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SENSORY ECOLOGY AND COGNITION IN SOCIAL DECISIONS

The challenge of detecting prey: Private and social information use in predatory bats

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Abstract

1. In the evolutionary arms race between predators and their prey, prey often evolve to be as cryptic as they can, while predators in turn hone their sensory strategies to detect prey. Examinations of the sensory strategies implemented by predators to detect their prey, as well as the ecological consequences of these interactions, are at the crux of understanding and predicting predator–prey dynamics.
2. We review the sensory strategies used by predators that rely on private information (attending directly to cues and signals generated by their prey) and those that gather social information (attending to the signals and behaviours of others). We focus our enquiry on bats, an ideal group to shed light on these questions given their ecological diversity, varied foraging strategies and wide range of social behaviours.
3. We discuss the costs and benefits of using private and social information for foraging. We investigate diverse strategies of information use and examine the effects different predatory strategies have on predator sensory systems.
4. We provide an overview of the sensory ecology of information use in hunting in bats and, by identifying current gaps in knowledge, highlight fruitful directions for future research.

KEYWORDS
acoustic cues, bats, eavesdropping, echolocation, mating signals, predator–prey interactions, prey detection, sensory strategies

1 | INTRODUCTION

Predators face a variety of challenges when capturing prey (Krebs & Davies, 1997). A critical first step in hunting, for instance, is early detection of prey. Finely tuned and sensitive systems allow predators an element of surprise, improving their chances of prey capture. Fish hunting in light-limited environments, for example, have widened lateral line canals that allow early and efficient detection of prey in the water column (Marshall, 1996) as well as in sandy and muddy substrates (Janssen, 1997; Schwalbe, Bassett, & Webb, 2012). Predators have evolved numerous sophisticated strategies to detect and recognize palatable food, but strong selection to avoid being eaten has resulted in elusive prey targets (Stevens, 2013).

In the arms race between predators and prey, predators have evolved the ability to exploit different types of information for prey capture. In this context, private or personal information involves information gleaned directly by the predators about prey. For example, predator use of sensory cues unintentionally emitted by prey is a widespread strategy for prey detection (Bradbury & Vehrencamp, 2011). A classic example of this hunting strategy is owls keying in on the rustles mice produce as they move through vegetation; mice in turn attempt to minimize the noise they produce to avoid detection (Konishi, 1973). Strong selection to reduce detection by natural

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enemies has finely tuned the behaviour of prey, resulting in an evolutionary race for survival with the predators' sensory systems both as a critical target of selection and as a selective agent that shapes prey's defence strategies. To detect the subtle cues emitted by their prey, predators have evolved sharply tuned sensory filters, such as barn owls' unique inner ear specializations, resulting in acute hearing ability (Dyson, Klump, & Gauger, 1998; Köppl, Gleich, & Manley, 1993). Across taxa, we find that the behaviour and sensory abilities of predators are honed to detect and localize prey cues (Stevens, 2013).

Another form of private information used by predators is eavesdropping on signals produced by their prey. In contrast to prey-emitted cues, such as incidental locomotion cues that are under strong selection to minimize attention, signals used by prey for intraspecific communication often evolve to be highly conspicuous, and inadvertently provide an ideal opportunity for predators to exploit them to attack the emitter. Even though eavesdropping on mating signals is a widespread strategy, its study has been largely anecdotal, lacking a strong conceptual framework (but see Bernal & Page, in prep; Peake, 2005; Zuk & Kolluru, 1998).

In addition to the private information gathered directly by attending either to prey incidental cues or prey communication signals, predators can obtain critical foraging information by attending to other predators. This information flow is similar to 'social information use' described in other contexts (Danchin, Giraldeau, Valone, & Wagner, 2004; Valone, 1989), but in the case of predation it specifically involves the use of information gained vicariously, not by attending to prey directly, but rather by attending to the signals and behaviours of other predators. For animals foraging in groups, social information use can be an effective foraging strategy that allows individuals to locate food sources that might be difficult to detect by single individuals (Giraldeau & Caraco, 2000). Information about prey location and prey quality can be extracted from the behaviour of conspecifics as well as heterospecifics with similar foraging needs. For instance, *Gyps* vultures forage collectively for carrion and use the information conveyed by other vultures as they descend to the carcass (Houston, 1974). Vultures, however, also rely on eagles that take carrion as a significant proportion of their diet; by attending to eagle foraging behaviour, vultures reduce their time of arrival to carrion food resources (Kane, Jackson, Ogada, Monadjem, & McNally, 2014). While foraging near others can increase competition, attending to the behaviour of other predators can outweigh these costs through increased prey capture per capita or reduced predation risk while foraging (e.g., Giraldeau, Valone, & Templeton, 2002; Ranta, Rita, & Lindstrom, 1993; Sharpe, Joustra, & Cherry, 2010).

In general, both using private information by attending directly to the cues or signals emitted by prey and using social information by keying in on the signals or behaviours of other predators are strategies that can improve foraging efficiency. Here, we review these diverse predatory strategies and the sensory ecology underlying them. We focus this enquiry on predatory bats. Bats are the most ecologically diverse group of mammals (Jones, Purvis, MacLarnon, Bininda-Emonds, & Simmons, 2002), employing a myriad of foraging strategies (Denzinger & Schnitzler, 2013) and a wide range of social behaviours (Kerth, 2008). As such, bats offer a robust window into the main venues in which attending to prey and attending to predators enhances predator foraging success.

In this review, we examine the costs and benefits of the diverse ways predators gather information. First, we discuss the strategies used by predators that gather private information attending directly to prey-emitted cues and signals. We then discuss predators that use social information, either in the form of eavesdropping on the echolocation signals of other hunting bats, or by observing their foraging behaviour. For each strategy, we evaluate the sensory adaptations that support those particular hunting modes. We conclude with an overview and synthesis of the challenges and benefits of these private and social approaches to finding prey. Ultimately, this review provides a current perspective on decades of research on bat foraging strategies, discussing pressing gaps in knowledge and fruitful venues of future research.

2 | PRIVATE INFORMATION USE

2.1 | Attending to prey-emitted cues

As prey move through the environment and perform basic functions, they cannot avoid emitting sensory information. Incidental cues are by-products of other functions of an animal's biology and are often under strong selection to be inconspicuous. Under the threat of predation, for instance, prey tend to minimize their emission of cues by reducing locomotor behaviour (e.g., Desy, Batzli, & Liu, 1990; Eilam et al., 1999; Hendrie, Weiss, & Eilam, 1998; reviewed in Apfelbach, Blanchard, Blanchard, Hayes, & McGregor, 2005), resulting in lower foraging rates (Brown & Kotler, 2004).

Attending to prey-emitted cues allows predators to hunt in environments in which prey are particularly challenging to detect or localize. While echolocation enables bats to navigate and forage in the dark (Griffin, 1958), allowing them access to otherwise inaccessible night niches, clutter is a significant impediment to the use of echolocation (Schnitzler, Moss, & Denzinger, 2003). When trying to locate prey in dense vegetation, for example, it is difficult to distinguish the returning echoes associated with one's target prey from the echoes emanating from surrounding clutter (Neuweiler, 1989; Schnitzler & Kalko, 2001). To overcome this challenge of echo overlap, bats often recruit a different sensory strategy—they listen for the sounds that their prey emit (Neuweiler, 1983). This hunting technique has been termed 'passive listening' and commonly takes the form of bats attending to the locomotion sounds of their prey (Jones, Page, & Ratcliffe, 2016).

Among the diverse range of bats that use incidental noises to detect and locate moving prey is *Mystacina tuberculata*, the New Zealand lesser short-tailed bat, one of only two extant species in New Zealand. Bats are the only native land mammals in New Zealand, and as such, they evolved with few competitors and under low predation risk. These conditions allowed New Zealand bats to fill

a wide range of foraging niches. For example, *M. tuberculata* spends approximately 40% of its foraging time on the ground (Daniel, 1979), more than any other bat species in the world. Foraging at ground level, however, comes with the challenge of locating prey hidden in leaf litter where echolocation is less effective. An experiment offering bats different sensory cues in isolation revealed that *M. tuberculata* uses both passive acoustics (the sounds of insects moving in leaf litter) and smell (olfactory cues of insects concealed in leaf litter) to find terrestrial prey (Jones, Webb, Sedgeley, & O'Donnell, 2003). Its large external ears (pinnae) and elongated, tubular nostrils enable *M. tuberculata* to attend to prey-emitted cues, and thus expand its foraging niche to the leaf-litter-covered ground (Carter & Riskin, 2006; Jones et al., 2003).

