

Tactics of evasion: strategies used by signallers to deter eavesdropping enemies from exploiting communication systems

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ABSTRACT

Eavesdropping predators, parasites and parasitoids exploit signals emitted by their prey and hosts for detection, assessment, localization and attack, and in the process impose strong selective pressures on the communication systems of the organisms they exploit. Signallers have evolved numerous anti-eavesdropper strategies to mitigate the trade-off between the costs imposed from signal exploitation and the need for conspecific communication. Eavesdropper strategies fall along a continuum from opportunistic to highly specialized, and the tightness of the eavesdropper–signaller relationship results in differential pressures on communication systems. A wide variety of anti-eavesdropper strategies mitigate the trade-off between eavesdropper exploitation and conspecific communication. Antagonistic selection from eavesdroppers can result in diverse outcomes including modulation of signalling displays, signal structure, and evolutionary loss or gain of a signal from a population. These strategies often result in reduced signal conspicuousness and in decreased signal ornamentation. Eavesdropping enemies, however, can also promote signal ornamentation. While less common, this alternative outcome offers a unique opportunity to dissect the factors that may lead to different evolutionary pathways. In addition, contrary to traditional assumptions, no sensory modality is completely ‘safe’ as eavesdroppers are ubiquitous and have a broad array of sensory filters that allow opportunity for signal exploitation. We discuss how anthropogenic change affects interactions between eavesdropping enemies and their victims as it rapidly modifies signalling environments and community composition. Drawing on diverse research from a range of taxa and sensory modalities, we synthesize current knowledge on anti-eavesdropper strategies, discuss challenges in this field and highlight fruitful new directions for future research. Ultimately, this review offers a conceptual framework to understand the diverse strategies used by signallers to communicate under the pressure imposed by their eavesdropping enemies.

Key words: anthropocene, communication, conspicuousness, detection, eavesdropping, localization, micropredator, parasites, parasitoids, predator–prey arms race, signal.

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I. INTRODUCTION

Exploitation of communication systems by eavesdroppers occurs across contexts, sensory modalities and taxonomic groups. Signals, by definition, target a specific receiver and have evolved under strong selection to accomplish a given function effectively (e.g. attract mates, deter rival males, warn others, inform parents of hunger levels). Eavesdroppers from other trophic levels exploit such signals to obtain valuable information on the presence, palatability and location of their prey or host, ultimately increasing their ability to detect, discriminate and attack their victim successfully. Such eavesdropping enemies fall into four main groups – predators, micropredators, parasites and parasitoids (Lafferty & Kuris, 2002). For simplicity, in this review we use the term ‘enemies’ unless referring to a specific trophic strategy. A complete list of terms and definitions can be found in the glossary (Table 1). Even though historically heterospecific eavesdropping studies have focused on animals, it is becoming increasingly apparent that eavesdropping is universal and wide-reaching (Bernal & Page, 2022). Eavesdropper–signaller interactions extend beyond the animal kingdom and are likely ubiquitous among other groups, including microbes and plants (Rebolledo-Gómez & Wood, 2019).

The widespread occurrence of eavesdropping enemies highlights the fact that classic, textbook definitions of communication based on dyadic interactions between a sender and a receiver (Fig. 1A) do not encapsulate the complexity of animal communication systems in the wild (Fig. 1B). A thorough understanding of communication systems requires including the multiple receivers associated with a given signaller in a communication network (McGregor, 2005). Signal evolution reflects the trade-offs inherent to communication as they are imposed by both target and non-target receivers. Indeed, eavesdropping enemies are considered one of the main counter-selective pressures limiting elaboration of mating signals and ultimately tempering sexual selection (e.g. Andersson, 1994; Endler, 1980; Tuttle & Ryan, 1981; Leavell *et al.*, 2022). Antagonistic selection imposed by eavesdroppers, however, is not limited to sexual communication systems. Signal structure and signalling behaviours of non-sexual signals have long been suspected also to be shaped by trade-offs imposed by predators (Marler, 1955), which are generally considered to impose critical costs mediating signal evolution (Bradbury & Vehrencamp, 2011). The long-standing assumption that communication signals are costly due to increased vulnerability to eavesdropping predators has been supported by

abundant anecdotal evidence. Over the last two decades, however, a growing number of experimental studies have provided direct empirical evidence across diverse systems revealing the intricate ways in which eavesdroppers affect both sexual and non-sexual communication systems (Bernal & Page, 2022). Here we capitalize on this recent increase in knowledge to synthesize current understanding of the strategies used by signallers to reduce the effect of interceptive eavesdropping by natural enemies.

Table 1. Glossary

Cue	An incidental feature that has not been modulated by natural selection to carry specific information for a receiver; it can benefit the receiver but does not benefit the signaller.
Eavesdropper	A non-target receiver that intercepts a signal.
Eavesdropping	The use of information in signals by those other than the primary target.
Kairomone	A semiochemical exploited by eavesdropping enemies to detect or locate their host or prey. For example, pheromones – semiochemicals that are produced by signallers to communicate with conspecifics – are often intercepted as kairomones by heterospecific eavesdroppers.
Micropredator	A predator that individually has limited effect on the fitness of its prey, as it does not individually kill its prey; a predator that feeds on multiple prey individuals in a single life stage and has density-dependent effects on its prey.
Parasite	An organism that obtains resources from its host but rarely kills its host; usually a parasite is much smaller than its host.
Parasitoid	An organism that is close in size to its host, has a similar lifespan to its host, and reproduces in or on the host, usually killing its host in the process.
Predator	An organism that consumes all or most of another organism; its prey is alive on first attack; usually a predator is larger than its prey.
Semiochemical	A chemical substance used for signalling/communication.
Signal	A trait that has evolved to change the behaviour of a receiver to the benefit of a signaller; a signal is modulated by natural selection to carry specific meaning in specific contexts; it has evolved for a specific role in communication.
Signal active space	Distance from the signaller over which a signal is detected and perceived by potential receivers.
Target receiver	An individual to which a sender transmits a signal.

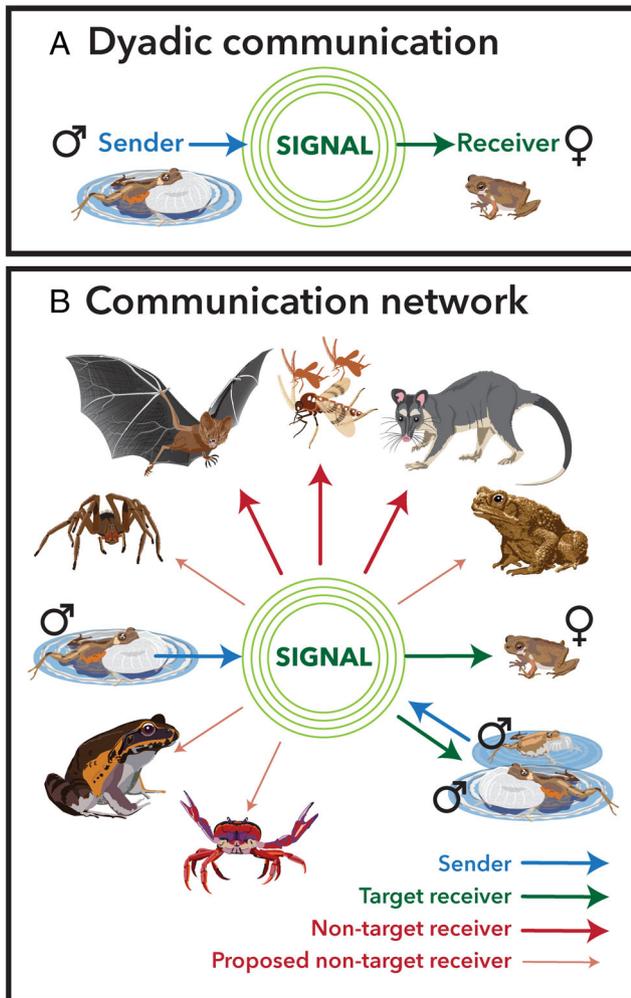


Fig. 1. Conceptual frameworks to investigate communication. (A) Traditional view of communication focusing on simple dyadic interactions, with a single sender and a single receiver. (B) A network view of communication in which multiple target and non-target receivers, including eavesdropping enemies such as predators, parasites and parasitoids, exploit a communication signal. Drawings illustrate these two approaches to understanding communication, using the túngara frog (*Engystomops pustulosus*) communication system as an example. In (A), a male frog produces a sexual advertisement signal to attract a female frog. By contrast, (B) depicts the complexity of the communication network in nature. This approach recognizes that male signals have a dual function and in addition to attracting females, they can also be used to compete with rival conspecific males. The sender thus also becomes a receiver as he interacts acoustically with other males. In the process of communicating with potential mates and with rivals, the signal attracts a variety of eavesdropping predators. Established eavesdropping interactions are depicted with thick arrows; hypothesized ones with thin arrows (see Page *et al.*, 2014). Drawings by Damond Kylo.

In contrast to prey traits that are targeted by non-eavesdropping enemies, signals and signalling displays are at the intersection of opposing forces: selection from target

receivers to facilitate communication, and eavesdropper-driven antagonistic selection to avoid conspicuousness. These conditions result in constraints that shape the fitness landscape modulating the defensive and evasive strategies of prey. Anti-eavesdropper strategies thus differ from responses to non-eavesdropping predators as they result from predator-prey interactions that are inextricably associated with information transfer. A recent meta-analysis of 78 experimental studies confirmed that eavesdropping predators, parasites and parasitoids can impose strong selection pressure on sexual signallers (White, Latty & Umbers, 2022). While the costs imposed by eavesdropping enemies are particularly apparent for mating signals that are subject to both natural and sexual selection (Zuk & Kolluru, 1998), wide-reaching effects extend beyond mating as many other behaviours require information transfer among interacting individuals (e.g. resource acquisition, parental care, and defence).

Similar to their non-eavesdropping counterparts, the ecological and evolutionary outcome of interactions between eavesdroppers and the organisms they exploit depends on the tightness of their associations. Overall, enemies that exploit communication systems can be considered to be opportunistic or specialized (Fig. 2). Opportunistic eavesdroppers capitalize on their general ability to detect and localize a wide range of signallers whose communication signals fall within their sensory range. By contrast, specialized eavesdroppers have adaptations that enable them to eavesdrop effectively on specific hosts/prey. While opportunistic eavesdroppers have loose relationships with the host or prey they attack, specialized eavesdroppers have tighter associations with their victims. This dichotomy, however, is not absolute. Eavesdropper strategies fall along a continuum of association patterns, from highly opportunistic to highly specialized (Fig. 2).

