducts of other organismal functions (**Figure 1B**). Cues can convey a great deal of information about the organism that produced them (its proximity, nutritional state, sex, etc.), but communication is not their primary function. Chemical cues, for example, tend to be metabolic byproducts of other physiological processes that are passively emitted by the signaler (**Figure 1B**).

While discriminating signals from cues is certainly problematic in animals too, it can be especially difficult when plants and microbes act as receivers because they often respond to signals physiologically rather than behaviorally. Moreover, in contrast to the animal visual and auditory signals that we understand fairly well, the chemical signals that plants and microbes use to communicate with each other can be tricky to decode due to their high dimensionality (Raguso, 2008). Later in this review, we will highlight how principles and predictions from the animal eavesdropping literature can help us distinguish between signals and cues in plants and microbes.

2. HOW DO PLANTS AND MICROBES COMMUNICATE?

Plants produce a wide array of visual, olfactory, and chemical cues to communicate with animal and microbial mutualists, as well as with each other (**Table 1**) (Heil and Karban, 2010; Caruso and Parachnowitsch, 2016). Beyond the familiar bright colors, sweet-smelling volatiles, and nectar rewards associated with floral displays, plants also communicate via volatile organic compounds ("VOCs") released from leaves, stems, and roots (Baldwin et al., 2006; Delory et al., 2016). These compounds diffuse through the air, water, or soil, and elicit responses from other plants, animals, and microbes (Baldwin et al., 2006; Heil and Karban, 2010). In addition to floral displays, an area in which plant communication is well-characterized is signal exchange between plants and mutualistic soil microbes. The root systems of nearly all land plants harbor mycorrhizal fungi that help their host plant tolerate drought and absorb soil nutrients (Bonfante and Genre, 2010). Legumes (plants in the family Fabaceae) also partner with soil bacteria called rhizobia to acquire nitrogen (Oldroyd, 2013). A crucial step in the formation of both mutualisms is chemical signal exchange, which plant and microbes use to locate and identify each other (Bonfante and Genre, 2010; Friesen, 2012; Oldroyd, 2013). These chemical conversations between plants and microbial mutualists occur via diffusible signals, such as flavonoids and strigolactones, and chemical gradients in the soil (Oldroyd, 2013).

Microbes also produce a wide array of secondary metabolites and respond to a broad range of chemicals in their environment and we are just starting to unravel the complex interactions and communication networks within microbial communities (**Table 1**) (e.g., Tan et al., 2014). Bacteria, for example, can transfer information through recognition of surface molecules (Blango and Mulvey, 2009), macromolecular contact-dependent delivery systems that transport effectors across cells (Hayes et al., 2010), small diffusible molecules and likely other physical forms of communication like sound waves (Matsuhashi et al., 1998), and electrical currents (Summers et al., 2010). The mechanisms of communication of microbes have mostly been described in bacteria; however, archaea, fungi, and protists all have their particular mechanisms of communication. In ascomycetes fungi, for example, complex chemical signaling is necessary to coordinate the fusion of germinating asexual spores in the formation and development of a fungal colony. This signaling system involves cell-cell contact and the alternation of signals and a coordinated rapid switch between two physiological stages (associated with signaling and response; Fleissner et al., 2009). And cell-cell signaling in social amoebas like *Dictyostelium discoideum* controls developmental programs (e.g., Bonner, 1970; Harwood et al., 1992; Pitt et al., 1992), kin recognition (Benabentos et al., 2009), multicellular aggregation (Tyson and Murray, 1989), behavioral changes (Darcy and Fisher,

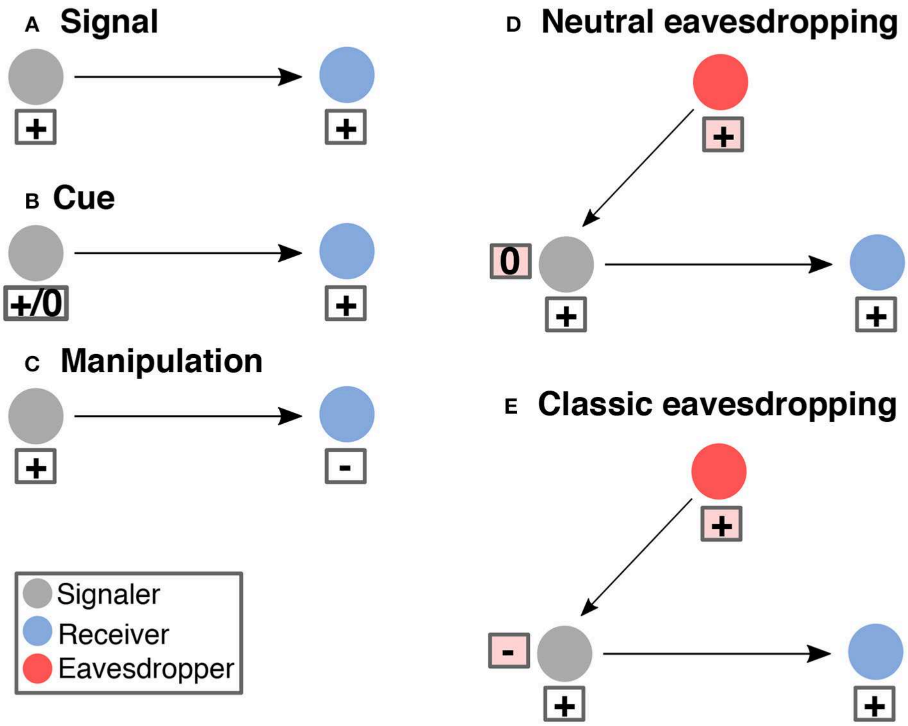

FIGURE 1 | Different kinds communication systems. A signal is produced by a signaler to obtain a response from a receiver **(A)**. Both signaler and receiver benefit from this interactions. Cues are unintended information that can be useful for the receiver **(B)**. A signaler can also exploit sensory biases in the receiver to obtain a benefit at the cost of this receiver **(C)**. Eavesdroppers intercept a signal to obtain beneficial information for them **(D,E)** often at the cost of the signaler **(E)**.