The challenge of finding prey in cluttered environments is not unique to New Zealand bats; the sensory strategy of attending to prey locomotion noises is widespread among bats foraging in cluttered environments. A widely used locomotion cue is prey walking sounds; bats attend to the walking sounds of a large variety of invertebrate and vertebrate prey (e.g., crickets: *Antrozous pallidus* [Fuzessery, Buttenhoff, Andrews, & Kennedy, 1993]; scorpions: *Otonycteris hemprichii* [Holderied, Korine, & Moritz, 2011]; katydids: *Myotis myotis* and *Myotis blythii oxygnathus* [Arlettaz, Jones, & Racey, 2001]; frogs: *Cardioderma cor* [Ryan & Tuttle, 1987]; and rodents: *Megaderma lyra* [Fiedler, 1979; Marimuthu & Neuweiler, 1987; Marimuthu, Rajan, Kandula, Parsons, & Jones, 2002]). Wingbeats are another common incidental prey cue generated as a by-product of locomotion; bats exploit these cues to hone in on flying insects. Bats targeting the fluttering sounds of moths are not surprising given the nocturnal habits of both groups; indeed, many bat species exploit this sensory strategy (e.g., *Myotis septentrionalis*, *Myotis lucifugus* [Ratcliffe & Dawson, 2003]; *Myotis evotis* [Faure & Barclay, 1992]; *Plecotus auritus* [Anderson & Racey, 1991, 1993]). Even bats with highly specialized neurological and morphological adaptations to use echolocation to detect fluttering moths also attend to the sounds produced by moth movements, underlying the importance of simply listening for prey-emitted locomotion cues (e.g., *Rhinolophus ferrumequinum*, Lattenkamp et al., 2018).

A less common prey-emitted cue used by bats are breathing noises. Vampire bats feed solely on blood and use a combination of sensory cues to find their hosts (e.g., Kurten, Schmidt, & Schafer, 1984; Schmidt, 1973). Common vampire bats, *Desmodus rotundus*, listen for the breathing noises of their hosts and have specialized neurons in the inferior colliculus that fire only in response to breathing noises (Schmidt, Schlegel, Schweizer, & Neuweiler, 1991). Vampire bats also have highly specialized low-frequency hearing, the lowest of any bat species tested to date, allowing them to detect low-frequency noises such as breathing sounds (Heffner, Koay, & Heffner, 2013). In fact, vampires are even able to classify the breathing sounds of different individual hosts (Gröger & Wiegrebe, 2006), enabling them to feed on the same individual host several nights in a row.

Prey-emitted cues offer reliable information about prey presence and location, and with the exception of the vampire example detailed above, generally do not require sophisticated tuning of the predators' sensory system. The desert-dwelling predatory bat, *Otonycteris hemprichii*, for example, feeds extensively on scorpions of diverse degrees of toxicity. These bats locate scorpions by attending to the rustling noises their prey make as they walk (Holderied et al., 2011). In an experiment quantifying bat response to three different scorpion species that vary in their levels of toxicity, *O. hemprichii* did not discriminate in their selection of scorpion prey. They captured and consumed highly toxic scorpions as readily as less toxic ones (Holderied et al., 2011). This lack of discrimination is not surprising given that there is little difference in the acoustic parameters of the rustling noises produced by scorpions of varying levels of toxicity (Holderied et al., 2011). Since prey-emitted acoustic cues offer little information to aid bats in the discrimination of one scorpion species over another when matched for size (Holderied et al., 2011), likely only predators that can tolerate the venom can exploit this prey. Even though the stinger of the scorpion rarely pierces the bat's skin, the bats consume the stinger along with the rest of the prey, suggesting that bats that consume scorpions may be resistant to their venom, an adaptation that may render the identification of toxic prey less important (Holderied et al., 2011). Supporting this idea, *Antrozous pallidus*, a New World bat that also consumes scorpions (Hatt, 1923; Johnston & Fenton, 2001), was recently shown to also be immune to scorpion venom (Hopp, Arvidson, Adams, & Razak, 2017). Given that pallid bats find other prey by attending to their locomotion cues (Bell, 1982; Fuzessery et al., 1993), they are likely to also use such cues to hunt scorpions. Convergence in predatory behaviour across Old (*O. hemprichii*) and New World (*A. pallidus*) scorpion predators provides an opportunity to examine information used to detect and recognize prey and additional traits that may have evolved in tandem.

Another intriguing example of predators exploiting incidental cues produced by their prey is bats that prey on other bats. While a number of predatory bat species have been documented to hunt smaller species of bats (e.g., *Cardioderma cor* [Csada, 1996], *Chrotopterus auritus* [Bonato, Facure, & Uieda, 2004], *Macroderma gigas* [Hudson & Wilson, 1986], *Nycteris grandis* [Hickey & Dunlop, 2000], *Trachops cirrhosus* [Bonato & Facure, 2000], *Vampyrum spectrum* [Navarro & Wilson, 1982]), little is known about the foraging behaviour underlying these predation events (Fenton, 2003). It has been hypothesized that predatory bats hone in on the echolocation calls produced by other bats as they forage for food or navigate the environment (Fenton, 2003). Behavioural experiments with *Nycteris grandis*, however, suggest that these bats attend not to echolocation calls but rather to the wingbeat sounds produced by the bats they hunt (Fenton, Gaudet, & Leonard, 1983). Further study across a range of bat-eating bats is necessary to better understand the sensory information bat predators use to hunt other bats.

In sum, prey-emitted cues are used opportunistically across a wide range of diverse predatory bats (Figure 1a). For bats that specialize on this prey detection strategy, adaptations that extend their sensory abilities beyond the range they use for communication and navigation enable them to exploit these resources in a more targeted