Opportunistic eavesdropping is a common strategy found across a wide range of taxa, likely due to considerable existing overlap between the sensory systems of eavesdropping enemies and their signalling hosts/prey. The widespread existence of broad, opportunistic eavesdroppers was recognized early on when Marler (1955, p. 7) suggested that vertebrate predators represent a ‘problem for insects which communicate by sounds.’ The suspicion that prey-emitted signals are in fact intercepted by predators was experimentally confirmed by Walker (1964), who broadcast katydid calling songs from a speaker to a domestic cat. These experiments offered the first-ever experimental evidence of a predator using sexual advertisement signals to identify and localize its prey. Since then, opportunistic eavesdropping has been documented across many taxa including birds (e.g. Igaune *et al.*, 2008), mammals (e.g. Tuttle, Taft & Ryan, 1981), anurans (e.g. Roberts & Uetz, 2008), fish (e.g. Godin & McDonough, 2003), and arthropods (e.g. Virant-Doberlet *et al.*, 2011). Investigations examining this eavesdropping strategy, however, are often limited to reports of anecdotal observations or studies showing that the signals can indeed attract the enemy. This narrow approach is probably due to the nature of encounters between opportunistic

eavesdroppers and their targets which makes them difficult to track and study systematically more deeply.

By contrast, specialized eavesdropping is a less-common strategy and it is used mainly by parasitoids. The costs of making an error differ along the eavesdropper–signaller relationship, reflecting the tightness of the eavesdropper–signaller relationship. Opportunistic predators often have little to lose when responding to prey signals, with low costs associated with errors in the assessment of those stimuli (e.g. Page *et al.*, 2012). Such low costs paired with the high potential benefits of obtaining a meal allow these eavesdroppers opportunistically to attack a broad range of prey. Specialized eavesdroppers such as certain parasitoids, by contrast, risk the future of their offspring and thus are confronted with strong selection for refined, efficient responses to signals emitted by their hosts. Accordingly, eavesdropping parasitoids have evolved specialized sensory adaptations to increase detection, localization or recognition of signals targeting other receivers. For example, acoustically orienting parasitoid flies that attack cicadas and crickets have sophisticated, highly sensitive ears that match the acoustic properties of their hosts' sexual advertisement songs. Among flies (Diptera), acoustic strategies to exploit host-emitted mating signals have evolved independently in Ormiini

(Cade, 1975; Lehmann, 2003) and Emblematomatini (Lehmann & Lakes-Harlan, 2019; Lakes-Harlan, Stölting & Moore, 2000; Lakes-Harlan & Lehmann, 2015; Soper, Shewell & Tyrrell, 1976), with female flies using insect calling songs (crickets or cicadas, respectively) to locate hosts for the deposition of their planidia (first-instar larvae). In both cases, the co-opting of general ear anatomy from originally vibration-sensitive scolopidial chordotonal organs in non-hearing flies has resulted in novel hearing organs specialized for eavesdropping on their hosts (Lakes-Harlan, Stölting & Stumpner, 1999). The independent evolution of unique hearing structures in these two separate Diptera lineages highlights the strength of selection promoting sensory adaptations for specialized eavesdropping behaviour in parasitoids.

Opportunistic and specialized eavesdropping strategies represent opposite ends of a continuum that illustrate the diversity of approaches used by signal exploiters. Particularly interesting are cases of eavesdroppers that integrate sensory and behavioural approaches from both strategies. The fringe-lipped bat (*Trachops cirrhosus*), for instance, has traits characteristic of both types of eavesdroppers. This species has a highly specialized auditory system that allows it to hear frog mating calls (Ryan, Tuttle & Barclay, 1983; Geipel

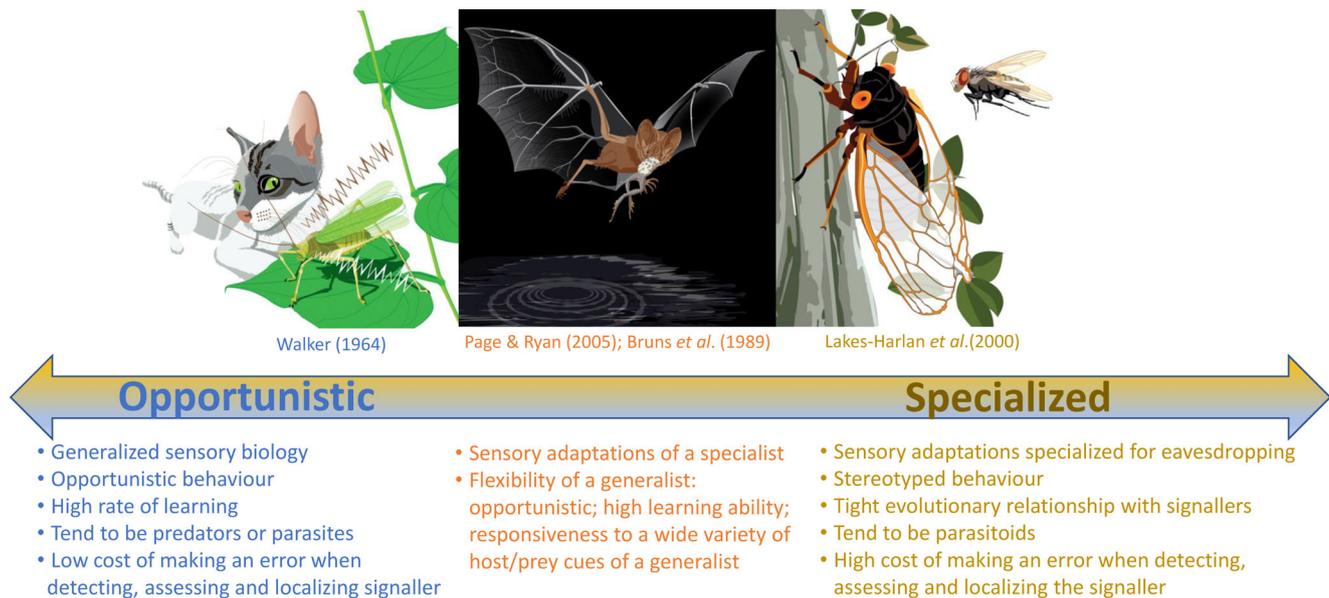


Fig. 2. Continuum of eavesdropping strategies. Eavesdropping behaviour can be generally divided into two broad categories. Opportunistic eavesdroppers are often predators and parasites that exhibit generalized sensory biology, attack a broad range of prey, show high learning ability in this foraging context, and incur low costs associated with eavesdropping errors (e.g. domestic cats using katydid calling song to hunt them opportunistically; Walker, 1964). Specialized eavesdroppers, by contrast, have tight evolutionary relationships with their hosts, and are often parasitoids with specialized sensory adaptations that enable highly stereotyped host-finding behaviour, with high costs associated with eavesdropping errors (e.g. the tight evolutionary relationship between parasitoid flies and their cicada hosts; Lakes-Harlan *et al.*, 2000). While these strategies represent extremes in the foraging approach and sensory features associated with eavesdropping behaviour, they reflect opposite ends of a continuum with diverse strategies in between, for example the frog-eating fringe-lipped bat (*Trachops cirrhosus*), which shows the sensory specializations of a specialist (Bruns *et al.*, 1989) but the flexibility, rapid learning and broad dietary breadth characteristic of an opportunistic eavesdropper (e.g. Page & Ryan, 2005). Drawings by Damond Kylo.

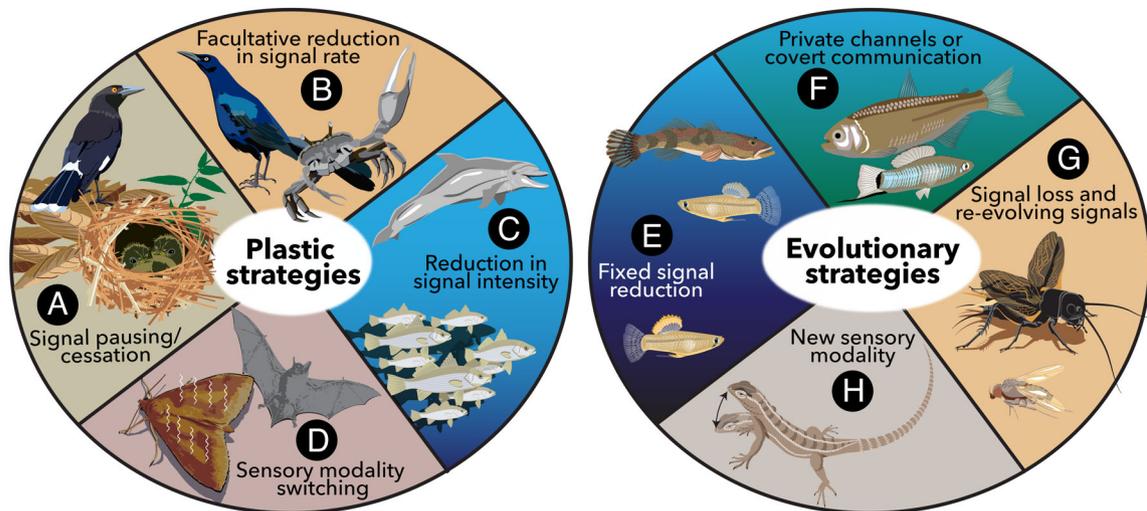


Fig. 3. Examples of anti-eavesdropper strategies. Prey employ a wide variety of plastic (left) and evolutionary (right) strategies to evade eavesdropping enemies. (A) Signal pausing/cessation. Nestling white-browed scrubwrens (*Sericornis frontalis*), stop calling when they hear the sound of a pied currawong (*Strepera graculina*), an avian predator, walking on leaf litter nearby (Haff & Magrath, 2010). (B) Facultative reduction in signal rate. Sexually advertising male fiddler crabs (*Uca beebei*), wave less in areas with high numbers of predatory grackles (*Quiscalus mexicanus*) (Koga *et al.*, 1998). (C) Reduction in signal intensity. Male silver perch (*Bairdiella chrysoura*), reduce the amplitude of their mating choruses in the presence of vocalizing bottlenose dolphins (*Tursiops truncatus*), predators that eavesdrop on silver perch mating calls (Luczkovich *et al.*, 2000). (D) Sensory modality switching. Lesser wax moths (*Achroia grisella*), stop their acoustic signals but continue releasing an advertising pheromone when insectivorous bats are present (Spangler, 1984). (E) Fixed signal reduction. Male Bahamas mosquitofish (*Gambusia hubbsi*), inhabiting water-filled vertical caves (blue holes) with high predator densities have less bright orange dorsal fins, which are attractive to females but also increase attractiveness to their predators, bigmouth sleepers (*Gobiomorus dormitor*) (Martin *et al.*, 2014; Heinen-Kay *et al.*, 2015). (F) Private channels or covert communication. Northern swordtails (*Xiphophorus nigrensis*) have ultraviolet ornamentation that increases their attractiveness to conspecific females but is not detectable by their main predator, the Mexican tetra (*Astyanax mexicanus*) (Cummings *et al.*, 2003). (G) Signal loss and re-evolving signals. In some populations of Pacific field crickets (*Teleogryllus oceanicus*), males have lost the ability to produce sound in the presence of *Ormia* parasitoid flies (Zuk *et al.*, 2006), in other populations males have evolved novel sexual acoustic signals (Tinghitella *et al.*, 2018). (H) New sensory modality. Blue-bellied *Sceloporus* lizards lost their blue bellies but gained an increased-intensity head-bobbing behaviour (Martins *et al.*, 2015). Drawings by Damond Killo.

et al., 2021). A long basilar membrane, high neural innervation in the apical portion of the cochlea, coupled with large pinnae, enable the detection of low-frequency sounds (Bruns, Burda & Ryan, 1989). But despite anatomical specializations pointing to adaptation of the *T. cirrhosus* auditory system for the detection of low-frequency frog calls, these bats also have traits characteristic of opportunistic eavesdroppers such as flexible behaviours and rapid learning abilities (Page & Ryan, 2005; Patriquin *et al.*, 2018) that result in exploratory tendencies that promote inspecting and attacking novel signalling prey (Page & Ryan, 2006; Dixon *et al.*, 2022). Indeed, the diet of *T. cirrhosus* is not exclusively frogs, but includes a broad range of other prey, including insects, birds, lizards and smaller species of bats (Jones *et al.*, 2020; Leal *et al.*, 2018), indicating that sensory specializations are not always associated with a tight coupling between eavesdropper and signaller. Overall, where eavesdroppers fall on the spectrum from opportunistic to specialized, and the sensory and behavioural abilities that accompany their eavesdropping strategies, shape the fitness landscape for the communication system of their hosts and prey.