1990; Dormann and Weijer, 2001), and the establishment of symbiosis (Shu et al., 2018).

3. EXAMPLES OF EAVESDROPPING IN PLANTS AND MICROBES

3.1. Plant-Animal Interactions

In plants, eavesdropping is most thoroughly understood in the context of plant-animal interactions mediated by floral displays (**Table 2**) (Schaefer et al., 2004). In many ways, flowers are analogous to the elaborate courtship displays that form the foundation of the animal eavesdropping literature. Flowers are visual (colorful) and chemical (scented) signals plants use to attract the animal pollinators they need to reproduce. The fitness benefit of floral signals for the plant, as well as the identity of the intended receiver, are clear and straightforward to measure. Species whose flowers share similar suites of traits (e.g., color, smell, shape) tend to be pollinated by the same animal taxa, a phenomenon known as a "pollination syndrome" (Fenster et al., 2004). The receiver of floral signals can often be identified based on these suites of shared traits, as well as models of animal sensory ecology that identify which species are capable of perceiving a given signal (Raguso, 2008; Schiestl and Johnson, 2013).

Flowers attract eavesdropping herbivores that damage leaf and stem tissue, rob pollen and nectar, and consume seeds. Using traps baited with individual components of the volatile cocktail produced by Canada thistle flowers, Theis (2006) demonstrated that some compounds attracted only pollinators, others attracted only herbivores, and some attracted both. Similarly, the dominant compound in the scent of flowers of the Neotropical orchid *Dichaea pendula* attracted bee pollinators and florivorous weevils (Nunes et al., 2016). These eavesdropping herbivores are a major source of selection on floral signals (Hanley et al., 2009; Kessler et al., 2013; Johnson et al., 2015; Santangelo et al., 2018). In a common garden, Santangelo et al. (2018) demonstrated that herbivores imposed stronger selection on inflorescence production and size than pollinators. A recent meta-analysis of phenotypic selection analyses came to a similar conclusion, finding that herbivore-mediated selection on floral traits was stronger than pollinator-mediated selection in two-thirds of cases (Johnson et al., 2015).

3.2. Plants as Eavesdroppers

Although controversial when first proposed, the idea that plants can receive and react to information is now firmly established (Heil and Karban, 2010; Kegge and Pierik, 2010; Karban et al., 2014; Caruso and Parachnowitsch, 2016). For example, plants respond to volatile compounds released by their herbivore-damaged neighbors by increasing their own herbivore resistance (Arimura et al., 2000; Dolch and Tscharntke, 2000; Dicke et al., 2003; Kegge and Pierik, 2010). Information is also transmitted from plant to plant through networks of mycorrhizal fungi that

TABLE 1 | Examples of signals and cues in microbes and plants.

Organism	Molecule or trait	Signal or cue	Specificity	Costs
Microbe	Oligo- peptides	Likely signal	Specific (differen-tiates between closely related strains)	Costly. Used by Gram-positive bacteria for quorum-sensing. The cost of synthesis of these peptides is relatively high even in the case of small peptides. These short peptides are highly specific signals: they often start as longer chains and have a series of post-translational modifications that allow for high specificity (Lyon and Novick, 2004; Keller and Surette, 2006).
Microbe	N-acyl homoserine lactone (AHL) autoinducers	Signal or cue	Variable	Cost varies. Synthesized from common metabolites. Their costs vary depending on the number of enzymatic steps required in their production (Fuqua et al., 2001; Keller and Surette, 2006).
Microbe	LuxS/auto-inducer-2 (AI-2)	Likely cue	Nonspecific	Not costly. AI2 is neither a very specific molecule, nor is it very costly (Keller and Surette, 2006). Instead, this molecule is generated by the degradation of a key metabolic compound (that is also involved in other forms of communication; Vendeville et al., 2005). Current evidence seems more consistent with AI2 acting as a cue of the presence and activity of other microbes, rather than as a specific signal that can be eavesdropped (Diggle et al., 2007).
Microbe	Nod factor	Signal	Specific (controls host specificity)	Likely costly. Nitrogen-fixing bacteria known as rhizobia initiate mutualisms with plants by producing lipo-chitooligosaccharide molecules called Nod factors. These signals mediate host-symbiont recognition, and are required for nodulation (Denarie and Debelle, 1996; Oldroyd, 2013).
Plant	Floral displays	Signal	Specific	Costly. The structure of the flower itself, as well as its coloration and pollinator rewards like nectar are all highly costly and tend to target specific pollinators (Pyke, 1991; Andersson, 2000; Fenster et al., 2004; Sletvold et al., 2016).
Plant	Strigo-lactones	Signal and cue	Variable	Strigolactone signaling is a key step in forming the mutualism between plants and arbuscular mycorrhizal fungi, and is upregulated during the establishment of symbiosis (Oldroyd, 2013; Waters et al., 2017). However, it is also a plant hormone that regulates shoot and root growth (Waters et al., 2017), so not all strigolactones exuded into the soil may be signals.
Plant	VOCs released in response to herbivores	Unknown	Variable	The volatile organic compounds (VOCs) plants release in response to herbivore or pathogen damage are metabolically costly (Hoballah et al., 2004).