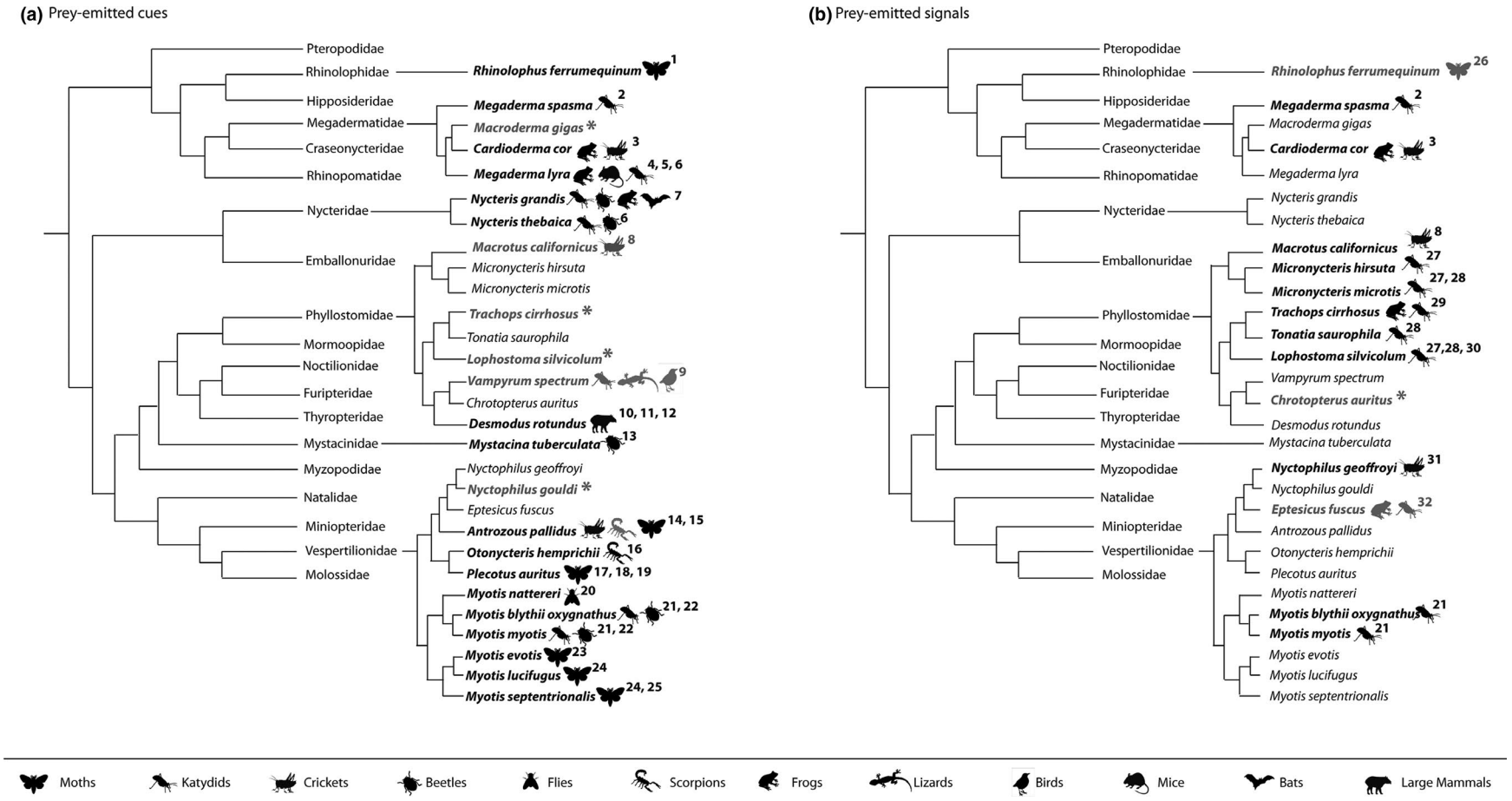

FIGURE 1 Phylogenetic relationships of predatory bats using prey-emitted cues (a) and signals (b). Illustrations adjacent to each species indicate the prey type hunted by each bat as suggested by observations (grey outlines) or demonstrated by experiments (black outlines). Asterisks indicate unpublished records of species suspected to use such cues or signals. Phylogeny adapted from Kaňuch, Aghová, Meheretu, Šumbera, and Bryja (2015), Roehrs, Lack, and Bussche (2010), Rojas, Warsi, and Dávalos (2016) and Stadelmann, Lin, Kunz, and Ruedi (2007). References for prey cue and signal use by bat species: [1]Lattenkamp et al. (2018); [2]Raghuram et al. (2015); [3]Ryan and Tuttle (1987); [4]Fiedler (1979); [5]Marimuthu and Neuweiler (1987); [6]Marimuthu et al. (2002); [7]Fenton et al. (1983); [8]Bell (1985); [9]Vehrencamp, Stiles, and Bradbury (1977); [10]Schmidt et al. (1991); [11]Gröger and Wiegrebe (2006); [12]Heffner et al. (2013); [13]Jones et al. (2003); [14]Bell (1982), [15]Fuzessery et al. (1993); [16]Holderied et al. (2011); [17]Anderson and Racey (1991); [18]Anderson and Racey (1993); [19]Coles et al. (2004); [20]Siemers et al. (2012); [21]Jones et al. (2011); [22]Arlettaz et al. (2001); [23]Faure and Barclay (1992); [24]Ratcliffe and Dawson (2003); [25]ter Hofstede, Ratcliffe, and Fullard (2008); [26]Alem et al. (2011); [27]Belwood and Morris (1987) (note that in this study, *Micronycteris microtis* is referred to as *Micronycteris megalotis* and *Lophostoma silvicolum* as *Tonatia silvicola*, reflecting the phylogenetic understanding at the time); [28]Falk et al. (2015); [29]Page and Jones (2016); [30]Patriquin et al. (2018); [31]Bailey and Haythornthwaite (1998); [32]Buchler and Childs (1981)

manner (see the Adaptations section below). Just as barn owls have shaped the defensive behaviour of rodents (Edut & Eilam, 2003), bats using prey-emitted cues likely have selected for corresponding defence strategies in their prey to reduce cue production and minimize detection. While prey defences to avoid consumption by bats are common (e.g., morphological defences such as spines, behavioural defences such as kicking and the production of startling sounds when handled, etc, reviewed in ter Hofstede et al., 2017), more subtle defence responses that curtail detection deserve further investigation.

2.2 | Eavesdropping on prey communication signals

As prey produce signals to communicate with conspecifics, predators exploit these signals to detect, assess and localize their prey (Zuk & Kolluru, 1998). Unlike prey-emitted cues that are under directional selection to limit information provided to predators, signals are at the crux of antagonistic selection by predators and selection to communicate with conspecifics. Predators that exploit mating signals exert selective pressures on their prey that oppose reproduction, a critical component of fitness. While sexual selection results in conspicuous and elaborate signals to entice potential mates (Laidre & Johnstone, 2013), modifications in signal structure and signalling behaviour to decrease conspicuousness can reduce predation risk and increase survival (Bernal & Page, in prep). To some degree, the fact that most prey must produce signals to find each other gives predators an edge in this arms race.

A number of bats eavesdrop on the mating signals of prey that communicate at night. Unlike other mammalian predators and birds (Bernal & Page, in prep), in bats eavesdropping on prey mating signals seems to be widespread. This strategy is found in at least three families of bats and it is used by species in both the New and Old World (Figure 1b). Katydids are common victims of eavesdropping bats. In a single Neotropical community, for example, at least four species of leaf-nosed bats hunt using the mating calls of these orthopterans (*Lophostoma silvicolum*, *Tonatia saurophila*, *Micronycteris microtis* and *Trachops cirrhosus*; Falk et al., 2015). Playback experiments using the mating calls of 12 katydid species in this community revealed that different species of bats prefer different acoustic features of the katydid calls, suggesting sensory niche partitioning among these different predators (Falk et al., 2015). Variation in predator response to the acoustic parameters of prey mating signals may result in low prey overlap and reduced competition.

Similarly, sensory niche partitioning has been suggested for the lesser and greater mouse-eared bats (*Myotis myotis* and *M. blythii oxygnathus*), Old World species which also eavesdrop on the calls of katydids (Jones, Page, Hartbauer, & Siemers, 2011). *Myotis blythii oxygnathus* show stronger predatory responses to the songs of katydid species than to prey movement sounds. But bats from its sibling species, *M. myotis*, respond more to prey rustling sounds than to katydid calling songs. In areas in which these predator species co-occur, variation in predator's acoustic preferences for prey could minimize their niche overlap, as suggested in the Neotropical example above. While similar sensory resource partitioning based on prey signals could occur among non-Chiropteran predators, to our knowledge no such cases are known. Indeed, eavesdropping predators from other vertebrate groups seem to be opportunistically hunting using mating signals, rather than being specialized in using this strategy (Bernal & Page, in prep; Zuk & Kolluru, 1998). As such, the lack of intra-guild competition is unlikely to result in partitioning of prey based on their signals.

Like katydids, frogs and toads also produce communication calls at night. While some anuran species are diurnal, in the majority of frogs and toads, males emit conspicuous, stereotypic calls at high repetition rates during the night, making the senders vulnerable to eavesdropping nocturnal predators like bats. It is thus surprising that few bats are known to exploit anuran mating calls to hunt their prey. The fringe-lipped bat, *Trachops cirrhosus*, attacks frogs by homing in on their mating calls as male frogs form choruses at ponds and puddles (Tuttle & Ryan, 1981). Similarly, the heart-nosed bat, *Cardioderma cor*, responds to frog calls with head movements and flight towards speakers broadcasting frog calls (Ryan & Tuttle, 1987). This commonality between a New and an Old World species is not surprising given the similarity in their feeding habits and the morphology of their pinnae (see more below under Adaptations). Interestingly, bat species that orient to frog mating calls often also attend to the calls produced by stridulating insects (Buchler & Childs, 1981; Falk et al., 2015; Ryan & Tuttle, 1987; Tuttle, Ryan, & Belwood, 1985). It is possible that attending to frog calls in these species may have arisen from, or in conjunction with, the ability to hunt using the songs of nocturnally signalling insects. Hunting both insect and anuran prey based on their calls also occurs in other taxonomic groups such freshwater birds which forage in the areas where many species of insects and frogs breed. Herons (Bell, 1979) and storks (Igaune, Krams, Krama, & Bobkova, 2008), for instance, both exploit the sexual advertisement calls of frog and insect prey. More studies that examine the use of prey signals by different groups are necessary to reveal parallels in strategies used by different eavesdroppers.

Moths are another group of nocturnal prey highly vulnerable to exploitation by bats. Greater horseshoe bats, *Rhinolophus ferrumequinum*, readily orient towards leks of singing male *Ascalenia grisella* moths, suggesting that bats use moth calling song displays to locate their prey (Alem, Koselj, Siemers, & Greenfield, 2011). Horseshoe bats are well known to use acoustic glints imprinted on the returning echoes of their echolocation calls produced by the fanning wings of their prey (Schnitzler, 1987; Schnitzler, Menne, Kober, & Heblich, 1983). While these bats likely are recruiting both avenues of information gathering, listening for moth calling songs as well as attending to their fanning wings, playback experiments evaluating bat responses to the calling songs of moths in the absence of acoustic glints are needed to determine whether the hunting strategies of greater horseshoe bats indeed involve eavesdropping (Alem et al., 2011). Evidence suggesting bat eavesdropping on moth calling song has also been found on the prey side (Nakano, Takanashi, Surlykke, Skals, & Ishikawa, 2013). Moths have been shown to reduce the loudness of their displays, producing a soft, low-amplitude song thought

to have evolved in response to strong selective pressure from eavesdropping bats (Nakano et al., 2009; Nakano & Nagamine, 2019).

Mating behaviour in general is risky but copulation in particular puts individuals in a vulnerable position, compromising both vigilance and defensive behaviours (Gwynne, 1989). Production of signals during copula is expected to further increase predation risk by broadcasting the location of the copulating pair to eavesdropping predators. While little work has been done in this area, Natterer's bats (*Myotis nattereri*) provide a robust case of increased conspicuousness and risk confronted by copulating pairs. In the wild, these bats are attracted to the buzzing sounds produced by house flies copulating and are more likely to attack copulating couples than walking flies (Siemers, Kriner, Kaipf, Simon, & Greif, 2012). It is unclear, however, if the sounds produced by the flies are courtship signals or incidental cues that result from the male positioning himself such that the female can thrust her ovipositor into his genital opening. Detailed descriptions of the mating behaviour of house flies are available (Murvosh, Fye, & Labrecque, 1964), but courtship signals are not mentioned and Siemers et al. (2012) conservatively refer to these copulation sounds as cues. Though little studied to date, exploitation of sounds produced during copulation could be an efficient predator strategy and may be a more common phenomenon that has currently been documented, both in bats and in other predators. Further investigation is needed to fully understand the potential risks to prey, and the potential advantages to predators, of cues emitted by prey during copulation.