In the evolutionary arm race with eavesdroppers, signalers are in a challenging situation as they are confronted with two difficult alternatives: engage in effective communication and risk parasitization or death, or play it safe but suffer costs resulting from not communicating (e.g. missed mating opportunities or other critical resources). Unlike prey attacked by predators using prey-emitted cues, such as incidental sounds produced during locomotion which are under selection to minimize attention, signalers attacked by eavesdroppers are often under selection to increase signal conspicuous to fulfil their function in communication. In this review, we provide an overview of the diverse strategies used by signalers to reduce predation risk by eavesdropping enemies. In particular, we examine the mechanisms involved in decreasing detectability, localizability and attractiveness to eavesdroppers both plastically at the individual level (Fig. 3, left panel), and evolutionarily, from a population perspective (Fig. 3, right panel). Focusing on animal systems, for which most evidence of anti-eavesdropping strategies has been identified, we identify overarching patterns as we highlight current challenges and fruitful opportunities for future

research to evaluate the role eavesdroppers play in shaping communication systems.

II. ANTI-EAVESDROPPER STRATEGIES

(1) Signalling displays

Signallers employ a battery of strategies to evade eavesdropper exploitation. Among non-animal systems, with the exception of flowers and floral signals, little is known about tactics deployed by signallers to deter eavesdroppers (Rebolleda-Gómez & Wood, 2019). Non-pollinators attracted to flowers steal nectar and disrupt pollination by deterring other flower visitors and are thus expected to have shaped the ecology and evolution of floral traits. Accordingly, hypotheses have invoked selection by those eavesdroppers to explain variation among plant species in flower number production (Pettersson, 1999), nectar volume, and eavesdropper-repellent traits (Ballantyne & Willmer, 2012). While investigation of eavesdropping behaviour in non-animal systems remains largely unexplored, our understanding of eavesdropping behaviour in animal systems is much broader. Animal anti-eavesdropper strategies include standard evasion responses common to general predator–prey interactions, such as limiting mobility and thus reducing associated locomotion cues. Motion is a salient cue (Geipel *et al.*, 2020) and the reduction and ultimately the cessation of motion is a critical first step in evading predator detection (e.g. Eilam *et al.*, 1999; Fenn & Macdonald, 1995; reviewed in Apfelbach *et al.*, 2005). But because eavesdroppers specifically attend to the communication signals of their hosts and prey, when faced with an eavesdropping enemy, evasion strategies often consist of modifying signalling displays or signal structure.

(a) Signal pausing/cessation

One effective anti-eavesdropper strategy is facultatively to pause or cease a signalling display in the presence of eavesdropping enemies. Diurnally calling brown frogs (*Rana uenoi*), for example, stop calling in the presence of daytime birds (Kim *et al.*, 2020). Gulf toadfish (*Opsanus beta*) also go silent when they hear dolphins (Remage-Healey, Nowacek & Bass, 2006), predators that can detect and respond to the advertisement calls of this fish species (Gannon *et al.*, 2005). Similarly, veeries (*Catharus fuscescens*) that hear owl calls during the dusk chorus stop singing sooner than conspecifics not exposed to such predation cues (Schmidt & Belinsky, 2013). Male wolf spiders (*Hygrolycosa rubrofasciata*) drastically decrease the drumming activity used to court females and often cease drumming altogether in the presence of predatory lizards (Kotiaho *et al.*, 1998). Katydid, both in temperate (Faure & Hoy, 2000; ter Hofstede & Fullard, 2008; Spangler, 1984) and tropical regions (ter Hofstede, Kalko & Fullard, 2010; Symes *et al.*, 2018), pause production of their calling song when they hear bat echolocation calls. The anti-eavesdropper strategy of signal cessation is not

limited to sexual signals. Nestlings of some avian species, for instance, assess danger independently of their parents and stop calling if they detect a predator nearby (Haff & Magrath, 2010; Magrath *et al.*, 2010; A in Fig. 3).

While the decision to stop signal production abruptly is likely modulated by specific trade-offs intrinsic to the signal's function, reducing detectability by limiting information intentionally released into the environment is an effective defence to evade detection and localization by eavesdropping predators. Curtailing a signal display reduces the likelihood of attack and increases the chances of survival if an attack unfolds. Flight cage experiments show that gleaning northern long-eared bats (*Myotis septentrionalis*) attack speakers broadcasting katydid calling songs but abort their attacks when the song stops (ter Hofstede, Ratcliffe & Fullard, 2008). Likewise, frog-eating bats show decreased localization ability when frog mating calls stop mid-attack (Page & Ryan, 2008).

The absence of signalling itself can be perceived as a cue of increased predation risk by individuals signalling within hearing range. In vocally lekking species such as frogs, such 'sound of silence' acts as an alarm cue to other callers, and can rapidly evoke call cessation across an entire chorus (Dapper, Baugh & Ryan, 2011). The relevance of this anti-eavesdropper strategy varies with chorus size. As the number of signallers in a chorus increases, the dilution effect results in lower *per capita* predation risk, and the anti-eavesdropping behaviour of pausing calling weakens (Jennions & Backwell, 1992). Silence as an alarm cue can also come from heterospecific signallers susceptible to shared eavesdroppers. For instance, frogs calling in mixed-species aggregations selectively attend to signals from sympatric heterospecifics to assess predation risk and to decide when to call (Phelps, Rand & Ryan, 2007).

In an analogous way, some males within a signalling population can adopt non-signalling strategies acting as satellites of signalling males. By quietly stationing themselves by signalling males, satellite males intercept approaching females, increasing mate acquisition without incurring signalling costs. This alternative mating strategy is common in crickets and frogs that produce acoustic advertisement signals to attract their mates (Gerhardt & Huber, 2002). Similar approaches by non-courting males that opportunistically take advantage of mates attracted by signalling conspecifics are known across taxa (e.g. acoustic signals in plainfin midshipman fish *Porichthys notatus*; Brantley & Bass, 1994) and signalling modalities [e.g. visual signals in ruff *Calidris pugnax* wading birds (Baguette, Bataille & Stevens, 2022); chemical signals in tephritid flies (Prokopy & Hendrichs, 1979)]. While sexual selection has been considered the main driver of alternative mating strategies (Oliveira, Taborsky & Brockmann, 2008), the role of natural selection has received less direct attention even though reduced eavesdropper-imposed predation has likely also shaped the evolution of non-signalling behaviours. Indirect evidence suggests that eavesdroppers may indeed be an important force selecting for less costly communication strategies. In the presence of

a model predator, for example, male guppies (*Poecilia reticulata*) decrease the use of courting tactics presumably to reduce their vulnerability to eavesdropping predators (Godin, 1995). Investigations of alternative reproductive strategies under the lens of anti-eavesdropper behaviours are promising avenues to understand these disparate behaviours more thoroughly.

(b) Reduction in signal rate

Rather than completely ceasing signal production, reduction of signalling rate is another common strategy used by signalers facing perceived predation risk. Brown anole lizards (*Anolis sagrei*), for example, decrease their push up rates when they perceive a model bird of prey resembling an American kestrel (*Falco sparverius*), a known lizard predator (Simon, 2007). Likewise, fiddler crabs (*Leptuca (Uca) beebei*) wave less in areas to which predatory grackles (*Quiscalus mexicanus*) are artificially attracted (Koga *et al.*, 1998; B in Fig. 3). In the visual realm of bioluminescent signalling by fireflies, males producing the highest flashing rates are most susceptible to exploitation by eavesdropping predatory *Photuris* fireflies (Lloyd & Wing, 1983; Woods *et al.*, 2007). Similarly, attractiveness of frogs to eavesdropping bats (Tuttle & Ryan, 1981) and midges (Aihara, de Silva & Bernal, 2016) increases with call rate. Individuals that perceive high risk of predation thus temporarily reduce their signalling rates. This plastic response, however, is also modulated by internal physiological factors associated with the function of the signal. In the case of mating signals, hormones associated with reproductive behaviour can increase motivation to signal counteracting perceived risk of predation (Kime *et al.*, 2007).

When predation pressure is consistently high over a long period of time, signal reduction can become fixed in a population. This pattern of fixed reduction is found in signals that cannot be readily reduced or turned off, such as pigmentation that varies in conspicuousness across populations in response to eavesdropper threat. Across islands in Greece, Aegean wall lizards (*Podarcis erhardii*) have duller sexual signals in populations where predation risk is higher (Marshall & Stevens, 2014). Similarly, in the Bahamas, male mosquitofish, *Gambusia hubbsi*, inhabit water-filled vertical caves (blue holes) and use their orange dorsal fins in courtship displays. In blue holes where predator densities are low, male dorsal fins are bright orange, but in areas with high predator density, males exhibit dull coloration (Martin *et al.*, 2014; E in Fig. 3). Bright orange dorsal fins are more conspicuous to predatory fish, and female mosquitofish prefer males with bright orange dorsal fins relative to their duller, high-predator counterparts (Heinen-Kay *et al.*, 2015). This visual signal reduction in response to predation is reminiscent of the pattern seen in stream populations of guppies in Trinidad where waterfalls demark stark shifts in predator abundance. Males in low-predator populations exhibit more and higher intensity blue and iridescent dots than those in high-predator populations (Endler, 1980). Guppies introduced into environments with different predation levels reveal that survival improves with adaptation to the new

predation conditions (Gordon *et al.*, 2009). Rapid evolutionary change of guppy male coloration (about three generations after introduction) is the outcome of the net effect of selection arising from reproductive success and mortality risk (Gordon *et al.*, 2015).