TABLE 2 | Examples of signaler/receiver/eavesdropper relationships in plants and microbes.

Signaler	Receiver	Eavesdropper	References
Orchid (*Dichaea pendula*)	Bee pollinator	Flower-feeding weevils	Nunes et al., 2016
Plant-parasitic nematodes	Conspecific nematodes	Host plant (*Arabidopsis*)	Manosalva et al., 2015
Plant-parasitic nematodes	Conspecific nematodes	Nematophagous fungi	Hsueh et al., 2013
Mammal host cells	Mammal host cells	*E. coli*	Lopes and Sourjik, 2018
Gram-negative soil bacteria	Gram-negative soil bacteria	*M. xanthus*, a predatory soil bacterium	Lloyd and Whitworth, 2017

connect their root systems (Dicke et al., 2003; Babikova et al., 2013; Song et al., 2014).

Parasitic plants use plant-emitted volatiles to locate new hosts (Runyon et al., 2006). Dodder (*Cuscuta pentagona*) is a obligately parasitic plant that does not photosynthesize: instead, it obtains nutrients by attaching itself to the shoots and leaves of other plants. Runyon and colleagues found that dodder seedlings grow toward the volatile cocktails of their host plants. Incredibly, this response is host-specific: seedlings could distinguish between preferred and non-preferred hosts on the basis of their volatiles (Runyon et al., 2006). In at least one instance, plant eavesdropping on belowground signals helps them avoid parasitism. Many plants are attacked by parasitic nematodes that inflict substantial damage by grazing on plant roots or invading the root system to live as endoparasites. A recent study found that nematode pheromones called ascarosides, intraspecific signals regulating nematode social behavior and development, trigger defensive responses in plants (**Table 2**) (Manosalva et al., 2015). Plants aren't the only eavesdroppers exploiting these nematode pheromones. Ascarosides also trigger nematophagous fungi, predators of soil nematodes, to form the trapping structures they use to ensnare their nematode prey (Hsueh et al., 2013).

3.3. Quorum-Sensing in Bacteria

One of the most studied mechanisms of microbial communication is quorum-sensing in bacteria (**Table 1**). Quorum sensing refers to genetic regulation based on the concentration of a signal called an autoinducer. Autoinducers are produced in small concentration by the signaler bacterial cell and only cause a response after they have reached a certain threshold concentration (Miller and Bassler, 2001; Waters and Bassler, 2005; Keller and Surette, 2006). This bacterial response involves the production of more autoinducer, causing a positive feedback loop (**Figure 2**). Quorum-sensing signals are hypothesized to help microbes evaluate both the physical (i.e., diffusion) and social (i.e., population density) properties of the environment (Cornforth et al., 2014). Microbes can use these concentration-based systems to evaluate p how fast an extracellular compound will diffuse away (Redfield, 2002), and to regulate metabolite production based on population density; in other words, it allows bacteria to invest in a coordinated response only once a threshold density has been reached (Miller and Bassler, 2001; Waters and Bassler, 2005; Keller and Surette, 2006; Hawver et al., 2016).

One of the clearest examples of eavesdropping in a microbial system involves quorum sensing. *Myxococcus xanthus*, a soil bacteria that feeds on other bacteria, eavesdrops on other bacterial signals to find its prey. It actively chases its prey and then is able to lyse and consume a wide range of bacterial species (Morgan et al., 2010). Like many animal predators, *M. xanthus* is able to eavesdrop on its prey signals and change its behavior accordingly. In this case, *M. xanthus* is able to recognize different quorum-sensing molecules (AHLs; **Table 1**) produced by Gram-negative bacteria, and respond by increasing predation activity (through increased motility, slower development of spores, increased germination of spores, and overall increased predation activity; Lloyd and Whitworth, 2017).

Eavesdropping on quorum sensing signals has been shown (through experiments and models) to increase eavesdropper fitness in soil bacteria, a hallmark of true eavesdropping (Chandler et al., 2012). Finally, LuxR/LuxI pair of genes show concordant patterns of evolution, suggesting co-evolution of signal and receptor (Lerat and Moran, 2004). Many bacteria have "solo" homologs of the LuxR-type protein (the response regulator) (i.e., in excess of those of the LuxI-type protein that functions as AHL synthase). Therefore, these bacteria can potentially respond to an autoinducer signal of another strain, but cannot produce their own, suggesting that eavesdropping could be on the purposes of these "solo" LuxR homologues (Case et al., 2008).