In general, exploiting the communication system of one's prey is an effective foraging strategy that provides several benefits. Predators can use this strategy to obtain information about the species identity of the sender, allowing them to make effective decisions about pursuing potential prey. Certain signal features can reveal prey quality, such as palatability or toxicity. The fringe-lipped bat, *Trachops cirrhosus*, for instance, relies on the mating calls of frogs as the first indication of prey palatability (Page, Ryan, & Bernal, 2014). Multiple layers of decision-making, however, are in place as safeguards to protect these bats from potentially lethal mistakes (Page, Schnelle, Kalko, Bunge, & Bernal, 2012). Even when acoustic features indicate that prey is safe to pursue, these bats employ both echolocation and chemical cues to verify prey palatability: frogs that are too large to attack or covered with toxic secretions are rejected before consumption. Using multiple sensory modalities in a multi-stage assessment process may facilitate the ability to learn novel associations between acoustic cues and prey quality in this species (Page & Ryan, 2005). It is likely that similar step-wise prey assessment processes occur in other eavesdropping predators, but this phenomenon requires further investigation.

When considering how bats' hunting strategies affect nocturnal signallers, which prey bats reject can also reveal interesting interactions. The signalling strategies of fireflies, for instance, have likely been shaped by predatory bats. Even though the conspicuous visual displays of fireflies offer ample opportunity for bats to depredate them, this prey is absent in their diets (Moosman, Cratsley, Lehto, & Thomas, 2009). Evidence that bats are deterred from consuming fireflies (Moosman et al., 2009; Vencl et al., 2016) and can quickly learn to avoid attacking them (Leavell et al., 2018) supports the long-standing, but previously untested, hypothesis that the flashing signals fireflies produce for intraspecific communication also serve as aposematic signals to deter predators like bats. Investigations that identify the role that bats may have played in constraining the signals and displays of nocturnal invertebrates that avoid them would be valuable to further understand the intricate ways in which predators shape the communication systems of their prey.

Since many anurans and insects aggregate to display in leks, eavesdropping on mating signals can result in the localization of productive prey patches. Big brown bats, *Eptesicus fuscus*, orient from long distances (>600 m) to frog choruses (Buchler & Childs, 1981). The diet of these bats, however, has been well studied and does not include frogs (e.g., Agosta, Morton, & Kuhn, 2003; Moosman, Thomas, & Veilleux, 2012). Rather it seems that areas of chorusing frogs are also areas of high insect abundance, and *E. fuscus* are using frog calls as an acoustic beacon to locate high-density areas of insect, not frog, prey (Buchler & Childs, 1981). Fringe-lipped bats, *Trachops cirrhosus*, and greater horseshoe bats, *Rhinolophus ferrumequinum*, discussed above, also home in on lekking males (Alem et al., 2011; Ryan, Tuttle, & Taft, 1981). Long-distance acoustic signals emitted by prey are thus used by bats to locate areas with high prey concentration and, once there, targeting individual calling males.

For predators, a potential downfall of exploiting readily available and conspicuous signals is that other predators can also be attracted to this prey in great numbers. Competition between eavesdropping predators may be slight though due to high prey abundance at leks. While there is tremendous variation in lek size between species and across environments (Andersson, 1994), signalling anurans and insects tend to be rich resources that are unlikely to be monopolized by single predators. Nevertheless, this type of resource can be ephemeral or at least highly seasonal. In both scenarios, eavesdropping predators need the flexibility to switch between prey types as they fluctuate in time or space. Fringe-lipped bats that eavesdrop on frog calls are highly adept at switching among prey across seasons. Their anuran prey mate mainly during the rainy season with a tremendous reduction in availability and diversity in the dry season. Fringe-lipped bats track these changes in prey availability by seasonally shifting the frog calls to which they are most responsive (Jones, Ryan, & Page, 2014). Different eavesdroppers, however, are expected to respond differently to seasonal changes in prey availability. For example, unlike fringe-lipped bats that have highly plastic behavioural strategies, frog-biting midges that use frog mating calls to locate calling males and obtain a blood meal seem to have a generalized acoustic template to respond to frog calls, and do not vary their acoustic preferences with prey availability (Legett, Baranov, & Bernal, 2017). Further investigation is needed to understand the diverse strategies used by eavesdropping predators and the sensory and cognitive adaptations they have evolved to confront temporal and spatial fluctuations in the abundance of their prey.

Among the bat species that eavesdrop on prey-emitted signals, several also attend to incidental cues emitted by prey. For example,

lesser and greater mouse-eared bats, *Myotis blythii oxygnathus* and *Myotis myotis* (Arlettaz et al., 2001; Jones et al., 2011), lesser false vampire bats, *Megaderma spasma* (Raghuram, Deb, Nandi, & Balakrishnan, 2015), and heart-nosed bats, *Cardioderma cor* (Ryan & Tuttle, 1987) all respond both to prey mating signals and to unintentionally produced sounds generated by their prey as they walk, fly and jump in their environment. While other bats known to attend to katydid songs, such as *Tonatia saurophila*, *Lophostoma silvicolum* and *Trachops cirrhosus* (Falk et al., 2015), have not been described to use incidental cues produced by their prey, field and flight cage observations indicate these species also use prey locomotion cues to hunt (R. A. Page, unpublished data). Given the significant challenges associated with using echolocation to detect prey in clutter (Neuweiler, 1989, 1990), it is likely that a large number of substrate gleaning bats rely on some sort of prey-emitted cues or signals to find their prey. The number of species currently documented to do so (Figure 1) is likely a gross underestimate, as robust experimental data are lacking for all but a handful of the substrate gleaners. Most mating calls of frogs and stridulating insects are restricted to sonic frequencies (Gerhardt & Huber, 2002) so bats that attend to these sounds require hearing sensitivity to these lower frequencies (see more under the Adaptations section below). In contrast, the sounds produced by prey walking or jumping on vegetation or leaf litter are broadband with strong components that extend into the ultrasound (Gröger & Wiegrebe, 2006). It is thus likely that bats that use prey-emitted signals also use incidental cues of their prey. Given the difference in frequency range of these prey stimuli and auditory specializations needed to detect much lower frequencies, the reverse scenario, bats that use prey-emitted cues that also use prey mating signals, is probably less common.

3 | SOCIAL INFORMATION USE

3.1 | Eavesdropping on echolocation calls

Echolocating bats emit high-frequency signals which bounce off elements in their environment or prey providing the bat with information about the environment or prey (Griffin, 1958). Echolocation calls, like communication signals, are prone to eavesdropping by other individuals. Aerial insectivores, that capture airborne prey in flight, rely on sophisticated echolocation systems to pinpoint their flying prey. As they home in on prey, they increase the repetition rate of their calls, culminating their hunting approach in a series of echolocation calls that are short in duration with a high repetition rate, enabling them to localize prey at close range (Griffin, 1958; Schnitzler & Kalko, 2001). In contrast to the passive listening bats that tend to have quieter echolocation calls (77–102 dB SPL at 10 cm, Faure, Fullard, & Barclay, 1990; Faure, Fullard, & Dawson, 1993; Miller & Treat, 1993; Surlykke, Jakobsen, Kalko, & Page, 2013), aerial insectivores (also called 'active listeners') tend to have loud echolocation calls, with search phases often exceeding 120 dB SPL at 10 cm from the bat's mouth (Surlykke & Kalko, 2008). While calls emitted during the terminal phase of the echolocation approach, or feeding buzz, are lower in intensity than the calls emitted in the search phase (Surlykke & Moss, 2000), feeding buzzes have sufficient energy to be used by eavesdropping bats as beacons indicating dense prey patches, such as insect swarms (Jones & Siemers, 2011). Indeed, eavesdropping on the echolocation calls of conspecifics to locate prey patches has been well documented across a diverse range of aerial insectivores (e.g., *Eptesicus fuscus* [Wright, Wilkinson, & Moss, 2011]; *Lasiurus borealis* [Balcombe & Fenton, 1988]; *Myotis lucifugus* [Barclay, 1982]; *Myotis yumanensis* [Balcombe & Fenton, 1988]; *Tadarida brasiliensis* [Gillam, 2007]). The strategy is not confined to eavesdropping on conspecifics; some bats are attracted to the feeding buzzes of heterospecifics as well (e.g., Barclay, 1982; Übernickel, Tschapka, & Kalko, 2013). Despite the potential benefits of social information use, however, not all bats attend to such information, even when available. Pipistrelle bats, *Pipistrellus pipistrellus*, for example, ignore playbacks of conspecific terminal buzzes broadcast from various locations across their habitat (Jonker, Boer, Kurvers, & Dekker, 2010). The degree to which bats eavesdrop on the echolocation calls of others is probably driven by the reliability of the information they can acquire privately and the costs associated with gathering social information (Valone & Templeton, 2002).