Genetic shifts in signal conspicuousness, such as those found in guppies and mosquitofish, are predominantly seen in the visual modality, where signals often cannot be flexibly adjusted in response to eavesdropper presence or absence. While some visual signalers have dynamic control over the ability to turn their signals on/off (e.g. dewlap displays in anoles), often the signals themselves remain consistently present independent of activation of courtship displays by signalers. In these cases, shifts in signal conspicuousness take place over evolutionary time rather than in the moment, resulting in different signalling patterns across populations with divergent predator communities. By contrast, transient and more flexible sensory signals, such as those associated with acoustic, vibratory, bioluminescent or chemical displays, can be facultatively diminished or turned off in response to eavesdropper presence.

Different sensory modalities also vary in their effectiveness at increasing the signaller's likelihood of survival when the signaller reduces, or completely stops, signalling. Signal reduction or cessation is highly effective when signalling in easily localizable sensory modalities, such as with visual or acoustic signals (Bradbury & Vehrencamp, 2000). By contrast, with less easily localized signals, such as volatile chemical signals that are often only loosely associated with the location of the sender, signal reduction or cessation may be a less-effective, and seldom used, anti-eavesdropper strategy. In such cases, cessation of volatile chemical signal production in response to eavesdropping enemies is expected to be uncommon. There is, however, variation in the opportunity that chemical signals provide for exploitation given the differences in a signaller's control of the duration of the signal presence. Some kairomones, chemical substances exploited by individuals of other species, allow eavesdroppers to locate and attack the signaller more reliably. Territorial marking illustrates this phenomenon as signalers consistently return to remark the location and conspecifics also visit those sites. *Ixodes neitzi* ticks perform chemotaxis aggregating in territorial marking pheromones of the East African klipspringer antelopes (*Oreotragus oreotragus*) where they wait for approaching hosts (Rechav *et al.*, 1978).

The cost of ceasing or reducing the frequency of a signalling display also varies depending on the signal's function. While the effect of truncating communication undoubtedly imposes negative consequences, benefits of signalers responding to predation risk by reducing signalling behaviour are counterbalanced by costs of missed opportunities associated with the communication goal. When considering the production of sexual signals, the signal reduction strategy decreases the likelihood of attracting a mate, thus directly affecting reproductive fitness (Kotiaho, 2001; Zuk & Kolluru, 1998). Given the high costs of limiting signal production and strong selection pressure for conspicuousness

imposed by mates, signallers producing mating signals tend to be the most vulnerable to exploitation. Their predictability in when or where they occur also makes them susceptible to specialized eavesdroppers. Begging signals are similar to mating ones in their conspicuous nature but their occurrence tends to be more uncertain in space and time, increasing the challenge for exploitation by non-target receivers. Signals with other functions, such as those mediating navigation, food acquisition or defence, are quickly reduced or ceased in the presence of eavesdroppers as part of generally reduced activity levels characteristic of increased risk perception (Daversa *et al.*, 2021).

Vulnerability to exploitation, and therefore anti-eavesdropper strategies, are also expected to vary by signal sensory modality. Overall, the larger the active space of a signal, the higher the likelihood the signal will be detected and potentially exploited by a non-target receiver. To some degree, a signal's active space, i.e. the distance from the signaller over which the signal is detected and perceived by potential receivers, can be predicted by fundamental properties of the signal in its specific sensory modality (Bradbury & Vehrencamp, 2011). The long-range transmissibility of airborne acoustic signals, for instance, results in such signals reaching receivers across large spaces. Similarly, chemical cues may reach non-target receivers over a wide area as they usually span medium to long distances. Accordingly, a recent meta-analysis confirmed high incidence of eavesdropping on both airborne acoustic and chemical signals (White *et al.*, 2022). A signal's active space, however, is only superficially evaluated when the sensory ability of the receivers is not considered. A signal may transmit over long distances but, if a limited number of receivers are able to detect and process it, the actual active space of the signal to exploiting enemies is smaller than predicted. Likewise, a signal can have a restricted range but expose the signaller to a large community of exploiters able to take advantage of this information. Substrate-borne vibrations, for example, have relatively short ranges but can be detected and potentially used by most organisms. Despite unfounded traditional assumptions that vibrational signals provide covert communication, these types of signals are one of the most taxonomically widespread forms of communication and vibration receptors are thus nearly ubiquitous across organisms (Cocroft & Rodríguez, 2005; Cocroft & Hamel, 2010). Vibrational signals are thus more susceptible to eavesdropping than originally thought and illustrate how human perception and methodological biases have influenced our understanding of signaller vulnerability (Virant-Doberlet *et al.*, 2019). The abundance of eavesdropping studies reporting exploitation of substrate-borne acoustic and chemical mating signals (White *et al.*, 2022) thus is likely to provide an incomplete view of signal susceptibility to eavesdroppers across sensory modalities.

(2) Signal structure alterations

Another strategy used by signallers to curtail exploitation risk is to continue signalling when eavesdroppers are present but

to modify signal structure to reduce signal detectability, localizability or attractiveness. These strategies involve the use of signal features that minimize cues available to eavesdroppers (i.e. cue denial; Searcy & Yasukawa, 2017), reflecting the intersection between responding to selection to avoid exploitation without overly compromising communication efficacy.

(a) Reduction in detectability

Signals can be modified to reduce the space over which detection occurs. Signals used over short ranges are typically inaccessible to eavesdropping enemies and provide privacy that results in diverse communication interactions. Courtship signals, for instance, illustrate the complex and unique interactions that arise when individuals interact over short distances. Courtship signals include tactile interactions, low-contrast coloration, subtle movements, low-amplitude calls, and contact chemicals (Bradbury & Vehrencamp, 2011). Similarly, signal properties that degrade rapidly in the environment like high-duty-cycle sounds, and highly volatile compounds, can be used effectively to limit the signal to target receivers. Alternatively, signallers can switch to a modality that reduces eavesdropper risk once the receiver is close by. Under the safety of communication interactions taking place at short range, receivers of long-range signals can now become active signallers. Females attracted to males producing long-distance mating displays, for example, may engage in signalling to assess mate suitability. In the few species in which female anurans produce acoustic signals, they vocally reciprocate male courtship signals by producing soft calls (Schlaepfer & Figueroa-Sandí, 1998). The contrast between short- and long-range communication highlights the weight that eavesdroppers impose on communication signals.

In systems in which long-range communication is necessary, a straightforward way to reduce the active space of an acoustic signal is to decrease the amplitude of the sound produced. Male silver perch, *Bairdiella chrysoura*, for instance, reduce the intensity of their mating choruses in the presence of vocalizing bottlenose dolphins, *Tursiops truncatus* – predators that eavesdrop on perch mating calls (Luczkovich *et al.*, 2000; C in Fig. 3). Similar to acoustic signals, higher amplitude electric signals result in increased predator detection (Stoddard, Tran & Krahe, 2019). There is evidence to suggest that electric fish will go silent when an eavesdropping predator (an electric eel *Electrophorus electricus*) approaches (Westby, 1988). Experimental studies show that instantaneous electric organ discharge (EOD) amplitude drops in *Brachyhyopomus* (formerly *Hypopomus*) *occidentalis* from Panama, in response to light touch as a proxy for predation threat (Hagedorn, 1995); more studies, however, are needed to show the degree to which electric fish can flexibly lower the amplitude of their electric signals in the context of perceived predation risk. Facultatively reducing the active space of signals provides flexibility for signallers to modulate their risk to eavesdroppers dynamically with predator presence, while maximizing reaching target receivers in under

low-predator-risk conditions. This strategy is thus expected across all sensory modalities in which senders can actively modulate signal intensity.

In populations with high selective pressure imposed by eavesdroppers, signal features that limit detectability to predators can become fixed. In electric fish, for instance, most gymnotiform species have signal adaptations that lower detectability of their signals to their main predator, electric eels (Stoddard, 1999). In addition, population differences in signal structure match differences in predation pressure between streams within the same drainage network. Given that low-frequency signals are most vulnerable to electric-sensing eavesdroppers (Stoddard & Markham, 2008), gymnotiform fish (*Brachyhyopomus occidentalis*) from populations with high incidence of eavesdropping catfishes (Siluriformes) produce EODs with an upward-shifted power spectrum compared to fish from populations with low predator density (Stoddard *et al.*, 2019). This shift in energy towards higher, safer, frequencies in high-predation populations is reminiscent of signal reductions in guppies and mosquitofish despite differences between the mechanisms involved in signal modification (reduction *versus* structural shift). Electric fish, however, also provide unique strategies in response to predators exploiting their signals. For instance, they deploy costly strategies that mask their own signals, reducing the active space to eavesdropping predators (Stoddard *et al.*, 2019). Weakly electric fishes in the genus *Brachyhyopomus* restrict the electric fields of their signals' low-frequency spectrum without affecting the higher frequencies, which maintains a larger active space. This spectral shift of the active space is accomplished by producing additional low-frequency electrosignals that mask the spectral components most vulnerable to eavesdroppers (Stoddard & Markham, 2008). Contrary to the common assumption that eavesdroppers curtail signal elaboration, in weakly electric fishes, signal exploitation by predators has resulted in higher signal complexity to cloak EODs from eavesdroppers (Stoddard, 2002). Such electric cloaking also unexpectedly increases the energetic cost of signalling rather than maintaining it by shifting signal structure or saving energy by reducing or ceasing signal production.

For senders emitting kairomones, semiochemicals that can attract parasites and predators, limiting the active space of the signal could involve strategies such as reducing the amount of chemical signal released into the environment. Studies that examine plastic and fixed adaptations in kairomone intensity in response to predation risk are needed to clarify the role this strategy may play in chemical signals. Changes in blend composition can also adjust overall signal detectability by shifting the chemical properties of the different compounds involved. Wisconsin pine engraver bark beetles (*Ips pini*) produce and are preferentially attracted to blends with intermediate ratios of the two stereoisomer compounds in their signals. By contrast, their two main predatory beetles, *Thanasimus dubius* and *Platysoma cylindrica*, prefer signals with mostly one or the other stereoisomer (Raffa, 2001; Raffa *et al.*, 2007). Across populations of pine engraver bark

beetles, shifts in the main compounds of their kairomones reflect differences in local eavesdroppers (Raffa, 2001). While differences in responses by predators and conspecifics to different blends suggest these kairomones have been shaped by selection imposed by eavesdropping enemies, it is unclear if these changes in signal structure modulate detectability, attractiveness or both. Disentangling detectability and behavioural responses like preference and attractiveness is a common challenge across sensory modalities that deserves further attention.