3.4. Host-Microbe Interactions

Bacteria are not the only ones that benefit from spying in microbial communication. Hosts also gather and react to crucial information about their biotic environment through eavesdropping in microbial quorum-sensing. The model legume *Medicago truncatula* modulates its gene expression in response to quorum-sensing autoinducers of a mutualist (*Sinorhizobium meliloti*) and a pathogen (*P. aeruginosa*) (Mathesius et al., 2003). Information flows in the other direction as well. Pathogenic microbes can eavesdrop on host signals to coordinate infection. In plant roots, for example, oomycete parasites can more easily find their host by eavesdropping on signals involved in attracting rhizobial partners (Hosseini et al., 2014). Inside the human gut *E. coli* and *Salmonella* respond to adrenaline and noradrenaline activating genes involved in virulence and motility (Lyte, 1992; Clarke et al., 2006). Similar eavesdropping mechanisms have been identified in plant pathogens. *Xanthomonas oryzae pv. oryzae* responds to the defense phytohormone salicylic acid by activating its quorum-sensing controlled virulence. More recently, Lopes and Sourjik (2018) showed that *E. coli* responds through chemotaxis to a wide array of hormones, and that the response (movement toward, or away from) is hormone-specific. The authors thus hypothesized that movement away from these hormones might allow the bacteria to escape certain host defenses (**Table 2**).

4. WHY STUDY EAVESDROPPING IN NON-ANIMAL SYSTEMS?

Organisms constantly respond to information in their environment, changing their growth, use of resources and ecological interactions. Thus, information plays an important role in ecological systems, mediating interactions, coexistence and community assembly (Kerényi et al., 2013; Juhász et al., 2017), and even affecting ecosystem functioning (Resco et al., 2009). Given the keystone ecological roles occupied by microbes and plants—both groups disproportionately influence nutrient cycling and overall ecosystem functioning—it is important to understand how they transmit and use information, and how as well as their information use shapes the stability of those systems. These communication networks pose a very interesting system to evaluate the ecological and evolutionary consequences of information transfer, signaling systems and eavesdropping.

Studying eavesdropping in non-animal systems has the potential to advance biological information theory in several ways. First, given the ecological and evolutionary significance of eavesdropping in animal systems, incorporating eavesdropping into plant and microbial biology is likely to yield new insights about the forces that shape information transfer. Second, expanding the study of eavesdropping beyond its traditional purview of behavioral ecology has the potential to generate new perspectives, and to test hypotheses that are difficult or impossible to test in most animal systems. Below, we outline how studies of eavesdropping could advance our understanding of plant and microbial communication biology, and how plant and microbial systems can be deployed to deepen our understanding of the evolutionary and ecological significance of eavesdropping.

4.1. Lessons From Animal Eavesdroppers for Plants and Microbes

What predictions and hypotheses from the animal eavesdropping literature are poised to advance our understanding communication biology in plants and microbes? With the notable exception of flowers and floral signals, it is often hard to distinguish between signals and cues in plants and microbes. Second, little is known about the fitness consequences of signaling in plants and microbes. With this in mind, we highlight two lessons from the animal eavesdropping literature that could significantly advance our understanding of the evolutionary

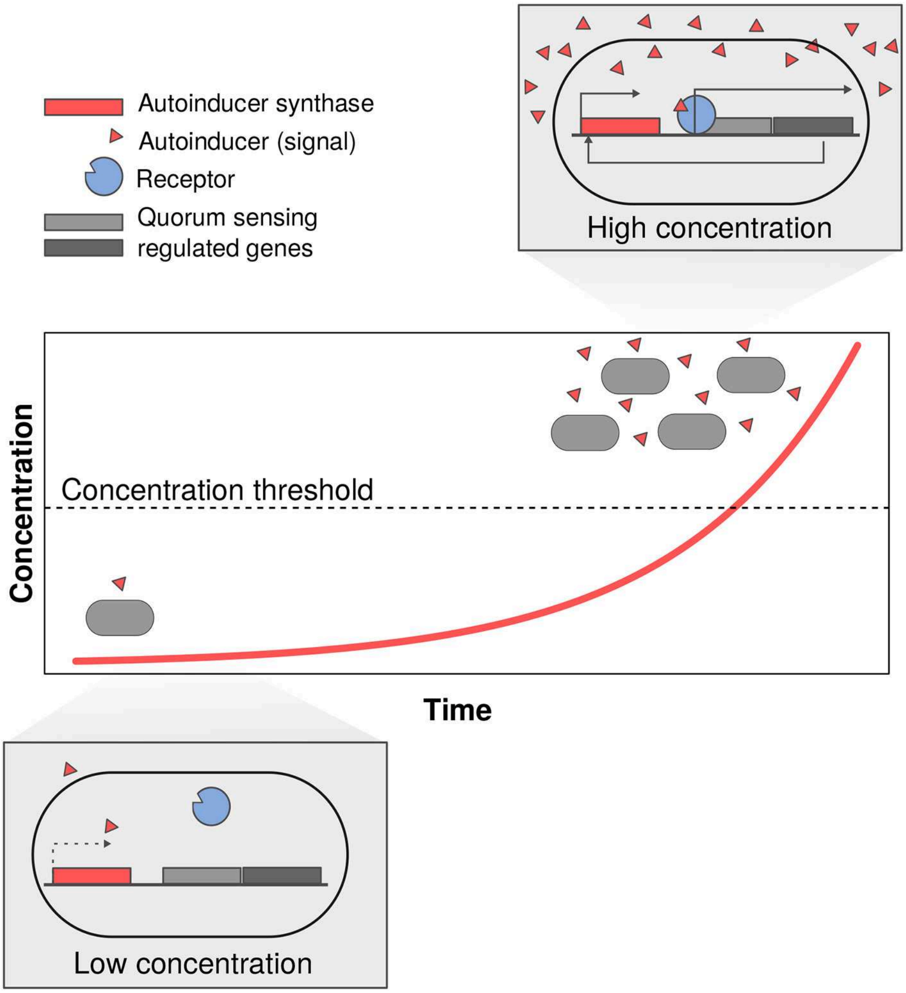

FIGURE 2 | Quorum sensing is a system of communication that relies on the concentration of an autoinducer. In this system bacteria are constantly producing a small amount of signal (autoinducers; red triangles). As bacteria reach a larger density the concentration of autoinducer increases until it crosses a threshold after which it binds to the receptor and induces changes in expression. This changes often lead to an increase expression of autoinducer and thus act as positive feedbacks in high concentration of signal.

