Eavesdropping on heterospecific alarm calls: from mechanisms to consequences

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ABSTRACT

Animals often gather information from other species by eavesdropping on signals intended for others. We review the extent, benefits, mechanisms, and ecological and evolutionary consequences of eavesdropping on other species' alarm calls. Eavesdropping has been shown experimentally in about 70 vertebrate species, and can entail closely or distantly related species. The benefits of eavesdropping include prompting immediate anti-predator responses, indirect enhancement of foraging or changed habitat use, and learning about predators. Eavesdropping on heterospecifics can provide more eyes looking for danger, complementary information to that from conspecifics, and potentially information at reduced cost. The response to heterospecific calls can be unlearned or learned. Unlearned responses occur when heterospecific calls have acoustic features similar to that used to recognize conspecific calls, or acoustic properties such as harsh sounds that prompt attention and may allow recognition or facilitate learning. Learning to recognize heterospecific alarm calls is probably essential to allow recognition of the diversity of alarm calls, but the evidence is largely indirect. The value of eavesdropping on different species is affected by problems of signal interception and the relevance of heterospecific alarm calls to the listener. These constraints on eavesdropping will affect how information flows among species and thus affect community function. Some species are 'keystone' information producers, while others largely seek information, and these differences probably affect the formation and function of mixed-species groups. Eavesdroppers might also integrate alarm calls from multiple species to extract relevant and reliable information. Eavesdropping appears to set the stage for the evolution of interspecific deception and communication, and potentially affects communication within species. Overall, we now know that eavesdropping on heterospecific alarm calls is an important source of information for many species across the globe, and there are ample opportunities for research on mechanisms, fitness consequences and implications for community function and signalling evolution.

Key words: alarm call, eavesdropping, interspecific eavesdropping, heterospecific eavesdropping, predation, anti-predator behaviour, mixed-species groups, information network, deception, mimicry.

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I. INTRODUCTION

Animals seek information about the world from a variety of sources, to reduce uncertainty and thereby enable adaptive behavioural decisions (Danchin, Giraldeau & Wagner, 2004; Dall *et al.*, 2005; Wagner & Danchin, 2010). Information comes from personal experience, or from signals or cues of members of the same or different species (Table 1 provides a glossary). Individuals gain information from the signals of other species either during communication or by eavesdropping. We define communication as entailing the use of signals that have evolved because they benefit the signaller by affecting the behaviour of an intended receiver, whose response has also evolved (Table 1; Maynard Smith & Harper, 2003). Familiar examples include flowers signalling to pollinators (Waser & Ollerton, 2006) and aposematic species signalling their noxiousness to predators (Ruxton, Sherratt & Speed, 2004). By contrast, eavesdropping entails using information from signals intended for others (reviews: Wiley, 1983; McGregor & Dabelsteen, 1996; Peake, 2005). For example, animals can locate suitable breeding habitat by eavesdropping on signals of other species (Pupin *et al.*, 2007), and predators locate prey by their mating calls (Ryan, 1985; Zuk & Kolluru, 1998).

Eavesdropping on the signals of other species is likely to provide a greater amount and broader range of information than from conspecific signals alone. In any natural community, most individuals are likely to be heterospecifics, so eavesdropping on heterospecific signals will usually increase the total amount of relevant information available (Seppänen *et al.*, 2007). Heterospecifics can also be better at detecting or signalling about relevant information than conspecifics, by virtue of their location and use of the habitat, sensory ability and types of signals (Goodale *et al.*, 2010). Furthermore, heterospecifics are not necessarily competitors, and so an individual potentially gains information without the burden of competition (Seppänen *et al.*, 2007).