As the active space of signals is reduced to decrease exploitation, costs from reduced communication to target receivers can be high. Some signallers have thus evolved to minimize detectability, biasing the active space of their signals specifically away from predators while still allowing detection by conspecifics. Compared to other sensory modalities, visual signals provide the clearest opportunity to restrict the active space selectively. Given that visual signals require a straight line of sight from signaller to receiver, signallers displaying coloration patches can restrict the viewing angle of their signals, limiting visibility to those only in specific positions relative to them. In iridescent butterflies, *Hypolimnas bolina*, males have ultraviolet markings on their dorsal wing surfaces that, despite having a narrow angular reflectance function, are visible to females as males fly directly above them during courtship. By positioning themselves above females, males maximize conspicuousness of a narrowly directed signal (White, Zeil & Kemp, 2015). Similar approaches, however, also work on signals with broader angular views than iridescent ones. Aegean wall lizards have ventrolateral coloration patches that are highly conspicuous to females and competing males but are not visible from the aerial perspective from which avian predators hunt the lizards (Marshall & Stevens, 2014). For signals using some sensory modalities, the active space may be constrained by the specific properties involved in signal transmission. For example, substrate-borne vibrations in organisms signalling on the stems of plants result in directional transmission of the signal (e.g. Caldwell *et al.*, 2010; Gibson & Cocroft, 2018). Similarly, transmission of kairomones is determined by air currents and can result in directional active spaces (Bradbury & Vehrencamp, 2011). Along those lines, it has been proposed that olfactory eavesdropping could have shaped the evolution of shortened odour trails or point-source-only scents to conceal insect nests (Nieh *et al.*, 2004).

Selection to reduce signal detectability is expected to exploit differences in sensory abilities between signallers and their eavesdroppers (Marler, 1955). Aerial alarms in birds, for instance, have been suggested to have been under selection to prevent detection by predators by using properties to which their enemies are less sensitive (Klump & Shalter, 1984). The Eurasian sparrowhawk (*Accipiter nisus*) has better hearing than their prey, great tits (*Parus major*), across most frequencies. The classic *seet* call of great tits that functions to alarm conspecifics, however, is produced at 8 kHz, a frequency at which the hearing threshold for sparrowhawks is about 30 dB higher than that of the great tits,

making the sparrowhawks much less sensitive to this call (Klump, Kretzschmar & Curio, 1986). Such signals to which eavesdroppers are less sensitive turn communication private.

Fundamental changes in signal structure away from the perceptual abilities of eavesdropping enemies can result in highly limited detectability for non-target receivers, known as private channels, or covert communication. For example, Northern swordtails (*Xiphophorus nigrensis*) have ultraviolet (UV) ornamentation that increases their attractiveness to conspecific females but is not detectable by their main predator, the Mexican tetra (*Astyanax mexicanus*) (Cummings, Rosenthal & Ryan, 2003) (F in Fig. 3). Similarly, the use of ultrasonic vocalizations by Philippine tarsiers (*Tarsius syrichta*) may reflect a strategy of private communication that reduces detection by predators, prey and competitors (Ramsier *et al.*, 2012). In addition to shifts in the range along a sensory modality used for signalling, signallers can use other dimensions of the signal physical properties that may obscure detection at the receiver. It has been proposed, for instance, that circular light polarization may also serve as a channel of covert communication in mantis shrimp (*Gonodactylaceus falcatus*) (Gagnon *et al.*, 2015) and some scarab beetles [Brady & Cummings, 2010; but see Blahó *et al.* (2012) and Horváth *et al.* (2014)]. Such communication channels may also be used by aquatic vertebrates like swordtail fish, in which polarized light modulates female preferences (Calabrese *et al.*, 2014), if their main predators are not sensitive to these stimuli. More investigations are needed to clarify further the use of polarized signals in conspecific communication and whether indeed these are covert to their enemies (reviewed in Marshall *et al.*, 2019). Similarly, senders may conceal their communication by de-emphasizing the chromatic contrast in their visual signals in the channel available to non-target receivers. Females of the false garden mantid (*Pseudomantis albobimbrata*) are chromatically cryptic to both target and non-target receivers but have achromatically conspicuous abdomens. In this system, reducing signal conspicuousness limits detectability to predators but also does so to potential prey (Barry *et al.*, 2015). Therefore, studies are needed to assess the relative contributions of selective pressures from eavesdropping enemies and reduced foraging opportunities driving the shift in signalling channel.

Eavesdroppers usually attend to signals in the same sensory modality used by target receivers. There are cases, however, in which eavesdroppers intercept signals in a different sensory modality entirely. Male field voles (*Microtus agrestis*), for example, scent mark their runways with semiochemicals that are chemically conspicuous to conspecifics. Avian predators can eavesdrop on these scent markings to locate areas rich in prey, not using the chemical modality, but with ultraviolet vision (reviewed in Honkavaara *et al.*, 2002). In a controlled experiment, Viitala *et al.* (1995) showed that Eurasian kestrels (*Falco tinnunculus*) are attracted to the UV component of vole scent markings. In northern Europe, vole populations fluctuate widely, and raptors are able to track them rapidly across great distances. Kestrels may use the UV component of male vole scent markings to scan large

areas and locate areas of high prey density (Viitala *et al.*, 1995).

To date, most attention has focused on investigating covert communication in airborne acoustic signals and visual signals. Substrate-borne vibrations were long assumed to provide private communication channels for animals using them. It is currently understood, however, that many animals use vibrational signals and have access to exploiting vibrational cues produced by others; thus, this sensory modality is less private than previously appreciated (Virant-Doberlet *et al.*, 2019). By contrast, the tighter association between stimuli and receptors makes chemical signals likely to provide opportunities for covert communication (Raguso, 2008; Bradbury & Vehrencamp, 2011). While interception of chemical signals by eavesdropping enemies has received limited investigation outside its use in pest control, the role and abundance of kairomones in ecological contexts has been recognized recently (Wyatt, 2014; Adams *et al.*, 2020). Investigating the potential for covert communication by addressing differential sensitivity to chemical signals by target and non-target receivers will provide a broader picture of trade-offs associated with communicating in this sensory modality.

Another strategy of increasing signal detectability is the use of multiple sensory modalities. Even though increased probability of detection by target receivers is considered an important advantage promoting the evolution of complex signals (Rowe, 1999; Hebets & Papaj, 2005; Partan & Marler, 2005; Partan, 2017; Higham & Hebets, 2013), it likely comes with increased exposure to eavesdropping predators. Surprisingly, despite the ubiquity and increasing study of complex communication in the last two decades, there has been surprisingly little research investigating the associated costs. One example is found in spider advertisement displays. Male *Schizocosa ocreata* wolf spiders engage in courtship behaviours that involve waving and tapping their forelegs displaying tufts of bristles on their forelegs and producing seismic signals. Conspecific females are more likely to respond to males when both sensory modalities are present (Uetz *et al.*, 2000; Uetz & Roberts, 2002) and detect such multimodal stimuli faster (Uetz, Roberts & Taylor, 2009), and as expected, these complex signals also increase risk of detection by predators. Predatory *Phidippus clarus* jumping spiders orient faster to *S. ocreata* males when signals include both visual and seismic components compared to only visual ones (Roberts, Taylor & Uetz, 2006).

Given the increased vulnerability of multimodal signals to predation, senders are expected to have the ability to adjust signal components dynamically under high perceived predation risk. As predicted, when insectivorous bats pass over displaying lesser wax moths (*Achroia grisella*), the moths stop their acoustic signals but can continue signalling by releasing an advertising pheromone (Spangler, 1984) (D in Fig. 3). By dropping the main acoustic component of the signal, the moths reduce their display to a modality not detected by the bats. A similar response can be seen in fireflies but over evolutionary time. The high nocturnal predation levels by *Photuris* predatory fireflies have promoted diurnal signalling

behaviour in some fireflies (*Lucidota atra*) which ultimately have switched from using bioluminescence to signalling through other sensory channels (Gronquist *et al.*, 2006). Katydid signal for mates both with acoustic calling songs, and through substrate-borne seismic communication, by tremulating their bodies. In habitats rich in gleaning bats that eavesdrop on katydid calling songs (Falk *et al.*, 2015), katydids reduce the acoustic component of their mating signal, producing extremely short, infrequent calls (<40 ms per call, with <10 s of total sound produced over the course of a full night; Symes, Page & ter Hofstede, 2016), relying more heavily on vibrational communication instead (Belwood & Morris, 1987). In open areas, where gleaning bats are rarely found, katydids signal to mates primarily with acoustic signals (Belwood & Morris, 1987). Examples of adaptive modality switching in response to eavesdropping enemies, however, are few. The growing number of researchers investigating multimodal signalling should consider both plastic and evolutionary modulation of the sensory channels used under diverse predation levels.

(b) Reduction in localizability

Signal modifications can also reduce the information available for eavesdroppers to localize the signaller. As calling individuals give away their position, adaptations in signal structure to hide the signaller's location have long been recognized in acoustic signals (Marler, 1955). This hypothesis has been examined in detail investigating the structure of avian alarm calls, which are produced in response to in-flight approaching predators such as owls and hawks. Aerial alarm calls produced by common chaffinch (*Fringilla coelebs*) were first proposed to have acoustic features that deny localization cues to predators (Marler, 1955). This idea that acoustic features of signals are the outcome of selective pressures imposed by predators to obscure the location of the signaller was extended more broadly across avian alarm calls. Support for this hypothesis comes from convergence among alarm calls on particular acoustic features that reduce localization ability by avian and mammalian predators. These eavesdroppers rely on binaural cues for sound localization so stimuli with high, narrowband frequency, as is characteristic of avian alarm calls, result in decreased ability to determine the location of a sound source. By contrast, calls directed to predators, like mobbing calls of songbirds, have broad frequency bands and are produced at high repetition rates, traits that make them easy to localize (Marler, 1955). Despite initial objections due to doubts about the mechanisms underlying localization ability in birds (Perrins, 1968; Rooke & Knight, 1977; Knudsen, 1980), adaptations of avian alarm calls to limit cues providing information about the location of the signaller to predators are well supported by the evidence (reviewed in Searcy & Yasukawa, 2017).

Similarly, by investigating the acoustic structure of signals and principles of sound localization, the role of eavesdropping predators has been considered for non-human primates and rodent vocalizations. While, unlike studies

investigating songbirds, few experimental studies have examined the costs imposed by predators on signallers producing alarm calls in mammals, observations suggest that at least in some groups there is increased risk for individuals producing such calls. Sciurid alarm calls to terrestrial predators, for instance, can increase risk to the signaller in some species (reviewed in Blumstein, 2008). In contrast to alarms calls made in response to aerial predators in which signallers quickly run into a burrow shortly after vocalizing, those produced in response to terrestrial predators come from signallers that remain in place as if communicating directly to the predator. Such disparate behaviours suggest sciurid alarm signals may have different target receivers. While aerial predators may be acting as eavesdroppers of information intended to communicate risk to others in the colony, terrestrial predators may be the target of alarm calls functioning as pursuit deterrents. Such different functions parallel those seen in songbird alarm and mobbing signals. Other lines of evidence, like increased crypticity of alarm calls under higher risk in some ground squirrels (Sherman, 1985) and marmots (Blumstein, 1995; Blumstein & Arnold, 1995), indicate that eavesdropping predators may shape these signals. It is unclear, however, whether the acoustic features of alarms calls elicited by terrestrial predators are more easily localized by their enemies than those produced towards aerial predators.