Numerous studies suggest that bats can benefit from foraging together (e.g., Brooke, 1997; Dechmann, Kranstauber, Gibbs, & Wikelski, 2010; Harten et al., 2018; Howell, 1979; Wilkinson & Boughman, 1998). For example, when attempting to locate ephemeral swarms of insects over large water bodies, the lesser bulldog bat, *Noctilio albiventris*, approaches feeding buzzes of conspecifics (Dechmann et al., 2009). While group foraging can be advantageous, facilitating the localization of ephemeral prey, there are also potential costs associated with attracting multiple predators to a foraging patch (Ranta et al., 1993). Too many individuals foraging in one place could result in high levels of competition. Another potential cost of attracting multiple individuals to the same feeding resource is that the echolocation signals of many bats in close proximity could interfere with one another, decreasing the ability of any one individual to efficiently detect prey. Greater mouse-tailed bats, *Rhinopoma microphyllum*, foraged together in moderately sized groups but tend to avoid high-density aggregations suggesting there is a trade-off in group size (Cvikel, Berg, et al., 2015). Moderately sized groups may reflect optimal number of bats aggregating to find prey, with attack sequences serving as beacons for patches of profitable prey, aiding others in prey detection. As the number of foragers in a dense area increases, however, too many bats in close proximity may result in signal interference, decreasing the efficiency of prey detection and capture (Cvikel, Berg, et al., 2015).

Bats are not the only echolocators in the animal kingdom. Odontocetes (toothed whales and dolphins, Kellogg & Kohler, 1952; Norris, Prescott, Asa-Dorian, & Perkins, 1961; Schevill & McBride, 1953), shrews (Siemers, Schauermann, Turni, & Merten, 2009) and tenrecs (Gould, 1965) echolocate, as do cave dwelling birds (e.g., cave swiftlets and oilbirds, Brinkløv, Fenton, & Ratcliffe, 2013). To date, however, eavesdropping on echolocation signals has only been studied intensively in bats. Especially in animals where echolocation can

potentially travel long distances (e.g., in ocean-dwelling mammals), it would be particularly relevant to investigate the possibility of eavesdropping on conspecific echolocation. Currently, there is only one study experimentally showing echolocation eavesdropping in odontocetes in captivity (Xitco & Roitblat, 1996), and one observation of this phenomenon in nature (Götz, Verfuß, & Schnitzler, 2006). While experimental investigation of eavesdropping on echolocation has proved challenging with odontocetes (reviewed in Gregg, Dudzinski, & Smith, 2007), this field provides fertile ground for comparisons between echolocation eavesdropping across disparate taxonomic groups.

3.2 | Attending to the behaviour of other predators

Social information is available to bats not just through eavesdropping on the echolocation calls of other bats, but also by attending to other foraging behaviours of fellow hunters, allowing individuals access to information that can increase foraging efficiency (Galef & Giraldeau, 2001). Indeed, there are many ways in which bats can acquire useful foraging information by attending to the behaviour of other hunters. The relative importance of eavesdropping on echolocation calls (as discussed in the section above) versus attending to non-vocal behaviours, however, is often challenging to unravel and requires further exploration. Often, both processes seem to be at play. In the flower-visiting bats, *Glossophaga soricina*, for example, individuals rapidly learn new flower locations in the presence of experienced conspecifics (Rose, Kolar, Tschapka, & Knörnschild, 2016). Bats are initially attracted to sensory stimuli given off by conspecifics as they forage, including echolocation calls successful foragers use as they home in on flowers. These calls draw the bat's attention to a particular area, with which it subsequently forms a positive association. Similarly, fringe-lipped bats, *Trachops cirrhosus*, initially seem to be attracted to the behaviour of a successfully foraging conspecific when it hears its loud chewing noises (Page & Ryan, 2006). Once its attention is captured, observing the conspecific's behaviour serves to draw the naïve bat's attention to the stimulus (in the case of *T. cirrhosus*, a sound), with which it subsequently forms a positive association. In both examples, attention is elicited both through the conspecific's echolocation calls and through its foraging behaviour (Page & Ryan, 2006; Rose et al., 2016).

Bats can acquire information not only from conspecifics but from heterospecifics as well. This seems to happen most frequently among species with some overlap in their foraging niche. From the eavesdropping side, for example, the lesser bulldog bats, *Noctilio albiventris*, attend to the echolocation calls of greater bulldog bats, *Noctilio leporinus*, and vice versa, but neither species is attracted to the echolocation calls of greater sac-winged bat, *Saccopteryx bilineata* (Übernickel et al., 2013). Likewise, cross-species social learning has been shown both between greater (*Myotis myotis*) and lesser (*Myotis blythii oxygnathus*) mouse-eared bats (Clarin, Borissov, Page, Ratcliffe, & Siemers, 2014) and between fringe-lipped (*Trachops cirrhosus*) and white-throated round-eared (*Lophostoma silvicolum*) Neotropical bats (Patriquin, Kohles, Page, & Ratcliffe, 2018). In both cases, these are sympatric species with overlap in the prey items upon which they forage.

A key adaption for recruiting information from con- and heterospecifics seems to be cognitive flexibility. Bats that can opportunistically observe and profit from the behaviour of other predators should possess flexible foraging templates, should have the ability to deviate from strict, stereotypical foraging behaviours and should be open to being influenced by the foraging success of others (Table 1). Comparative studies have examined the traits associated with behavioural flexibility in bats and have found that bat species with high degree of behavioural flexibility in their foraging behaviour have significantly larger relative brain sizes (Ratcliffe, Fenton, & Shettleworth, 2006). While similar predictions could be made for the propensity for social learning in bats, broadscale investigations of this behaviour across bats are still lacking. Social learning studies in bats, recently scarce, are beginning to be more common (reviewed in Wright, 2016). Perhaps in the years to come we will be able to use comparative analyses to assess the traits that favour social learning in bats as well as those characteristics associated more broadly with social information use.

While passive transfers of information are by far the most common, with one individual opportunistically gleaning information by observing the foraging behaviour of another, active transfer of information, or teaching, can also be a powerful tool for acquiring information (e.g., meerkats: Thornton & McAuliffe, 2006; dolphins: Bender, Herzing, & Bjorklund, 2009; pied babblers: Raihani & Ridley, 2008; reviewed in Hoppitt et al., 2008). Teaching *sensu* Caro and Hauser (1992) is an interesting subset of social learning that has been little studied in bats, with only one documented case to date (Bunkley & Barber, 2014). While systematic, experimental studies of teaching in bats are lacking, indirect evidence points to the possibility that active transfer of information might be more common than currently documented. Bats are long-lived animals that typically give birth to a single pup, with mothers and pups often associating for long periods of time. Proximity sensor data have shown that in fringe-lipped bats, *Trachops cirrhosus*, mothers associate with young post-weaning, not only at the roost, but at foraging sites as well, suggesting the potential for vertical transfer of foraging information (Ripperger et al., 2016). The common big-eared bat, *Micronycteris microtis*, provision young with live prey for up to five months after weaning; it has been hypothesized that this extended provisioning period serves to teach young prey handling skills, as they consume large and well-defended prey (Geipel, Kalko, Wallmeyer, & Knörnschild, 2013).

Social learning can be an efficient strategy for bats to obtain hunting information (reviewed in Wilkinson & Boughman, 1999; Wright, 2016). Social information acquisition, however, does not have to involve learning. Indeed, traditional definitions of social information have explicitly excluded social learning (Danchin et al., 2004; Valone, 1989; Valone & Templeton, 2002). In bats, the role of social information use, both through eavesdropping on echolocation calls and by attending to the behaviours of other hunters, whether through learning or otherwise, is an area in need of widespread, comparative study (Wright, 2016).

TABLE 1 Comparison of the different features involved in the main information venues used by predatory bats

Information venue	Source	Selection on emitter	Constrained by	Adaptations by predators	Benefits to predator	Costs to predator
Attending to prey-emitted cues	**Private** • Prey movement • Prey breathing	Minimize detection	Environment Locomotor ability Physiology	**Enlarged pinnae** **Elaborate pinnae** Mid-frequency hearing (12–25 kHz) Enlarged inferior colliculus	Detection of otherwise cryptic prey Allows prey detection in cluttered environments	Cues provide little information about prey (e.g., species identity, palatability)
Eavesdropping on prey-emitted signals	**Private** • Prey communication signals	Conceal information (Signal crypsis) • Modifications in signal structure • Plastic signaling behavior	Communication function	**Enlarged pinnae** **Elaborate pinnae** Low-frequency hearing (<5–15 kHz) Enlarged inferior colliculus	Highly conspicuous and highly localizable signals Species palatability confirmation Detection of highly abundant prey patches Risk prone prey	Seasonal Often ephemeral
Eavesdropping on bat echolocation	**Social** • Echolocation calls of other predators	Production of less conspicuous echolocation calls • Differentiation of frequencies used • Reduction in call production	Environment	Enlarged inferior colliculus	Detection of highly abundant prey patches Honest signals	Acoustic interference Inaccuracy of public information Competition
Attending to the behavior of other predators	**Social** • Hunting behavior and hunting strategies of other predators	Subtle hunting behaviors	Environment	Cognitive flexibility	Detection of highly abundant prey patches Discovery of novel foraging behaviors or novel prey species	Inaccuracy of public information Competition

Under 'Adaptations by predators', black text depicts hypothesized adaptations that require further investigation; bold text indicates traits for which there is empirical evidence supporting the hypotheses that such features are indeed adaptations.