Table 1. Glossary of terms

Term	Context of production or definition	Typical response of receivers	Other usage
Signal	Feature that has evolved specifically because its effects on other individuals on average benefit the signaller. A signal has an 'intended' audience.	Depends on the type of signal. Receivers are selected to respond only if on average they benefit from the response.	—
Cue	Feature or presence of an individual that affects the behaviour of others but has not evolved for that purpose.	Depends on the type of cue. Receivers are selected to use any information from others that is of benefit.	—
Communication	Interaction between individuals entailing the use of signals evolved for that purpose.	Receiver is selected to respond to a signal only if on average it benefits from that response.	—
Eavesdropping	Reception and use of a signal that was intended for others; in this review synonymous with 'interceptive eavesdropping', *sensu* Peake (2005).	Response depends on the type of signal and the eavesdropper. Eavesdroppers can be conspecifics, heterospecifics, predators or prey.	'Interceptive eavesdropping' contrasts with 'social eavesdropping', which is gaining information from the communication interactions between others (McGregor & Dabelsteen, 1996; Peake, 2005; Searcy & Nowicki, 2005).
Alarm call	Call prompted by the presence of a predator or other threat such as a brood parasite. (Definitions focus on predators, but brood parasites are also often relevant.)	A variety of anti-predatory responses, depending on the type of alarm call.	Sometimes restricted to calls intended to warn others, usually conspecifics, about a predator (also called 'warning signals'), and so excluding calls directed to a predator itself, such as startle signals or signals of unprofitability.
(a) Flee alarm call	Call prompted by a hunting predator, often posing immediate danger. Those to raptors in flight are often called 'aerial alarm calls'.	Prey individuals become cryptic, flee to cover, or become vigilant (sometimes looking upwards to aerial calls).	Sometimes called 'warning calls'. Can be named after the type of threat, such as 'hawk' or 'eagle' alarm, or acoustic features, such as the 'seet' alarm call of some species.
(b) Mobbing call	Call prompted by a perched predatory bird or terrestrial predator, that is not posing an immediate threat. Potentially directed to other prey or to the predator.	Prey species approach the caller; give mobbing calls, and harass the predator. Predators may give up the hunt and leave. Vulnerable individuals such as young may become silent or cryptic rather than approach.	Can be called an 'assembly' alarm, 'terrestrial' alarm, or named after the prompt, such as 'leopard' or 'snake' alarm. Calls that are directed to a predator can be called 'defence calls'.
(c) Distress call	Call prompted after an individual is cornered, attacked or captured.	Prey species may approach. The attacking predator may be startled or deceived; other predators may approach.	Can be named after acoustic properties, such as 'hiss' or 'rattle' calls. Also called 'victim signals'; some may act as 'distraction calls'. Calls that threaten a predator can be called 'defence calls'.

Table 1. Continued

Term	Context of production or definition	Typical response of receivers	Other usage
(d) Graded alarm call	Call that varies quantitatively according to some property of the predator, such as its proximity. May therefore indicate urgency or degree of risk.	Prey species modify response according to quantitative features of the call. Responses include taking more immediate action to calls encoding greater urgency.	When related to degree of danger, called an 'urgency-related' or 'risk-based' alarm call.
(e) Referential alarm call	Call given to a specific type of predator or threat.	Prey respond in ways appropriate to avoiding that type of predator or threat.	Also called 'functionally referential' or 'predator-specific' alarm calls, or named after specific predators, such as 'eagle', 'leopard' and 'snake' alarms.
(f) Alert call	Call prompted by the presence of a predator or other threats or disturbances, so not only a subset of alarm calls.	Conspecifics become alert and respond differently according to the context.	May be called a 'general alarm call', because given to a broad range of threats or disturbances.
Sentinel call	Call given by an individual that signals it is vigilant, including when predators are absent. May vary with the sentinel's assessment of current risk.	Listeners may reduce vigilance and increase feeding rate when a sentinel is on duty and calling.	Also called a 'watchman's song' when given to indicate the absence of danger. Some 'contact calls' and 'close calls' may also serve this function.

We use alarm calls as model signals to examine eavesdropping because they can provide a wealth of information about predators, they are relevant to most species, and have broad ecological and evolutionary importance (Kostan, 2002; Seppänen *et al.*, 2007; Goodale *et al.*, 2010; Schmidt, Dall & van Gils, 2010; Zanette *et al.*, 2011). Alarm calls are widespread in birds and mammals, and while primarily used to warn conspecifics about predators or to deter predators, individuals often gain information about danger from the alarm calls of other prey species (Caro, 2005). Furthermore, alarm calls can encode information about the type of predator or degree of risk, both of which are relevant in selecting anti-predator responses. At a larger ecological scale, communities of species may form information networks, in which individuals gain information about danger from many species, and with differences among species in the production and reception of information (Holt, 2007; Goodale *et al.*, 2010; Schmidt *et al.*, 2010). Eavesdropping on alarm calls can also lead to different types of interaction among species, and so can have evolutionary as well as ecological consequences. Depending on the costs and benefits to the caller and listener, there could be evolution of signalling to thwart eavesdropping or to facilitate either deception or communication (Kostan, 2002; Dabelsteen, 2005).