Target and non-target receivers often depend on similar sensory mechanisms to localize signallers. Therefore, when effective communication requires target receivers to find the source of the signal accurately, as is the case for mating signals, concealing location information to limit eavesdropper interception also disrupts communication. In those cases, dynamically adjusting signal components provides a solution to reduce localizability under high-risk conditions. Male túngara frogs (*Engystomops pustulosus*), for example, produce a frequency-modulated whine to which they can facultatively add secondary components ('chucks'). Mating calls with chucks are more attractive to female túngara frogs (Ryan, 1985) but also to eavesdropping frog-eating bats (*T. cirrhosus*; Tuttle & Ryan, 1981) and frog-biting midges (*Corethrella* spp.; Bernal, Rand & Ryan, 2006). In addition, chucks have acoustic properties expected to maximize binaural comparisons allowing localization such as short duration, broadband frequency, and clear onsets and offsets. Accordingly, frog-eating bats show better localization performance when approaching calls containing chucks than those without them, especially under complex habitat conditions (Page & Ryan, 2008). While it is unclear if chucks also facilitate call localization for female túngara frogs, calling males producing calls with chucks provide additional location cues available to bats attacking them. Thus, calling males adjust whether they add chucks to their calls based on perceived eavesdropper risk and competition with rival neighbouring males. When calling individually, they produce calls without chucks but under the increased protection of calling in a chorus, they append these secondary components (Ryan, 1985). Dynamic modulation of signal structure or signal types based

on perceived eavesdropper risk provides a compromise for signallers in need of signalling despite the imminent danger.

Alternatively, signallers may increase the challenge of being localized by limiting their signalling displays. While reducing signal rates is an obvious way to obscure the signaller's location, more sophisticated strategies have evolved. Recent studies, for example, have provided a communication network perspective on the unusual synchronous calling behaviour of some anurans. Male pug-nosed tree frogs (*Smilisca sila*) call relatively infrequently (1.7 calls/min; Tuttle & Ryan, 1982) and when they do, they synchronize their calls with their neighbours at extremely short latencies (7–79 ms; Ryan, 1986). Frog-eating bats and frog-biting midges are preferentially attracted to male pug-nosed tree frogs that alternate their calls with their neighbours (Legett, Page & Bernal, 2019). Therefore, call synchrony is a strategy that can reduce the signallers' vulnerability to acoustic eavesdroppers. Equivalent results have been found in the Ryukyu Kajika frog (*Buergeria japonica*) in which males also form synchronous choruses (Legett, Aihara & Bernal, 2021). While early work had proposed predators' preferences for out-of-synchrony choruses (Tuttle & Ryan, 1982), until recently the effects of synchronization on eavesdroppers were unclear. By producing calls that closely follow those of other males, pug-nosed tree frog males also exploit an auditory illusion in the eavesdroppers that limits their ability to localize the signalling male (Legett, Hemingway & Bernal, 2020). When two sounds are produced in synchrony, many acoustically sensitive animals exhibit a perceptual localization bias that favours the first, leading sound over the second one – known as the precedent effect (Wallach, Newman & Rosenzweig, 1949). Due to this illusion, receivers perceive both sounds as if they are originating from the source of the first, leading sound even though the two calling males are separated in space. Both frog-eating bats and frog-biting midges are susceptible to this illusion, preferentially attacking males calling first over those that follow closely. While signallers taking advantage of sensory illusions of their enemies is likely more widespread than currently recognized, the evolution of this strategy requires that target receivers are not deceived. In the case of call synchronization by pug-nosed tree frogs and Ryukyu Kajika frogs, relaxed selection from females likely promoted the evolution and maintenance of this behaviour (Legett *et al.*, 2019, 2021).

The ability to obscure cues that facilitate localization is limited in some sensory modalities. While examples abound in acoustic signalling, concealing localization cues when communicating with visual or chemical signals is less common. Visual signals, for instance, require a direct line of contact between signaller and receiver, directly providing the location of the signaller to the observer. Thus, reducing localizability of visual signals often requires switching to a channel of covert communication, a topic discussed in Section II.2.a. For chemical signals, the mechanism of scent dissemination determines the ability of the sender to decouple its signal from its location. For scents applied to a solid substrate, the signaller can be physically dissociated from the signal. In

most cases that strategy provides protection from eavesdroppers but some scents, such as territorial marks, can reveal activity of the signaller in a given area and thus are ideal locations for eavesdropping enemies to wait for the return of their victim (Carroll, Mills & Schmidtman, 1996; Rechav *et al.*, 1978). When odorants are released into a fluid medium (e.g. water or air), signallers can employ passive dissemination of the chemical, or can use self-generated currents (Bradbury & Vehrencamp, 2011). Male sac-winged bats (*Saccopteryx bilineata*), for example, hover in front of females, fanning their wings to direct their odorant to females (Voigt & von Helversen, 1999). Cases of active generation of currents to direct scents preferentially to target receivers are well recognized, but it is unclear whether senders have evolved strategies to direct scent currents away from potential eavesdroppers. Lastly, scents applied directly to the body of the signaller cannot be decoupled from the signaller's location. All three scent-dissemination mechanisms, however, depend on receivers tracing a chemical plume towards its source, a task that may appear trivial. Tracing kairomones over long distances in real-world conditions, however, can be a remarkable challenge as turbulent fluid-flow environments stretch and twist the filaments of chemical plumes. It is expected that signallers exploit fluid-flow environmental conditions to limit the ability of eavesdroppers to pinpoint their location accurately. Along those lines, it has been proposed that hedgerows and forest edges can be used by chemically signalling prey as these habitats generate odour shadows that may shield them from eavesdropping enemies (Bradbury & Vehrencamp, 2011). Evaluation of anti-eavesdropper strategies to conceal cues that facilitate localization of signallers producing kairomones deserves further attention. Finally, examination of how eavesdropper risk may shape strategies to conceal the location of signallers displaying non-acoustic signals are likely fertile grounds to uncover intricate ways in which context dependency facilitates communication in a network.

(c) Signal conspicuousness

Signal conspicuousness has long been assumed to increase predation risk. The connection may seem clear at first glance, but vague use of the term 'conspicuousness' has complicated identification of the mechanisms underlying receiver responses. For example, conspicuousness can involve differences in signal detectability, localizability, or preference by a receiver. That is, the receiver's sensitivity in a given sensory modality can result in different behavioural responses to signal variation. Similarly, inherent localization abilities of receivers can modulate behavioural responses to signals. In addition, receivers that detect different signals equally well and can localize signallers producing such signals with similar accuracy, may still be more attracted to one over the other. Such preferences can result from signals eliciting different degrees of neural stimulation or involving particular cognitive processes, like higher memorability or lower habituation rates (Ryan & Cummings, 2013). Moreover, differences in

detection, localizability, and preferences among signals can act together to modulate decision making in both target and non-target receivers. Signal conspicuousness is assumed to tap into those processes resulting in increased attractiveness. This approach can be problematic as conspicuousness may be inferred using increased attractiveness, without direct evaluation of the mechanisms underlying the response of the receiver, and is compounded by the problem that human observers are often biased towards sensory channels they themselves can perceive. With the rapid advancement of the field of sensory ecology over the last several decades, experimental approaches have been developed to identify more robustly factors contributing to conspicuousness (Dusenbery, 1992; Stevens, 2013).

Given the exaggerated nature of mating signals, they have been at the centre of conversations about signal conspicuousness. The risk taken by males displaying such signals was recognized early on (Darwin, 1871), and since then, increased risk of attack by predators and parasites on males due to sexual differences in conspicuousness has been demonstrated in numerous studies [but see Raghuram *et al.* (2015), ter Hofstede *et al.* (2017), and Torsekar, Isvaran & Balakrishnan (2019)]. In wall lizards (*P. erhardii*), for example, males use bright sexual signals to display to females, who in turn are duller and more camouflaged. Experiments using artificial wall lizard models show that, as predicted by their differences in conspicuousness, males are more likely to be attacked by predators (Marshall & Stevens, 2014). While most extreme between the sexes, differences in conspicuousness extend to within-male variability which results in the raw material for sexual selection to act upon.

Across many taxa, there is strong female preference for more elaborated mating signals with mates favouring intricate appendages, bright contrasting coloration, and in general, signals with ‘greater quantity’ (Andersson, 1994; Ryan & Keddy-Hector, 1992). Such increased attractiveness to target receivers is also assumed to increase attractiveness to predators and parasites (Magnhagen, 1991; Zuk & Kolluru, 1998; Kotiaho, 2001). This increase in attraction is the case in túngara frogs in which, as described above, males facultatively add secondary-component ‘chucks’ to their whine increasing the attractiveness of their mating call to conspecific females (Ryan *et al.*, 2019) but in doing so, they also increase their attractiveness to eavesdropping bats and midges (Ryan, Tuttle & Rand, 1982; Page, Ryan & Bernal, 2014; Bernal *et al.*, 2006). Similarly, a recent study in water anoles (*Anolis aquaticus*) experimentally confirmed that more conspicuous dewlap coloration increases predation attacks, as previous correlational studies have suggested. Anole models with redder dewlaps were attacked more than twice as often as less-conspicuous models with less-red dewlaps (Swierk *et al.*, 2021). Relatively few studies, however, have empirically examined the relationship between predation risk and increase conspicuousness in coloration. Evidence from fairy-wrens (*Malurus* spp.) raises questions about the long-standing hypothesis that conspicuous plumage increases predator attraction. Attack rates on models

mimicking variation in conspicuousness across males and females show that, contrary to expectations, dull female models were attacked at similar rates to the conspicuous models of males and females across habitats (Cain *et al.*, 2019). Within-species investigations in this group suggest conspicuousness may interact with other factors, resulting in more complex patterns than originally expected. In male superb fairy-wrens (*Malurus cyaneus*), individuals with bright plumage were more cautious than their duller counterparts: they were more likely to flee in response to alarm calls, took longer to emerge from cover, and spent more time being vigilant and foraging in cover than their dull counterparts (McQueen *et al.*, 2017). This risk-averse behaviour is in line with other studies showing that more conspicuous individuals show stronger anti-predator behaviour to compensate for their increased conspicuousness (Husak *et al.*, 2006; Journey *et al.*, 2013). Consistently, eavesdropping predators are one of the potential selective pressures hypothesized to have shaped the evolution of alternative reproductive strategies (Oliveira *et al.*, 2008).