4 | SENSORY ADAPTATIONS FOR OBTAINING FORAGING INFORMATION

Sensory adaptations reflect an animal's foraging needs (Stevens, 2013). Bats that use passive listening to help them detect and locate prey have evolved auditory specializations to hone in on prey-emitted sounds (Hemingway, Dixon, & Page, in press; Razak, 2018). The most conspicuous of these adaptations is prominent pinnae or external ears (Figure 2). This characteristic is so striking that upon capturing a bat, even without knowing anything about its foraging behaviour, its predominant foraging strategy can often be predicted just by observing the morphology of its ears (Figure 2; R. A. Page, unpublished data). Bats with large external ears relative to the size of the head tend to be slow flying, passive listening gleaners, while bats with smaller external ears tend to be fast flying, open space hunters that rely extensively on echolocation to hunt insects in flight (Gardiner, Codd, & Nudds, 2011). Large pinnae increase impedance matching between airborne vibrations and the ear drum, improving the transmission of quiet, prey-emitted sounds to the tympanic membrane (Obrist, Fenton, Eger, & Schlegel, 1993). The gleaning bats *Megaderma lyra* and *Macroderma gigas*, for example, have highly sensitive hearing in the 10–20 kHz frequency range. This high sensitivity is partly due to their large pinnae that result in a gain for frequencies within that range (Guppy & Coles, 1988; Obrist et al., 1993). In fact, without the pinnae, there is a frequency-dependent reduction in neural threshold sensitivity of up to 10–15 dB in *M. gigas* (Guppy & Coles, 1988). Not all large-eared bats are listening for prey sounds, however (Obrist et al., 1993). Some are listening for their own faint echolocation calls. Bats attacking prey sensitive to ultrasonic sounds, for example, have evolved faint echolocation calls that overcome the prey's hearing ability, and have large ears to hear these quiet calls. The aerial hawking barbastelle bat, *Barbastella barbastellus*, for instance, hunts tympanate moths by using low-amplitude echolocation calls and has large pinnae that allow it to receive the faint echoes (Goerlitz, ter Hofstede, Zeale, Jones, & Holderied, 2010).

The ears of passive listening bats can detect such disparate noises as prey rustling sounds, the mating signals of stridulating insects and frogs, or even the breathing sounds produced by potential mammal hosts (e.g., Arlettaz et al., 2001; Gröger &

FIGURE 2 Characteristics of the pinnae of predatory bats that use different foraging strategies. Bats that detect prey by attending to prey-emitted cues (a), eavesdropping on prey communication signals (b) and eavesdropping on the echolocation signals of other bats (c). The prominent, enlarged ears of bats that listen for prey cues (a) and prey signals (b) facilitate the detection of quiet, low-frequency prey sounds. Photo credit: https://www.MerlinTuttle.org

Wiegrebe, 2006; Jones et al., 2003; Page & Jones, 2016). These sounds consist mainly of frequencies in the sonic range. In the first case, as animals walk through the environment and their bodies and feet come into contact with the substrate around them, they produce broadband clicks with variable amplitudes, bandwidths and click intervals (Goerlitz & Siemers, 2007). While these rustling sounds can extend well into ultrasonic frequencies, most of their energy is found at relatively low frequencies (8–20 kHz; Guppy & Coles, 1988; Obrist et al., 1993). The mating signals of insects and frogs consist of even lower frequencies. These signals vary tremendously in structure but most insect songs and frog calls fall between 2–15 kHz and less than 5 kHz, respectively (Gerhardt & Huber, 2002), although some katydids emit higher frequency signals (Montealegre-Z, Morris, & Mason, 2006; Simmons, 2009). Finally, as mammals breathe, their inhalations and exhalations produce broad frequency band sounds mainly below 20 kHz (Gröger & Wiegrebe, 2006).

While prey-emitted sounds span a broad range of frequencies, with incidental cues such as rustling noises and other locomotion noises tending to be more broadband and higher in frequency than mating signals such as frog and insect calls, bats that attend to prey-emitted sounds must have auditory sensitivity well below the frequency range used for echolocation. The full range of echolocation call frequencies used by bats is broad (9–210 kHz, Fenton, 1999; Fenton, Jacobs, Richardson, Taylor, & White, 2004; Jacobs, 2000), but echolocation calls typically have frequencies above 40 kHz (Hubner & Wiegrebe, 2003; Razak, Fuzessery, & Lohuis, 1999). Interestingly, audiograms show that most bat species have quite

good hearing sensitivity in frequencies much lower than the frequencies of their echolocation calls (e.g., Dalland, 1965, Fay, 1988; Heffner et al., 2013; Neuweiler, 1984; Ryan, Tuttle, & Barclay, 1983; Schmidt, Turke, & Vogler, 1983, Wenstrup, 1984; reviewed in: Moss & Schnitzler, 1995; Altringham, 2011). Most bats are quite sensitive to frequencies between 12 and 25 kHz (Neuweiler, 1990; Figure 3). Sensitivity to frequencies within this range has been proposed to be a vestige of the ancestral state of bats, when insectivorous protobats used prey-generated noises to hunt their prey (Schnitzler et al., 2003). Many species of bats have since evolved away from this mode of hunting, most notably the aerial insectivorous bat species that hunt flying prey on the wing, relying purely on echolocation to do so. Sensitivity to lower frequencies remains (Neuweiler, 1990), however, providing a potential window for detection of sonic, prey-emitted signals and cues by predators across the order Chiroptera.

This hypothesis for low-frequency sensitivity as an ancestral trait predicts that a sensitivity window exists for many bat species to take advantage of lower frequency prey sounds. On the whole, however, there should be greater selective pressure to have lower frequency sensitivity on bats that attend to prey-emitted cues and signals, in contrast to bats that rely predominantly on echolocation to find prey. While auditory sensitivity has been investigated in bats for decades, audiograms exist for only a tiny fraction of the over 1,300 extant bat species world-wide. Furthermore, variation in methods limit the feasibility of comparisons of auditory sensitivity across species. For example, auditory brainstem recordings (e.g., red bats, *Lasiurus borealis*, Obrist & Wenstrup, 1998), behavioural tests based on unconditioned responses (e.g., fringe-lipped bats, *Trachops cirrhosus*, Ryan et al., 1983), and single auditory neuron recordings (e.g., common long-eared bats, *Plecotus auritus*, Coles, Guppy, Anderson, & Schlegel, 1989) vary greatly in their sensitivity, making direct comparison across methodologies problematic. Issues associated with comparing different methodological approaches to assess hearing sensitivity in bats have been discussed before (Heffner et al., 2013). In addition, auditory sensitivity is not always achieved in the same way, further complicating comparisons across taxa; different species can evolve different mechanisms to increase their auditory sensitivity to low frequencies, as has been the case in small rodents (Webster & Plassmann, 1992) and small mustelids (Heffner & Heffner, 1985).

Recognizing the limitations involved, as a first step we compared the auditory sensitivities of four species tested with the same methodology (conditioned suppression/avoidance) to examine the predicted disparity in low-frequency sensitivity in bats with different foraging strategies. While we compared auditory sensitivity for only a limited set of species, as predicted, bats that attend to prey signals and cues are indeed sensitive to lower frequencies than bats that eavesdrop on the echolocation calls of other bats (Figure 3). In addition, in contrast to the highest audible frequencies that are driven by the echolocation calls of each species, the lowest audible frequencies are extended in the species that attend to prey-emitted cues and signals (Figure 3).