This review examines the extent, benefits, mechanisms and consequences of vertebrates eavesdropping on the alarm calls of other species. We focus on prey species gathering information on danger from other prey species, rather than predators eavesdropping on signals from their prey, for which there is already a rich literature (e.g. Ryan, 1985; Haff & Magrath, 2011; review: Zuk & Kolluru, 1998). We first describe and define alarm calls, survey the extent of eavesdropping on heterospecific alarm calls, and consider the benefits of eavesdropping. We then assess the evidence for learned and unlearned mechanisms for recognizing heterospecific alarm calls, what constraints there may be on detection or recognition, and how these constraints affect eavesdropping networks within communities. Most of the review focuses on eavesdroppers, using the working assumption that callers are not affected by eavesdropping, but we then consider the evolutionary consequences that follow when callers benefit or suffer a cost from the response of eavesdroppers. We conclude by summarizing current knowledge and opportunities for research.

II. VERTEBRATE ALARM CALLS AND EXTENT OF EAVESDROPPING

We start by considering what information is potentially available to individuals that eavesdrop on the alarm calls of other species, and then assess the evidence that individuals often do use that information. We therefore

outline the different types of avian and mammalian alarm calls, and the information they convey to conspecifics, before surveying the extent of eavesdropping.

(1) Information from alarm calls

Many species of birds and mammals give specific calls when a predator is nearby or attacks (Klump & Shalter, 1984; Zuberbühler, 2009). Following these authors, we use the term 'alarm call' to refer to all such calls, despite diversity in acoustic structure, context and potential function. Alarm calls are classified in many ways, including by the degree or type of threat, response elicited, presumed state or intention of the caller, or acoustic structure (Table 1). The proliferation of terms reflects differences in alarm call use among species, and what is known about the context of production and function in different species. Calls directed to predators are sometimes considered signals of unprofitability or deterrence rather than alarm calls (Caro, 2005; Bradbury & Vehrencamp, 2011). However, both conspecifics and predators are likely to respond to calls given when a predator is nearby, so we consider as an alarm call any call that prompts an anti-predator response in conspecifics, even if the predator also responds.

In this review we refer as far as possible to alarm calls by the information conveyed, as revealed by the context of production and response of listeners to playback experiments. A focus on information is helpful because it is widely used and encapsulates the context of production, receiver response and ecological consequences (Caro, 2005; Dall *et al.*, 2005; Seppänen *et al.*, 2007; Zuberbühler, 2009; Schmidt *et al.*, 2010; Seyfarth *et al.*, 2010; Bradbury & Vehrencamp, 2011; but see Stegmann, 2013, for a diversity of views). Playback experiments are important in judging the information conveyed because they isolate response to the putative alarm call from other cues or signals, including from the predator itself (Seyfarth, Cheney & Marler, 1980*a,b*). The degree of specificity in alarm calls varies greatly among species and alarm call types (see below; Table 1), but many species have three common types of alarm calls: (*i*) flee alarm calls, given in response to immediate danger from hunting predators, and causing others to become cryptic or to flee; (*ii*) mobbing alarm calls, which are given to predators not posing immediate danger, and causing others to approach and monitor or harass the predator; and (*iii*) distress alarm calls, given when an individual is attacked or captured, which might startle the predator or recruit others to help the caller. There have been relatively few studies of distress calls, so the review primarily discusses flee and mobbing alarm calls.

Alarm calls can convey information on the type of predator, with different degrees of specificity. In a now classic example, vervet monkeys, *Chlorocebus pygerythrus*, produce acoustically distinct alarms calls to different predators, and conspecifics respond appropriately to playback of these calls (Seyfarth *et al.*, 1980*a,b*). For example, individuals look down after playback of 'snake' mobbing alarms, and look up and run to cover after 'eagle' flee alarms. Subsequent playback studies have shown that other mammals and birds possess alarm calls that convey information on predator type (Evans, Evans & Marler, 1993; Zuberbühler, 2009; Suzuki, 2012). Some species, such as redfronted lemurs, *Eulemur fulvus*, and Verreaux's sifakas, *Propithecus verreauxi*, have both context specific and general alarm calls: they give 'aerial' alarms to raptors, and 'general' alarms to raptors, terrestrial predators and in social contexts (Fichtel & Kappeler, 2002).

Alarm calls can also provide information on the urgency of the threat or degree of danger (Zuberbühler, 2009). In some cases the same type of alarm call is modified according to the level of risk. For example, white-browed scrubwrens, *Sericornis frontalis,* include more elements in their aerial alarm calls when a predatory bird is flying closer (Leavesley & Magrath, 2005), and black-capped chickadees, *Poecile atricapillus*, include more 'dee' elements in mobbing calls to species of perched raptor that pose a greater threat (Templeton, Greene & Davis, 2005). In other cases, including in several species of terrestrial rodents, individuals give different types of alarm calls in more and less risky situations (Blumstein, 1999*a*). For example, gerbils, *Rhombomys opimus,* change the timing and structure of alarm calls as humans approach (Randall & Rogovin, 2002).