As discussed in previous sections, anti-eavesdropper strategies often result in reductions in signalling displays and signal structure to minimize the ability of eavesdroppers to detect and localize the signaller. Eavesdroppers, however, do not always curtail the sexual ornamentation of their hosts or prey. In aggregations of sexually signalling bush-crickets and cicadas, the opposite seems to occur. Under the pressure of acoustic parasitoid flies, males calling in a chorus compete against other males and benefit from singing fast and loud to be selected rapidly by females (Lehmann & Lakes-Harlan, 2019). This strategy results in increased signal conspicuousness as males bet on securing a mate. Attracting a female allows males to stop calling, dropping off from the signalling pool during their refractory period which ultimately reduces their parasitism risk. In a similar vein, male variable field crickets (*Gryllus lineaticeps*) do not reduce signal conspicuousness in response to an eavesdropping fly (*Ormia ochracea*) that attacks them. Males from high-risk populations, where chances of attack by these deadly parasitoids are elevated, sang equally frequently as males from low-risk populations (Beckers & Wagner, 2012). These findings may reflect increased sexual selection in high-risk populations, but further work is necessary to understand better the mechanisms underlying this unexpected lack of signal reduction. Even though it is surprising to find cases of signallers not reducing their signals, or even ramping them up, in the face of danger, we are just beginning to understand the complex, combined dynamics converging on signallers by their social environment and by eavesdropping enemies (e.g. Leavell *et al.*, 2022). Evolutionary responses to eavesdroppers that result in changes in life-history strategies rather than signal reduction or alterations may be more widespread than previously anticipated and offer unique opportunities to examine the diversifying effects of these enemies. As with the field crickets that do not change their signalling display in the face of high parasitoid pressure, signallers could be selected to ‘signal fast and die young’, generating different strategies

among or within populations. Evaluating such potential diversifying effects of eavesdroppers deserves further attention.

Overall, while preference of eavesdroppers for more conspicuous signals is common, promising areas of research are likely to come from examining the mechanisms underlying such preferences as well as additional factors that modulate attraction of enemies to more conspicuous signals. Previously rarely considered forces such as heterospecific competition, for instance, can change the payoffs associated with attraction to more conspicuous signals. In stingless bees, the dominant eavesdropper (*Trigona hyalinata*) avoids higher and more conspicuous levels of pheromone produced by competitors from another species (*Trigona spinipes*) as such scent represents increased difficulty to compete for a food source (Lichtenberg *et al.*, 2014). By contrast, and contrary to expectations, these eavesdropper bees are more attracted to lower, less-conspicuous pheromone levels, as they indicate relatively undefended resources. This case illustrates the potential of additional factors and species interactions at shifting signal preferences by eavesdroppers that can result in them unexpectedly preferring less-conspicuous signals.

(3) Losing signals and evolving new ones

Evolutionary loss of traits has been a recurring phenomenon that is widespread across taxa. Historically, evolutionary biologists have focused on loss of organs which tend to leave obvious, morphological clues behind. This field has received, however, recent increased attention due to novel techniques available to examine genetic and developmental pathways (Sadier, Sears & Womack, 2022). Similar to organs and other morphological traits, signals and signalling behaviours can be lost as their fitness payoffs are tipped in favour of the costs imposed on them. Costs imposed by eavesdropping enemies can drive the evolution of communication systems and, in doing so, they have the potential to put signallers in an evolutionary situation where extreme solutions such as signal loss are favoured. Not surprisingly, the factors that promote evolutionary loss of signals are the same ones that are at play in losing other traits (Heinen-Kay & Zuk, 2019).

Perhaps the best-recognized example of signal loss due to eavesdropper pressure comes from Pacific field crickets (*Teleogryllus oceanicus*) on the Hawaiian island of Kauai where males turned silent to evade acoustically oriented parasitoid flies (*O. ochracea*) (Zuk, Rotenberry & Tinghitella, 2006). Males from the novel and silent morph, known as ‘flatwings’, lack the file and scraper used for sound production and over a short amount of time (20 generations) became the prevailing morph in the population (90% of males). Similar to organs that are lost during evolution, the song of crickets left a trace behind as flatwing males still go through the behavioural motions of the courtship display (Schneider *et al.*, 2018). Evolutionary song loss resulted from the disappearance of structural components of the stridulating apparatus but left behind a behavioural vestigial trait. While vestigial structures are a common and well-recognized phenomenon in

morphological traits (reviewed in Sadier *et al.*, 2022), behavioural examples are less abundant.

The rapid evolutionary change in signalling in Pacific field crickets continues to highlight the lability of communication systems under strong eavesdropper selective pressure (reviewed in detail in Heinen-Kay & Zuk, 2019). Field crickets on another island in the Hawaiian archipelago, Oahu, convergently evolved silent males *via* a different genetic pathway (Pascoal *et al.*, 2014). In addition, on Molo-ka'i Island males have evolved a novel mating song using structurally different wing morphology which produces unique acoustic features unlike those that are characteristic of songs produced by species in this clade (Tinghitella *et al.*, 2018). This new and highly variable song, called ‘purring’, is attractive to female field crickets but not to *O. ochracea*, their eavesdropping enemy (Tinghitella *et al.*, 2021). Purring is thus an evolutionarily novel signalling strategy that results in covert, or private, communication (G in Fig. 3). The recent encounter of this signaller and its eavesdropping enemy have provided a unique opportunity to document rapid evolution of a communication system driven by signal exploitation. While Pacific field crickets colonized the Hawaiian Islands several hundred years ago (Tinghitella *et al.*, 2021; Zhang *et al.*, 2021), the parasitoid fly attacking them colonized this area more recently; it arrived sometime before 1989 from North America (Eldredge, Evenhuis & Hawaii Biological Survey, 2003). The combination of the recent origin of this interaction, the strong selective force imposed by abundant parasitoids, the cricket's short generation time, and its ability to evolve quickly, have resulted in the diverse anti-eavesdropper strategies observed so far.

Rapid evolution of secondary sexual traits, such as the signal changes occurring in Hawaiian field crickets, seems to be rare (Svensson & Gosden, 2007). The general phenomena of losing and re-evolving signals due to eavesdroppers, however, could be more common than previously expected. Katydid, for example, have lost their airborne sexual signals in forested populations, where gleaning bats are present (Belwood & Morris, 1987). Similarly, several lines of evidence suggest firefly mating flashing signals have been lost under selection from eavesdropping enemies. Geographic variation in flashing patterns of lampyrids reveals signal loss in some high-predation areas (Lewis & Cratsley, 2008). A phylogenetic approach also showed independent losses of bioluminescent courtship signals across North American *Photinus* fireflies likely associated with predatory eavesdropping *femme fatale* lightning bugs, *Photuris* spp. (Stanger-Hall & Lloyd, 2015).

Evolution of novel signals that are less susceptible to exploitation by eavesdropping enemies (H in Fig. 3) is also rare. Similar to the Hawaiian field crickets that regained an acoustic signal after losing it, blue-bellied *Sceloporus* lizards lost their blue bellies but gained an increased-intensity head-bobbing behaviour (Martins *et al.*, 2015). Origin of a novel signal, however, does not need to follow losing a previous one and can, instead, evolve to amplify an already

existing signal. This is the case for UV ornamentation in northern swordtails (Cummings *et al.*, 2003). The relatively scarcity of examples in non-visual sensory modalities could be explained by fewer constraints narrowing sensitivity of sensory filters in other modalities, by biases in experimental approaches, or both. Heinen-Kay & Zuk (2019) discuss key contributors that promote loss of sexually selected signals and could provide a useful foundation to contrast this phenomenon across sensory modalities.

III. EVADING EAVESDROPPERS IN THE ANTHROPOCENE

Human-driven rapid environmental changes modify community composition and in doing so, can alter interactions between eavesdropping enemies and their victims. As species' ranges shift, or as translocations take place, novel eavesdroppers can disrupt long-established communication networks. When curly-tailed lizards (*Leiocephalus carinatus*) were introduced to the Bahamas, brown anoles suddenly gained a visually oriented predator that could tap into their communication signals. As the curly-tailed lizard became a main predator, brown anoles decreased the amplitude of their head-bobs, a display used in territorial defence and mate attraction, on islands where this predatory lizard was present (Steinberg *et al.*, 2014). This study illustrates how non-native eavesdroppers can select for the rapid reduction of signal conspicuousness, resulting in a decrease in a signal's active space, ultimately depressing the reproductive success of signalling individuals. As prey or host are translocated, absence of eavesdroppers at new locations can also result in new fitness landscapes for communication systems. Jackson's chameleons (*Trioceros jacksonii xantholophus*) accidentally brought to the Hawaiian island of Oahu, for instance, encountered fewer predators than in their native range and thus experienced relaxed selection against conspicuous signals (Whiting *et al.*, 2022). Over the course of five decades, local adaptation to this novel environment with few eavesdroppers led to higher conspicuousness of social colour signals during courtship and male contests, and lower crypsis in response to predators, compared with their native counterparts. Despite the strikingly rapid effects of eavesdroppers in this well-studied system, the role of introduced eavesdroppers on communication systems and the absence of such enemies in the introduced ranges of their victims has received limited attention.

Similarly, urbanization often disrupts species interactions and can shape the presence and abundance of non-target receivers. In urban areas of Panama, túngara frogs occupy signalling spaces free from eavesdropping enemies, since their main eavesdroppers, frog-biting midges and frog-eating bats, are absent in cities (Halfwerk *et al.*, 2019; McMahon, Rohr & Bernal, 2017). Urban túngara frogs thus experience relaxed natural selection which, coupled with more intense sexual selection due to lower numbers of female túngara

frogs *per capita* in urban choruses, results in the production of more attractive, more conspicuous signals in the city (Halfwerk *et al.*, 2019). It is unclear, however, how widespread disrupted communication networks may be in cities. Given that urbanization often increases the representation of species that are foraging generalists rather than specialists (McKinney, 2006; Sorace & Gustin, 2009), a shift from specialized to opportunistic eavesdroppers is expected in urban areas. In addition, as urban animals often display higher cognitive abilities than their rural counterparts (Johnson & Munshi-South, 2017; Lee & Thornton, 2021), opportunistic eavesdroppers with high learning abilities may expose signalers to unprecedented challenges. Our understanding of non-target receivers associated with urban signals, and how those interactions change fitness payoffs for signallers, is still in its infancy. Studies examining how living in cities differentially shapes communication networks across sensory modalities are necessary to understand signal dynamics in an increasingly urbanized world.