forces shaping plant and microbial communications systems: (1) How to distinguish between signals and cues; and (2) Are a eavesdroppers a major agent of selection shaping the evolution of plant and microbial signals?

4.1.1. Distinguishing Between Signals and Cues

Distinguishing between signals and cues, as we noted earlier in this review, is a key step in establishing signaler-receiver relationships, and discriminating between intended receivers and eavesdroppers. In both plant and microbial systems, it remains challenging to establish that the compounds that elicit responses from plants and microbes are true signals, rather than cues. For example, while some volatile organic compounds released by plant leaves in response to herbivores are probably produced with the purpose of signaling—they are synthesized *de novo* in response to damage—others are mere byproducts of rupturing tissues and cells (Baldwin et al., 2002). From an evolutionary perspective, the distinction between signals and cues is an important one, given that signals and cues are governed by distinct selective pressures. By definition, signals and cues are associated with different fitness consequences for the signaler: while the receiver's response to a signal increases the signaler's fitness, cues may be selectively neutral, beneficial, or harmful for the individual that produced it (Laidre and Johnstone, 2013). Therefore, eavesdroppers almost always impose conflicting selection on signals, but not necessarily on cues.

There are three key properties of signals that distinguish them from cues. First, signals tend to be costly and specific, while cues are often cheap and non-specific (**Table 1**) (Grafen, 1990; Endler, 1992; Johnstone, 1998; Searcy and Nowicki, 2005). For example, flowers attract specific pollinators, and there is strong evidence that elements of floral displays are costly to produce (Knauer and Schiestl, 2015). The same is true for some of the molecules bacteria employ for quorum sensing (**Table 1**).

Second, relative to cues, signals are detectable. The reliability and detectability of cues is highly variable. Detectability depends on the state of the receiver (e.g., which receptors are being expressed), its genotype and the environmental context. Selection for signaling, by contrast, makes signals readily detectable by the intended receiver and in the appropriate context (Endler, 1992). As an example, it remains ambiguous whether the volatiles plants release are true signals, or merely cues whose primary function is something other than communication. Addressing this question can be tricky because herbivore damage necessarily releases some compounds as a direct result of wounding; many compounds implicated in plant-plant communication are plant hormones that play important roles in internal plant signaling as well (Heil and Karban, 2010); and most laboratory-based experiments that measure plant responses to volatiles use much higher volatile concentrations than are ecologically realistic (Baldwin et al., 2002). One possible way to resolve this question is to search for volatiles that exhibit heightened detectability (e.g., released at high initial concentrations or over especially long time periods) (Baldwin et al., 2002, 2006; Caruso and Parachnowitsch, 2016).

Finally, signal production (and specifically, the response a signal elicits in a receiver) increases signaler fitness. In plants and microbes, while the fitness consequences for the receiver are clear, the fitness consequences for the emitter are murkier (Karban and Maron, 2002; Heil and Karban, 2010). In quorum-sensing bacteria, it is not always clear who benefits from these interactions and at what cost for the other players. In mammals, for example, the immune system responds to *P. aeruginosa* quorum-sensing signals, but increasing evidence suggests that this response is not beneficial for the host and instead promotes *P. aeruginosa* establishment (reviewed in Kariminik et al., 2017). In leaf-epiphyte communities there are a number of strains that produce the same AHL, influencing motility in *Pseudomonas syringae* and therefore reducing its ability to colonize the host (Dulla and Lindow, 2009). However, the fitness consequences of this signaling system for the different players involved are not clear, nor why cross-communication has been maintained in different species that compete for some of the same resources.

Clever experimental manipulations have recently been deployed to decode the fitness consequences of information transfer in non-animal systems. Two powerful tools—available in model systems amenable to genetic manipulation—are "mute" organisms, which do not emit volatiles, and "deaf" organisms that lack the chemical receptors necessary to respond to them (Pierik et al., 2003; Baldwin et al., 2006; Paschold et al., 2006; Dicke and Baldwin, 2010). Comparing the fitnesses of mute and wild-type individuals is one way to quantify the benefits and costs of signaling for the signaler. An alternative approach is to measure the fitness consequences of being paired with a deaf partner that is unresponsive to a signaler's signal.