Some species communicate simultaneously about the type of predator and urgency of danger. For example, meerkat, *Suricata suricatta,* alarm calls vary according to both the type of predator and the degree of danger it poses (Manser, 2001), and playbacks reveal differences in response according to both predator type and call urgency (Manser, Bell & Fletcher, 2001; Manser, Seyfarth & Cheney, 2002). More broadly, communication about predator type and risk can be closely related, and sometimes difficult to discriminate, because different predators can pose different risks and there can be a continuum between signalling about predator type and urgency (Owings & Morton, 1998; Blumstein, 1999*b*).

Although not alarm calls, 'sentinel calls' indicate the absence of danger or provide an indirect estimate of current risk, and so are relevant to listeners in adjusting anti-predator behaviour. For example, meerkats and pied babblers, *Turdoides bicolor*, acting as sentinels for a foraging group regularly give sentinel calls in the absence of danger, prompting others to reduce their vigilance (Manser, 1999; Hollén, Bell & Radford, 2008). The sentinel calls of pied babblers also provide an estimate of current risk, and calls indicating low risk lead to reduced vigilance and increased foraging success by listeners (Bell *et al.*, 2009). Even within foraging groups, meerkat individuals that have briefly scanned for danger give a distinct 'guarding close call', and playback of this call again reduces vigilance of listeners (Townsend, Zöttl & Manser, 2011). Animals can

therefore gain information about risk from signals that indicate either the presence of risk – alarm calls – or absence of risk – sentinel or comparable calls. We consider only sentinel-calling species that also produce alarm calls, so that the sentinel calls indicate the presence of an individual that could warn directly of danger. By contrast, we do not consider cases in which courtship or other calls by heterospecifics indicate that a predator is unlikely to be present, such as frog choruses (Phelps, Rand & Ryan, 2007).

(2) Extent of interspecific eavesdropping

Consistent with the wealth of information potentially available from alarm calls, eavesdropping occurs in a great diversity of species (Table 2). There have been playback experiments on at least 74 species in 41 families including birds, mammals and lizards, most of which show clear anti-predator responses. Individuals can eavesdrop on closely related species, or members of different families, orders and even vertebrate classes. Research so far has not been aimed at providing unbiased estimates of the proportion or types of species that eavesdrop, nor at assessing the characteristics of species from which they gain information, so analyses of published data cannot be extrapolated to species in general. In particular, experiments are likely to have been done on species suspected of eavesdropping, and it is possible that positive results are more readily published. Nonetheless, we now know that eavesdropping is common in a variety of species. For example, eavesdroppers can lack their own alarm calls (e.g. lizards: Vitousek *et al.*, 2007; Ito & Mori, 2010), rarely give alarm calls (e.g. mule deer, *Odocoileus hemionus*: Carrasco & Blumstein, 2012), or regularly give alarm calls, such as many birds and mammals (review: Zuberbühler, 2009). Eavesdroppers can range from solitary species to highly social ones (Carrasco & Blumstein, 2012). Published results suggest that birds could be a more common source of information about danger than are mammals, perhaps by virtue of their excellent vision, position in the habitat, foraging ecology and common alarm calls (Sections III.3, VI.1). More mammal species have been shown to eavesdrop on birds (11/30 eavesdropping mammals), than birds on mammals (2/41 birds). The three species of lizards also eavesdrop on birds, strengthening this association.

III. BENEFITS OF EAVESDROPPING

The diversity of eavesdropping species that respond appropriately to heterospecific alarm calls implies that individuals often gain useful information about danger from the calls of other species. In this section we consider the benefits of eavesdropping, including allowing immediate anti-predator behaviour, and gaining longer-term and indirect benefits. We also consider what benefits can be obtained from heterospecifics beyond that gained from conspecific calls. These benefits are not mutually exclusive, and could vary within and among species.