Factors other than listening to prey-emitted sounds, however, could also promote sensitivity at low frequencies. Sociality, for instance, has been proposed to favour low-frequency hearing given that pup isolation calls, critical for offspring survival, are produced at low frequencies (from 13 to 30 kHz; Bohn, Moss, & Wilkinson, 2006; Gould, Woolf, & Turner, 1973). Supporting the

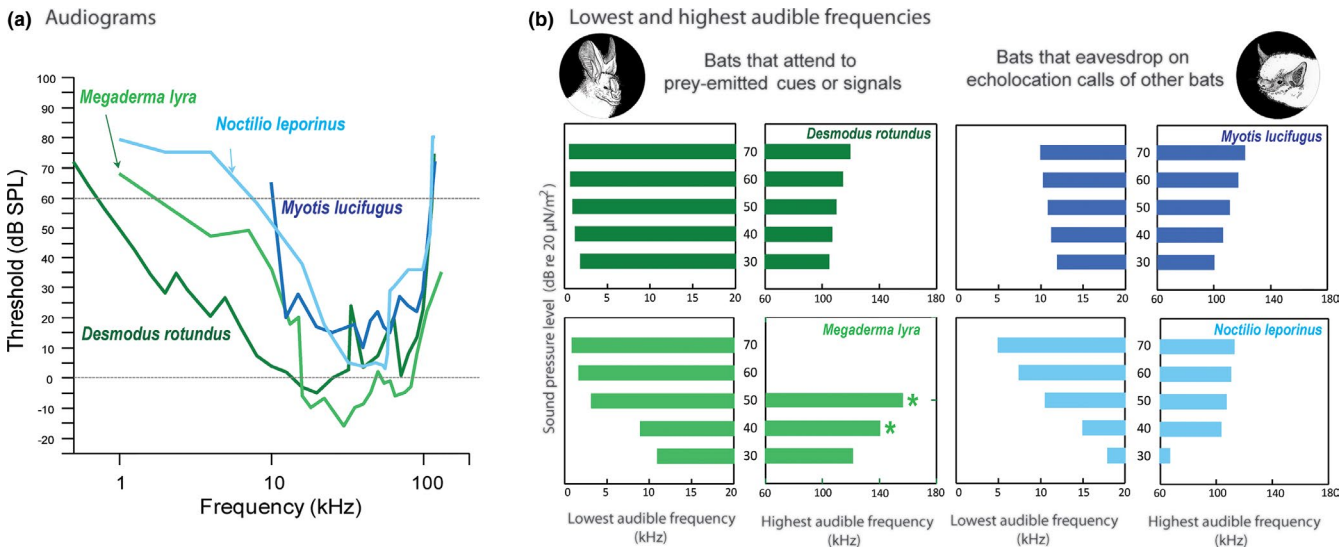

FIGURE 3 Frequency sensitivity of representative predatory bats that use different foraging strategies: two species that attend to prey-emitted signals and cues (green) and two species that attend to the echolocation calls of other bats (blue). Absolute thresholds (a) and lowest and highest audible frequencies at sound pressure levels (SPL) ranging from 30 to 70 dB (b) are shown for each species. All audiograms were collected using operant conditioning suppression–avoidance training. Data compiled by Rickeye Heffner (http://www.utoledo.edu/al/psychology/research/psychobio/audiograms2.html) from original studies as follows: *Desmodus rotundus* (Heffner, Koay & Heffner 2013); *Megaderma lyra* (Fay, 1988; Neuweiler, 1984; Schmidt et al., 1983), *Myotis lucifugus* (Dalland, 1965) and *Noctilio leporinus* (Wenstrup, 1984). Asterisks indicate extrapolated data for *M. lyra*. Bat drawings by Gabriela Sincich

role of perceiving pup isolation calls as the selective pressure for maintaining low-frequency hearing in bats, a cross-species analysis found that low-frequency hearing is correlated with the frequency of pup isolation calls (Bohn et al., 2006). Another hypothesis for the retention of low-frequency hearing is so that bats can detect the locomotion sounds of their own predators and thus avoid predation themselves. To our knowledge, however, the role of predators in influencing bat hearing remains unexplored. Overall, a deeper understanding of the factors driving the auditory adaptations associated with different foraging strategies, and other factors potentially modulating bat hearing, requires comparisons across a wide range of bat species tested using a consistent methodology and incorporating a phylogenetic approach.

Given that attending to prey acoustic cues was likely the ancestral state in bats (Jones et al., 2016; Schnitzler et al., 2003), and that bats have largely retained an ability to hear low frequencies, it is surprising that there are not more bat species known to use passive acoustic hearing for hunting. Only about a third of bat families have species suspected or experimentally shown to use prey-emitted cues or signals (Figure 1). It is surprising that there are not more species from more families that exploit these sources of information if most bats are indeed able to detect such cues and signals, even if only at relatively high intensities. Experimental challenges of disentangling the specific information sources used when hunting, coupled with a lack of in depth study for most species, may explain this information gap. Robust studies usually focus on bat species that can be kept easily in captivity and that respond well to behavioural assays in captive conditions. Currently, for instance, a deep body of literature on fringe-lipped bats provides a foundation for eavesdropping in bats (reviewed in Page & Jones, 2016). The restriction of our in depth knowledge of the use of passive listening in predatory behaviour to this and few other species, however, biases our understanding of this hunting strategy across bats.

To begin to correct this bias, alternative paradigms for conducting playback experiments are opening new doors in our understanding of bat eavesdropping behaviour. In lieu of experiments in captivity, field playback experiments provide an opportunity to investigate species in their natural environment. For example, baiting mist nests with calling katydids can reveal eavesdropping bat species, using mist nets with silent (female) katydids as controls (Belwood & Morris, 1987). Similarly, speakers broadcasting prey mating calls can be placed near mist nets (Tuttle et al., 1985), with mist nets accompanied by silent speakers serving as controls. More elaborate questions can be pursued by setting up speakers broadcasting different acoustic stimuli and video recording bats hunting in nature. This approach has been valuable to examine the predation pressure imposed by eavesdropping bats on their sexually signalling prey (Halfwerk et al., 2019; Legett, Page, & Bernal, in press; Trillo, Athanas, Goldhill, Hoke, & Funk, 2013; Trillo et al., 2016). This simple yet efficient experimental paradigm can be implemented to assess communities of eavesdropping bats, compare the abundance and distribution of these predators and identify the specific prey they are targeting. Overall, studies that address the effects of a wide range of eavesdropping bat species on their prey's signals across environments are necessary to improve our understanding of how these predators shape the community of nocturnal signallers. As more and more bat species are tested, both through controlled laboratory-based experiments and with the addition of the field-based assays described above, we should develop a better understanding of the range of signals and cues predatory bats attend to across time and space.

While sensitivity to 12–25 kHz seems to be common across bats (Neuweiler, 1990), lower frequency hearing is much rarer. For clarity, we distinguish between what we term 'mid-frequency' sensitivity (12–25 kHz) and 'low-frequency' sensitivity (<5 kHz to 15 kHz, Table 1) in bats. While somewhat overlapping, these frequency ranges tend to allow predators access to two separate pools of information: locomotion sounds such as wingbeats and rustling noises (accessible through 'mid-frequency' sensitivity, 12–25 kHz), versus the sounds of sexually signalling insects and frogs ('low-frequency' sensitivity, <5 kHz to 15 kHz). It is possible that bats that initially attended to the cues produced by moving prey, later evolved additional sensitivity in the lower frequencies, thus expanding their auditory repertoire to include access to frog and insect mating signals. The fringe-lipped bat, *Trachops cirrhosus*, for instance, has a peak of auditory sensitivity below 5 kHz matching the frequency range of most frog mating calls (Ryan et al., 1983). Its ability to detect these lower frequencies seems to be unusual in bats and is supported by a variety of adaptations in the inner ear including a long basilar membrane, increased innervation in the part of the cochlea that detects low-frequency sounds, and a large baso-apical stiffness difference (Bruns, Burda, & Ryan, 1989). Hearing sensitivity to low frequencies for *T. cirrhosus* is probably a key adaptation to exploiting frog mating calls. Studies of the hearing sensitivities of a variety of passive listening predators across a broad range of frequencies would provide valuable insights into the sensory mechanisms underlying this foraging behaviour. Examination in particular of the hearing sensitivity of species like *Cardioderma cor* that also eavesdrop on frog calls would be important to better understand the adaptations underlying this predatory strategy.

In addition to the adaptations described above, it has been hypothesized that having a large inferior colliculus is another adaptation for passive listening, with a more developed inferior colliculus enabling bats to process multiple streams of information (Baron, Stephan, & Frahm, 1996). While bats that listen for prey-emitted sounds do not rely primarily on echolocation to find their prey, they do use echolocation during their attacks for spatial navigation and landing control. As such, bats that rely on prey-emitted sounds need to process both the high frequencies of their echolocation calls and the much lower frequencies of the prey sounds. These multiple streams of information pose a processing challenge (Barber, Razak, & Fuzessery, 2003; Fuzessery et al., 1993). Since the inferior colliculus processes both sonic and ultrasonic sounds, adaptations in this brain region are expected (Baron et al., 1996). Contrary to this prediction, however, comparative studies have found no evidence that the inferior colliculus is larger in passive listening bats than in their active listening counterparts (Ratcliffe et al., 2006). This unexpected finding could be due to lack of detailed behavioural investigations across diverse bat species, misinforming comparative studies. For example,

species assumed to be aerial hawkers, relying exclusively on echolocation to find airborne prey, have subsequently been found to also glean prey on substrate using prey-generated sounds, and vice versa (e.g., *Myotis septentrionalis* and *Myotis lucifugus*: Ratcliffe & Dawson, 2003; *Otonycteris hemprichii*: Hackett, Korine, & Holderied, 2014). It is thus possible that our current understanding of bat foraging strategies and its relationship to the inferior colliculus is yet lacking.