4.1.2. Do Eavesdroppers Shape Signal Evolution in Plants and Microbes?

The extent to which eavesdropping has shaped the evolution of information transfer systems deserves more consideration in non-animal systems. In animals, eavesdropping is a significant evolutionary force (Burk, 1982, 1988; Zuk and Kolluru, 1998). Signals that are intercepted by eavesdroppers are shaped evolutionary time by receiver-imposed selection favoring conspicuousness and eavesdropper-imposed selection favoring limited detectability (Zuk and Kolluru, 1998). The evolutionary impact of eavesdroppers is most evident in animal sexual signals. When eavesdropping predators are common, sexual signals tend to be less conspicuous than in populations where predation is rare (Endler, 1978). Over longer timescales, coevolutionary arms races between signalers, receivers, and eavesdroppers have been hypothesized to drive signal elaboration, facilitate speciation, and favor the evolution of novel signals (West-Eberhard, 1983; Zuk and Kolluru, 1998; Hoskin and Higgie, 2010). Finally, eavesdroppers may contribute to the maintenance of variation in signals by imposing fitness costs on the individuals that produce the most attractive signals (Strauss and Irwin, 2004; Heath and Stinchcombe, 2014; Wood et al., 2018). In the case of microbes, facultative cheating (eavesdropping) has favored the coexistence of multiple quorum sensing alleles in *Bacillus subtilis*, a classic case of balancing selection (Pollak et al., 2016).

Do plant and microbial signals reflect an evolutionary compromise between communicating with intended receivers and avoiding eavesdropping antagonists, as is the case with animal sexual signals (Zuk and Kolluru, 1998)? With the exception of floral signals, this question is relatively unexplored. Approaches that leverage the tools of evolutionary genomics have the potential to shed light on these processes. For example, a comparison of evolutionary rates of autoinducer synthetases and receptors between allopatric and sympatric bacteria could provide some insight into the importance of eavesdropping for microbial competition. In plants, the role of eavesdroppers in driving prezygotic reproductive isolation merits further investigation. If neighboring plant populations encounter different eavesdroppers that are attracted to different characteristics of a signal, selection to evade detection by local eavesdroppers could drive signal divergence, resulting in a breakdown of communication between signaler-receiver pairs from different populations.

Two plant signals where the evolutionary consequences of eavesdropping deserve to be explored in more detail are the root exudates plants use to communicate with mutualistic microbes, and floral volatiles. Many signals that plants use to communicate with microbial mutualists are also implicated in pathogenesis (Oldroyd, 2013).Furthermore, the ability to form mycorrhizal and rhizobial mutualisms is associated with susceptibility to parasites (Miller, 1993; Wood et al., 2018), consistent with the hypothesis that parasites rely on some of the same signals as mutualists to locate plant hosts. Second, in a recent review, Caruso and Parachnowitsch (2016) proposed a new eavesdropper on floral volatiles: other plants. They suggested that plants may eavesdrop on their neighbors' volatiles, arguing that eavesdropping on floral volatiles would be an effective way for plants to gain information about mating opportunities in their local neighborhood. Whether this eavesdropping occurs and how it might shape the evolution of floral signals remains to be tested.

Signal honesty is another foundational concept from the animal literature that deserves more extensive exploration in microbes and plants. Dishonest or manipulative signals are those where the signaler obtains a benefit at a cost to the receiver (**Figure 1C**). For example, flowers without pollinator rewards might either mimic other high reward flowers or exploit the sensory biases of the intended pollinators (e.g., Schiestl, 2004; Peter and Johnson, 2008). Manipulative signals exploit sensory biases to elicit a response in the intended receiver, usually at a fitness cost for the receiver (Laidre and Johnstone, 2013). These dishonest signals are a central component of plant reproductive biology: many plants produce deceptive flowers that advertise but do not offer a food reward; others mimic the smell of rotting flesh to attach carrion-feeding insects (Raguso, 2008). It is important to empirically determine whether a signal is dishonest. Some apparently honest signals may in fact be manipulative, and signals that appear to be dishonest may not be. For example, floral nectar is often assumed to function as a pollinator attractant, but its evolutionary ecology is surprisingly poorly understood (Parachnowitsch et al., 2019). Pyke (2016) argues that floral nectar should be considered a manipulative signal rather than a pollinator attractant, because it influences pollinator behavior. These studies illustrate that a detailed understanding of a signal's natural history—its ecology and function—is crucial.

Whether eavesdroppers intercept dishonest or manipulative signals, and what the fitness consequences of interception are for the signaler, receiver, and eavesdropper remain unknown. The maintenance of honest signals has a deep history of study in animal signals, and, generally speaking, the costs associated with producing a signal that honestly reflects the signaler's condition are thought to prevent cheaters from "faking it" (Hamilton and Zuk, 1982; Laidre and Johnstone, 2013). By imposing additional costs on the signaler, eavesdroppers may play an important role in enforcing signal honesty. However, signal honesty in general, and the role of eavesdroppers in particular, have received relatively little attention in non-animal systems (Knauer and Schiestl, 2015). One intriguing reason that manipulative signals deserve more attention in the context of eavesdropping is that eavesdropping on deceptive signals is likely to be costly for eavesdroppers, limiting the potential for eavesdroppers to exploit the signal. Generally speaking, data on the costs of eavesdropping are scarce in plants and microbes. One case in which costs limit the potential for eavesdroppers to capitalize on signal interception is found in a *Pseudomonas* example outlined earlier in this review. Mutant cells that fail to produce a quorum signal pay a high pleiotropic cost because the signal is required to regulate internal metabolic processes as well (Dandekar et al., 2012). Future studies should explore the generality of this result: are pleiotropic costs of eavesdropping primarily a characteristic in quorum-sensing bacteria, or does pleiotropy constrain eavesdropping in other systems and circumstances?