Noise and light pollution, which are intrinsically associated with human settlements but often also extend beyond cities, can interfere with the ability of target and non-target receivers to respond to signals. An increasing number of studies have evaluated how acoustic noise pollution affects the timing or structure of animal signals (reviewed in Gomes *et al.*, 2022). Fewer studies have examined how eavesdroppers are affected by noise pollution but it is evident that this type of habitat degradation can affect the ability of eavesdropping parasitoid flies (Phillips *et al.*, 2019) and micropredator midges (McMahon *et al.*, 2017) to locate their victims (field crickets and frogs, respectively). In a parallel manner, pollution along other sensory modalities can also result in signal disruptions and alterations (Dominoni *et al.*, 2020; Lürding & Scheffer, 2007; Seehausen, Alphen & Witte, 1997). Non-toxic concentrations of chemical pollutants, including apparently harmless substances, can disrupt chemical information transfer among animals. Such chemical info-disruptors directly interfere with the communication process; a growing number of studies documents how they can induce maladaptive responses from senders and receivers (reviewed in Lürding & Scheffer, 2007). Chemical info-disruptors are also expected to hamper signal exploitation by eavesdroppers but to our knowledge, the effect of chemical pollution on communication networks has yet to be examined. Across sensory modalities, different types of pollution may act as info-disruptors and potentially shift the point of junction between natural and sexual selection.

Differential sensory abilities and responses to sensory pollution among target and non-target receivers are expected to modulate the outcome of signallers and their enemies. When non-target receivers are more sensitive to the predominant form of sensory pollution, the communication network can become simplified and turn into dyadic communication (i.e. sender to target receiver without exploitation from eavesdropping enemies; Fig. 1A). This higher sensitivity to pollution occurs in frog-biting midges that eavesdrop on túngara frog calls. These midges are highly sensitive to both acoustic

noise and artificial light at night (ALAN), which both independently and together disrupt the ability of these eavesdropping micropredators to cue in on frog calls to obtain a blood meal (McMahon *et al.*, 2017). Acoustic traps and cameras used that eavesdropping enemies that are common in the forest, like frog-eating bats and opossums, are largely absent in urban areas (Halfwerk *et al.*, 2019). Given that túngara frogs are resilient to both light and noise pollution, while their non-target receivers are not, their complex communication network (Fig. 1B) turns into a dyad (Fig. 1A) as a result of human-driven changes in the sensory environment. An alternative scenario in which target receivers are more sensitive than their eavesdroppers to sensory pollution is also plausible. This unfortunate outcome would break down communication, with signallers unable to reach target receivers, with the additional negative consequence that only non-target receivers would maintain responsiveness to the signal, resulting in potentially disastrous consequences for the signallers.

Communication systems have also evolved under environmental conditions that are currently changing rapidly due to climate change. Accordingly, an increasing number of studies reveal that stressors associated with climate change have deleterious effects on communication systems, in particular affecting chemical communication in aquatic systems (reviewed in Roggatz *et al.*, 2022). The consequences of climate change extend beyond aquatic systems to other signalling environments. In two subspecies of Mediterranean blue tit (*Cyanistes caeruleus caeruleus* and *Cyanistes caeruleus ogliastrae*), increasing temperatures have been associated with plastic responses in ornamented signals that have resulted in duller and less chromatic coloration in both males and females (López-Idiáquez *et al.*, 2022). The response of non-target receivers to signal alterations, such as those seen in structural coloration in blue tits or the chemical signals of many aquatic species, are likely to be system and signal specific, resulting in some cases in unpredictable outcomes. An example of such complex consequences is illustrated by hoverflies (*Episyrphus balteatus*) that use kairomones present in the waste product excreted by aphids (*Acyrtosiphon pisum*) ('aphid honeydew') to find aphid colonies to lay their eggs. Under elevated CO₂ conditions, the kairomone is qualitatively and quantitatively different but the eavesdropping hoverflies do not seem affected given that they do not change their searching or oviposition behaviours (Boullis *et al.*, 2018a; Boullis, Francis & Verheggen, 2018b). Ultimately, however, evidence suggests that decreased alarm pheromone emissions under such elevated CO₂ concentrations result in a lower number of eggs laid by the flies at the aphid colony (Verheggen *et al.*, 2008).

Apart from climate change-induced alterations of signals, long-term environmental changes can also affect the phenology of signalling displays. It is well-recognized that rising temperatures and changes in precipitation patterns have resulted in phenological advancement for many organisms (reviewed in Inouye, 2022). Such species-specific changes in phenology are likely to cause temporal mismatches among signallers, target and non-target receivers paralleling those described for other types of species interactions (e.g. Visser,

Marvelde & Lof, 2012). Similarly, the well-characterized shifts in species abundance and distribution in response to climate change (e.g. Chen *et al.*, 2011) are expected to interfere with communication networks. While the relevance of climate change-induced informational mismatches among species at a community level has been recognized (Parejo, 2016), studies that examine the behaviour and sensory ecology of eavesdropping enemies to evaluate the consequences of climate change stressors on signals are necessary to obtain a complete picture of how communication networks are currently being shaped.

In general, the mechanisms used by eavesdroppers and their victims to cope with rapid anthropogenic environmental change parallel those of other organisms. Evidence of contemporary adaptive evolution is scarce (Lambert *et al.*, 2020; Svensson & Gosden, 2007) but plasticity and phenotypic flexibility are more likely strategies to be deployed to adjust successfully to novel conditions. When considering specifically the task of communicating, however, signallers with the ability to communicate using multiple sensory channels may benefit by being able to cope better with noise introduced by rapid environmental change (reviewed in Partan, 2017). As different components of multimodal signals may have redundant or amplifying functions (Partan & Marler, 2005), it has been proposed that multimodality can allow signallers and receivers to shift from noisy to more quiet channels to avoid signal interference (Brumm & Slabbekoorn, 2005; Hebets & Papaj, 2005). A relatively small number of studies have investigated signal adjustments along multiple sensory channels in response to novel environmental conditions but shifts in sensory channels used in response to natural, abiotic conditions provide interesting hints at expected transitions. Partan (2017) provides a detailed overview of those responses highlighting common shifts in the sensory modalities deployed in the face of signal interference; under high acoustic noise conditions, signallers often shift from acoustic to visual or seismic signals; when the visual environment is degraded, switches from visual signalling to seismic or chemical signals take place. The consequences of such signal adjustments across sensory modalities in terms of eavesdropper-imposed selective pressures, however, deserve further attention.

IV. FUTURE DIRECTIONS

Throughout this review, we have highlighted fertile approaches and directions for future research to understand anti-eavesdropper strategies better. Here we address additional avenues critical to address as the field develops. A growing body of empirical work highlights how eavesdropping enemies impose selective pressures, ultimately shaping communication systems. While an expanding number of studies have provided rich and varied examples, deepening our knowledge of how widespread and diverse these strategies are, much of our fundamental conceptual understanding

still comes from a limited number of eavesdropper–signaller interactions for which deep investigations have been performed (e.g. field crickets and *Ormia* parasitoid flies; guppies and their piscivore fish predators; túngara frogs, frog-eating bats and frog-biting midges). Detailed, integrative studies of additional taxonomic groups are needed to obtain a more robust perspective of the diverse ways in which these interactions unfold in the wild. Similarly, most of our understanding comes from acoustic and visual signalling. Studies investigating eavesdropping on chemical signals beyond the context of pest management (e.g. Adams *et al.*, 2020) and seismic signals (e.g. Hamel & Cocroft, 2019) underscore the complex and diverse nature of strategies to communicate in a world where non-target receivers are universal. Previous studies have also focused on individual signal components or signalling modes, and although multimodal communication has attracted increasing attention in recent years, there has been surprisingly little research investigating the costs associated with signalling in different sensory modalities (Partan, 2013).

As we continue to expand our understanding of the multiple players involved in a communication network, interactions among multiple signallers attacked by the same eavesdroppers should be considered. This perspective already has provided previously unsuspected fitness consequences of signalling in mixed-species aggregations (Trillo *et al.*, 2016) and has identified unique outcomes of signal evolution and interactions among heterospecifics signalling together (Trillo *et al.*, 2019; Goodale, Ruxton & Beauchamp, 2019). As studies are broadening to examine the effect of heterospecific eavesdroppers beyond the exploitation of mating signals to include signals used across all contexts (Bernal & Page, 2022), the inevitable and sometimes unforeseen ecological consequences of signal exploitation are becoming more evident. We are, however, just beginning to understand the community-level effects of eavesdropping behaviour, a promising direction given the abundant cascade effects from these interactions that could trickle across the community. Some eavesdroppers, for instance, are disease vectors (e.g. eavesdropping frog-biting midges that transmit anuran trypanosomes; Bernal & Pinto, 2016) and could thus be active modulators of disease dynamics in the community. In addition, eavesdropping enemies can shape interactions at previously unappreciated trophic levels, playing an important role in non-animal systems (e.g. microbial and plant systems; Rebollada-Gómez & Wood, 2019). Such eavesdropper interactions affecting primary producers could have bottom-up effects unconsidered so far.

More broadly, as technological advances continue to progress, making instruments more widely available to quantify signals across all sensory modalities, to monitor signalling behaviours remotely, and to understand the genetic and developmental pathways underlying those traits, our knowledge of anti-eavesdropper strategies is expected to grow in new, exciting directions. To understand fully the ecology and evolution of signals, it is necessary to incorporate examinations that include both target and non-target receivers, and their diverse effects on communication systems.

V. CONCLUSIONS

- (1) Eavesdropper strategies fall along a continuum from opportunistic to highly specialized, affecting the tightness of the relationship between eavesdroppers and signallers and resulting in differential pressures on communication systems.
- (2) Signallers engage in a broad variety of plastic and fixed anti-eavesdropper strategies to curtail signal detection and localization, including modulation of signalling displays, shifts in signal structure, and evolutionary loss or gain of a signal from a population, which ultimately reduce the likelihood of successful attacks by eavesdropping enemies and modulate information transfer to target receivers.
- (3) Most studies examining the ecology and evolution of anti-eavesdropper strategies address exploitation of mating signals using visual and airborne acoustic displays, with deep examinations restricted to a limited number of systems. Further research on less-studied sensory modalities, like electric and substrate-borne signals, is necessary to establish sensorially and taxonomically broad patterns of signal ecology and evolution.
- (4) Across sensory modalities, anti-eavesdropper strategies often result in reduced signal conspicuousness. While eavesdroppers have the potential to curtail signal ornamentation, these enemies can also promote signal ornamentation. We posit that cases of this unexpected outcome may be more common than previously anticipated.
- (5) Technological advances making equipment more widely available to quantify and reproduce signals have expanded opportunities to examine sensory modalities previously erroneously assumed to be less prone to signal exploitation, providing fertile avenues for broadening our understanding of communication networks.
- (6) Future research should examine communication networks, considering that these systems are embedded in ecological communities, and directly address the cascade effects that eavesdroppers have beyond the signallers they attack.
- (7) Anthropogenic changes provide valuable, yet underused, opportunities to assess natural experiments in which communication networks are simplified or expanded and are thus promising avenues to examine the consequences of network alterations on signals. In addition, investigations of the factors determining the outcome of communication systems confronted with novel, human-imposed stressors will illuminate our understanding of rapid signal evolution.

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