5 | DISCUSSION AND PERSPECTIVE

In this review, we have discussed information-acquisition strategies predators use to take advantage of cues, signals or behaviours that are not intended for them. These diverse information-gathering strategies impose different selective pressures on prey and predators and are constrained by diverse factors (Table 1). Each strategy is also supported by a variety of sensory adaptations. While there is overlap between traits that allow bats to be able to exploit prey cues, prey signals and the echolocation calls of other bats, in general, each of these information-gathering strategies is associated with distinct benefits and costs (Table 1).

Predators that eavesdrop on prey mating signals can obtain detailed information about their prey, including species identity, palatability and precise location. As Belwood and Morris (1987) phrase it, prey mating signals tend to be 'species-specific, unambiguous, and highly localizable.' In contrast, prey-emitted cues offer much less detailed information. Generally, bats do not seem to use prey-emitted cues for prey identification or discrimination, but rather as an opportunistic way to detect and locate prey.

Sexually advertising males are heavily invested in the process of attracting mates. As such, eavesdropping predators can take advantage of the fact that when they are sexually signalling, prey tend to be more risk prone, and less vigilant, than they otherwise would be (Bernal, Rand, & Ryan, 2007). The use of prey mating signals also allows predators to profit from patches of highly abundant prey. Many insects and frogs aggregate to display for mates at night. Eavesdropping predators attending to their mating calls, in particular if they can detect them from large distances, can efficiently circumvent spatial heterogeneity in prey abundance. Given the many advantages (Table 1), it is thus unexpected that so few bat species exploit the mating signals produced by their prey (Figure 1b). While the low number of confirmed cases could be due to sampling biases, it is possible that the necessary sensory infrastructure is difficult to evolve. More studies that broadly examine this hunting strategy and the sensory adaptations it requires would provide valuable insights into this conundrum.

Analogous to eavesdropping on prey mating signals, attending to echolocation calls of other individuals can be a powerful strategy to detect abundant prey patches such as ephemeral swarms of insects (Dechmann et al., 2009). An added benefit is that echolocation hunting calls, particularly the feeding buzzes produced immediately prior to prey capture, are honest signals of prey presence. Competition for food resources and acoustic interference from the echolocation calls of others may increase the costs of this strategy as the number of predators increases (Table 1). The added benefit of eavesdropping on other predators is expected to decline after an intermediate, optimal group size (Cvikel, Berg, et al., 2015). Selection imposed by eavesdroppers is expected to promote features that minimize exploitation by other individuals such as differentiation of echolocation calls and reduction of call production (Table 1). Similar signal changes are used by bats to minimize jamming (e.g., Bates, Stamper, & Simmons, 2008; Chiu, Xian, & Moss, 2008; Gillam, Ulanovsky, & McCracken, 2007; Ulanovsky, Fenton, Tsoar, & Korine, 2004) but have not been described in the context of reducing eavesdropping. The adaptations involved in the ability to process echolocation calls of other individuals, in addition to one's own echolocation calls, and the contexts in which jamming constrains foraging in concentrated prey patches in nature, demands more attention (Cvikel, Levin, et al., 2015).

In contrast to the honest and immediate nature of the information received when eavesdropping on echolocation calls, attending to the behaviours of other predators can result in inaccurate, or outdated information (Rendell et al., 2011). In spite of this potential drawback, social information is a particularly valuable strategy when information from other sources is limited. Bats provide an exciting opportunity to evaluate the role of ecological context on the use of social information and social learning.

In general, we see several broad patterns in the bat species that employ these different information-gathering strategies. Bats that use prey-emitted cues and signals tend to be gleaners—hunters that take prey off of substrates, whether it be off of vegetation, the leaf-litter-covered ground or some other cluttered surface (Figure 4). For bats in these cluttered environments, echolocation for prey finding becomes extremely difficult if not impossible for most species (Neuweiler, 1990), so prey-emitted sounds offer critical information on prey presence and location that would otherwise be lacking. The second broad trend that emerges is that bats that attend to the echolocation calls of other bats tend to be aerial insectivores (Figure 4). Again, this pattern matches the particular ecological challenges of this group of bats. Aerial insectivores, the bats that hunt flying prey in flight, have loud, far-travelling echolocation calls that include distinctive feeding buzzes when foraging (Surlykke & Kalko, 2008). In contrast, the calls of gleaning species tend to be quieter, usually lacking the feeding buzz component altogether (Neuweiler, 1990). Although gleaners and aerial insectivores differ in the use of prey and predator sounds, both groups have a propensity for social learning. While social learning has only been shown in a handful of bat species, it seems to be found across taxonomic groups and foraging guilds. Learning from other predators does not seem constrained by the specific hunting strategies associated with particular echolocation patterns (aerial insectivores vs. gleaners), as seems to be the case for other information gathering strategies.

In this review, we have discussed two forms of private information use, attending to prey-emitted cues and eavesdropping

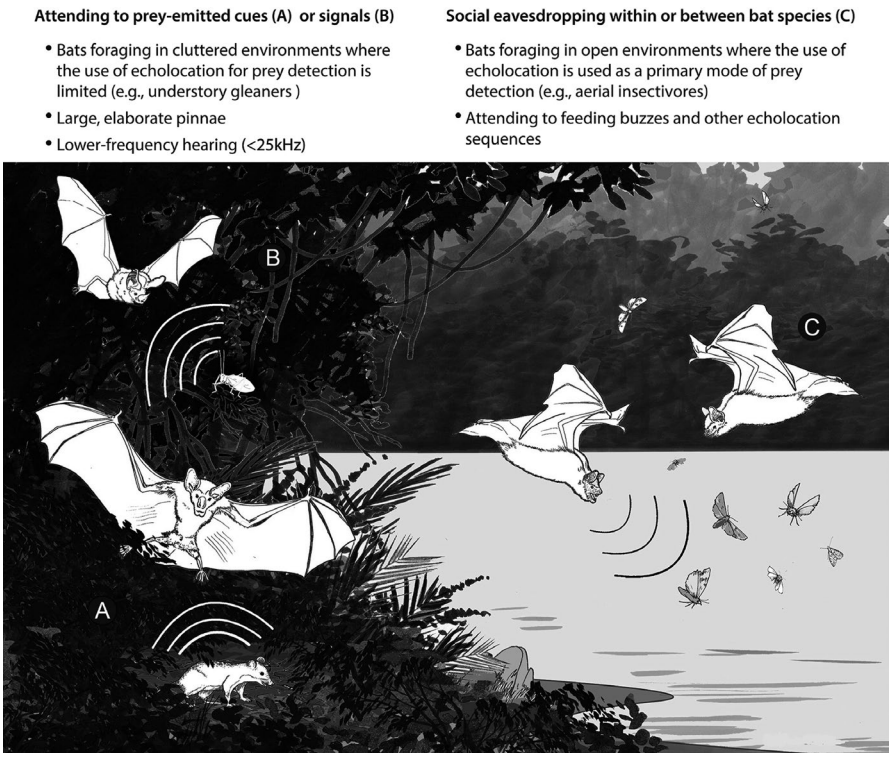

FIGURE 4 Graphic overview of the main information sources used by predatory bats as a function of habitat type. Foraging strategies include attending to prey-emitted cues (a), eavesdropping on prey communication signals (b) and eavesdropping on the echolocation signals of other bats (c). Illustration by Gabriela Sincich

on prey communication signals, and two forms of social information use, eavesdropping on bat echolocation calls and attending to other forms of bat foraging behaviour. We also considered social learning as a venue in which bats can obtain hunting information. Individuals face trade-offs associated with each of the strategies we discussed (Galef & Giraldeau, 2001). Acquiring information oneself can be both time consuming and risky; using socially acquired information can be an efficient way to avoid these potential costs (Kendal, Coolen, & Laland, 2009). While echolocation calls, in particular the feeding buzzes, of other hunting bats unequivocally inform eavesdroppers of prey presence, other forms of socially acquired information can be inaccurate or outdated. Bats returning to a roost, smelling strongly of a particular fruit, for example, may be accurate indicators of fruit abundance, but these scents could also reflect a food resource that has already been depleted and thus conveys social information that is no longer relevant or useful (O'Mara, Dechmann, & Page, 2014; Ratcliffe & ter Hofstede, 2005). Theory predicts that individuals should selectively use both private and social information, balancing their use of each depending on circumstance (Laland, 2004). While studies of other taxa have indeed shown this selective use to be the case (reviewed in Kendal, Coolen, Bergen, & Laland, 2005; Rendell et al., 2011), few studies have examined this trade-off in bats. The little work that has been done reveals that bats do indeed employ foraging strategies that balance the costs and benefits of social versus private information (Jones, Ryan, Flores, & Page, 2013). More investigation is necessary to fully understand the diverse strategies used by bats to balance the trade-offs associated with different types of information use.

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AUTHORS' CONTRIBUTIONS

R.A.P. and X.E.B. conceived the review topic, searched the literature, discussed emergent patterns and wrote the manuscript.

DATA AVAILABILITY STATEMENT

This review does not report new raw data. Rather, we review published literature and investigate patterns in previously published data. All studies used in this review are cited in the text and referenced in the Reference section.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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