4.2. Plants and Microbes Unlock New Questions: Non-animal Models of Eavesdropping and Communication

Theories of animal communication can help guide research in the much less known world of plant and microbial communication. Often the literature in these communication systems comes from physiological and molecular studies that are more interested in the molecular mechanisms than in the ecological and evolutionary consequences. This means, on the one hand, that plant and microbial communication theory is lacking with respect to our knowledge in animal systems. But, on the other hand, it means that the mechanisms of signaling and perception are often well described—the molecular tools to study these systems and their consequences have already been developed. This provides multiple advantages for using microbial and plant systems to explore the ecological and evolutionary consequences of eavesdropping from new perspectives.

4.2.1. Evolutionary Genetics of Eavesdropping

To date, work on the evolutionary implications of eavesdropping has focused disproportionately on selection imposed by eavesdroppers on signals and signalers. However, selection is only one of two factors that influence evolutionary change (**Figure 3**). In the classic framework of quantitative genetics, trait evolution is determined by selection acting on the trait and its genetic correlation with other traits (**Figure 3**) (Lande and Arnold, 1983; Via and Lande, 1985; Brodie III et al., 1995). A genetic correlation between two traits arises when the same genes influence both traits, or when the genes influencing the two traits are tightly linked to each other (Falconer and Mackay, 1996). Genetic correlations are evolutionarily important because selection on a correlated trait causes indirect change in the focal trait by targeting the same underlying genes.

Using this quantitative genetic framework, eavesdropping can be incorporated into models of signal evolution by modeling signal detectability by intended receivers and eavesdroppers as two separate traits of the signaler that are genetically correlated (**Figure 3**) (Via and Lande, 1985). For example, attractiveness to pollinators and apparency to herbivores are both traits that can be measured on a focal plant. If, pollinators and herbivores home in on the same floral volatile, attractiveness to pollinators is genetically correlated with apparency to herbivores, and evolution of increased volatile production will attract more herbivores alongside pollinators. However, if pollinators and herbivores detect different volatiles, an evolutionary change in the volatiles that attract pollinators will not increase the plant's apparency to eavesdropping herbivores. Modeling signal detectability by receivers and eavesdroppers as traits of the signaler means that this framework is generalizable and can be applied to any signaler-receiver-eavesdropper triangle, regardless of study system.

As long as eavesdroppers impose fitness costs on signalers, a positive genetic correlation between signal detection by receivers and eavesdroppers will constrain the evolution of signal detectability, because any change in the signal that increases detection by receivers will increase apparency to eavesdroppers. When the two traits are uncorrelated, however, selection is free to reshape signals by exaggerating the features perceptible by eavesdroppers and minimizing those perceptible by eavesdroppers. Understanding the genetic correlation between detection by receivers and eavesdroppers is crucial to fully incorporate eavesdropping into models of signal evolution. Yet while we know a great deal about the fitness consequences of

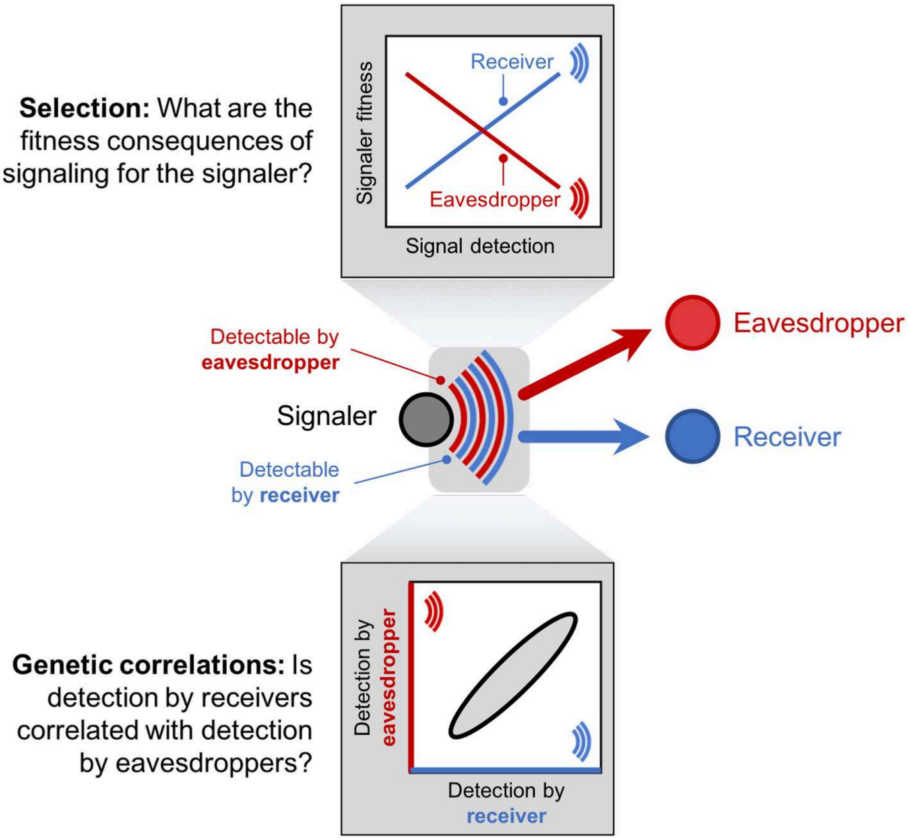

FIGURE 3 | Signal evolution is governed by two elements: selection (the fitness consequences of signaling for the signaler) and genetic correlations (the relationship between signal detectability by receivers and signal detectability by eavesdroppers). Selection **(top)** imposed by eavesdroppers can be quantified by measuring the relationship between signaler fitness and signal detection by eavesdroppers. Genetic correlations **(bottom)** can be measured by treating signal detectability by eavesdroppers and receivers (the blue and red components of the signal in this diagram) as two separate traits in the signaler (i.e., two separate properties of the signal itself). When signal detection by eavesdroppers is positively correlated with detection by receivers, as illustrated in this example, eavesdroppers will influence how signaler-receiver communication evolves.

eavesdropping for signalers (**Figure 3**, top panel), few studies have measured the genetic correlation between signal detection by receivers and eavesdroppers (**Figure 3**, bottom panel), perhaps because measuring genetic correlations requires breeding designs and large sample sizes (Falconer and Mackay, 1996). By leveraging the quantitative genetic approach described above to model evolutionary change in multiple correlated traits, we can fully incorporate eavesdroppers into our framework of signal evolution, and advance our understanding of how constraint imposed by eavesdroppers has shaped signals and communications systems over evolutionary time.

4.2.2. Experimental Ecology and Evolution of Signals

Due to the molecular characterization of communication systems in bacteria, and the ease with which their genomes can be engineered, bacteria communication can be easily manipulated to measure the fitness effects of different quorum-sensing mutations in different ecological contexts (see, for example, Popat et al., 2012. In plants, this kind of genetic engineering is restricted to a few organisms (e.g., Pierik et al., 2003; Paschold et al., 2006), but plant genetics are easy to manipulate through planned crosses.

In bacteria, for example, genetic manipulation could illuminate the fitness costs and benefits of eavesdropping in the context of cooperation and cheating within the same bacterial species. These systems are susceptible to invasion by cheaters that gain the benefits without paying the costs. This is analogous to intraspecific eavesdroppers in animals, like satellite males, that are able to obtain the overall benefits of other male calls without paying for the costs of producing the signal (e.g., Olzer and Zuk, 2018). However, given the particular properties of quorum-sensing, there can be different kinds of quorum sensing cheaters. They could be (1) insensitive to the signal and therefore not produce more signal and other public goods, (2) use information from the signal without secreting public goods (eavesdroppers), or (3) respond to the signal by producing more signal stimulating the production of more public goods by others (manipulation). The frequency and consequences of these different kinds of cheaters have rarely been studied and different mutations lead to different consequences and a diversity of ecological and evolutionary dynamics that would be hard to predict from communication theory alone. In *Pseudomonas aeruginosa*, for example, it is common to find mutants that are insensitive to quorum-sensing signals (e.g., Cabrol et al., 2003) and these cheaters readily evolve in environments were cheating is beneficial (Sandoz et al., 2007). In contrast, "eavesdropper" mutants that cannot produce the autoinducer (even if they can sense others responses) pay significant pleiotropic costs because this autoinducer is necessary for regulation of other metabolic processes (Dandekar et al., 2012).

Furthermore, the ease of manipulation in these systems can allow us to investigate the ecological evolutionary consequences of signals produced not by the signaler itself, but their associated bacteria. In hyenas, for example, social odors that indicate species identity, sex and reproductive state are produced by bacterial fermentation in their odor glands (Theis et al., 2013). Similarly, microbes from flowers can alter the volatile composition affecting pollinator visitation (Herrera et al., 2013; Good et al., 2014; Schaeffer et al., 2017). What are the consequences of these signaling symbiotic associations? What are their evolutionary consequences? Manipulating the association between microbes and plants can be a fruitful strategy to evaluate the contributions of the microbiome for fitness and how these associations might affect evolution (Lau and Lennon, 2011, 2012).

Finally, using experimental evolution, it is possible to evaluate the evolutionary consequences of eavesdropping in microbes (and even in plants). In a recent example, Kimura et al. (2016) conducted directed evolution to increase the receptor sensitivity to a particular autoinducer. This study was motivated by increasing our understanding of the receptor function and activity, but similar methods can be used to understand the fitness effects of increased sensitivity and specialization under different ecological contexts (e.g., in the presence/absence of eavesdroppers or in the presence of eavesdroppers with varying degrees of fitness impacts on the signaler).

5. SUMMARY

There are few clear examples of eavesdropping in microbial and plant communication. In this review, we argue that studies in these systems have been focused on the immediate causes and molecular mechanisms, while the evolutionary consequences are often overlooked. It is often hard to determine the "intentions" of a signaler (even worse if they are so unlike us). These organisms, however, provide great systems to test theoretical predictions and advance our understanding of biological communication. Furthermore, plants and microbes play important roles in their environments shaping the function of whole ecosystems. In principle, we might expect eavesdropping to have large-scale consequences that ramify up to the ecosystem scale. For example, signal exploitation by eavesdroppers could influence community composition and assembly although to our knowledge such an effect has not yet been empirically demonstrated. Finally, understanding the ecological and evolutionary consequences of eavesdropping and communication in plants and microbes can have important effects on agriculture and human health. Intercepting quorum-sensing signals has been proposed as a potential alternative to classic antibiotics (Roy et al., 2011) but a better understanding of genetic correlations, costs, and pleiotropic effects would give us a better idea of the potential for these methods to work over time.

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MR-G and CW conceived the paper, reviewed the literature, and wrote the manuscript.

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