(1) Immediate anti-predator benefits

(*a*) Types of response

Eavesdropping on heterospecific alarm calls signalling immediate danger is likely to reduce the probability of being captured or detected by predators. Heterospecific flee alarm calls often cause individuals to flee to cover. For example, superb fairy-wrens, *Malurus cyaneus,* usually flee immediately to cover after playback of aerial alarm calls of several species (Magrath, Pitcher & Gardner, 2007, 2009; Magrath & Bennett, 2012). Similarly, playback studies on mammals show that golden-mantled ground squirrels, *Callospermophilus lateralis,* and yellow-bellied marmots, *Marmota flaviventris*, flee to refuge after the other species' alarm calls (Shriner, 1998); bonnet macaques, *Macaca radiata,* flee to cover in response to alarm calls of sambar deer, *Rusa unicolor*, and two species of langur (Ramakrishnan & Coss, 2000); and red squirrels, *Sciurus vulgaris*, flee to Eurasian jay, *Garrulus glandarius*, alarm calls (Randler, 2006). Instead of fleeing, individuals can become cryptic to alarm calls indicating immediate danger, which should reduce the risk of detection. For example, both downy woodpeckers, *Picoides pubescens*, and Carolina chickadees, *Poecile carolinensis*, freeze and become silent after playback of heterospecific aerial alarm calls (Sullivan, 1984*a*; Hetrick & Sieving, 2012), and older nestlings of ground-nesting white-browed scrubwrens become silent to playback of brown thornbill, *Acanthiza pusilla*, mobbing alarm calls, which are often given to predators on the ground (Haff & Magrath, 2012). In one case individuals even change colour, probably to increase crypsis against their background, after heterospecific alarm calls: Koch's giant day gecko, *Phelsuma kochi*, darkens more quickly and dramatically after playback of Madagscar paradise flycatcher, *Terpsiphone mutata*, alarm calls than after playback of song (Ito, Ikeuchi & Mori, 2013).

Many species increase vigilance after hearing heterospecific alarm calls, which is likely to improve their ability to detect predators or gather information about the type of danger (Caro, 2005). For example, playback of heterospecific alarm calls given to raptors usually prompts pied babblers to increase individual vigilance and group sentinel behaviour (Ridley, Raihani & Bell, 2010). Similarly, banded mongooses, *Mungos mungo*, increase vigilance after playback of plover alarm calls given to humans (Müller & Manser, 2008); impala, *Aepyceros melampus*, do so after playback of baboon, *Papio hamadryas*, alarm calls given to terrestrial predators (Kitchen *et al.*, 2010); and Madagascan spiny-tailed iguanas, *Oplurus cuvieri,* increase vigilance

Table 2. The outcome of playback experiments testing for eavesdropper response to heterospecific alarm calls. The response columns show the number of (a) eavesdropping species and (b) species pairs, and how they responded to playback, scored as a clear anti-predator resonse, weak response, or none. The 'eavesdropping species' response is the strongest shown by that species to any heterospecific alarm playback, so a species is tabulated as having no response if it did not respond to any species tested, if more than one was tested. The 'species pairs' response tabulates unique eavesdropper:caller pairs, and so can have multiple entries for a single eavesdropping species. Studies were included if the subjects were adults or free-ranging individuals living sympatrically with the playback species, and the sample size was ≥8 and so adequate to detect clear effects

Eavesdropper	Caller	(a) Eavesdropping species[a,b] response to playback:			(b) Species pairs[b,c] response to playback:			Sources
		Clear	Weak	None	Clear	Weak	None	
Birds Non-passerine (7 orders; 7 families, 8 species)	Bird (6 families, 7 species)	6	0	0	7	0	0	1–6
	Mammal (1 family, 2 species)	2	0	0	3	0	0	7, 8
Passerine (20 families, 33 species)	Bird (13 families, 21 species)	29	0	4	36	1	8	9–31
	Mammal	0	0	0	0	0	0	—
All birds (8 orders; 27 families, 41 species)	*Bird (17 families, 26 species)*	*35*	*0*	*4*	*43*	*1*	*8*	—
	Mammal (1 family, 2 species)	*2*	*0*	*0*	*3*	*0*	*0*	—
	Total (18 families, 27 species)	***37***	***0***	***4***	***46***	***1***	***8***	—
Mammals Carnivores (1 family, mongooses, 3 species[d])	Bird (3 families, 5 species)	3	0	0	6	0	0	12, 32, 33
	Mammal	0	0	0	0	0	0	—
Primates (4 families, 10 species[a])	Bird (4 families, 4 species)	3	0	0	4	0	0	34–37
	Mammal (6 families, 12 species)	9	0	0	13	0	0	34, 38–44
Ungulates (2 orders; 3 families, 7 species)	Bird (1 family, Musophagidae)	1	0	0	1	0	0	45
	Mammal (4 families, 4 species)	2	2	2	2	3	2	46–48
Rodents (1 family, scuirids, 6 species[a])	Bird (3 families, 4 species)	2	1	1	2	1	1	49–52
	Mammal (1 family, scuirids, 4 species)	2	1	0	3	1	0	49, 53, 54
Lagomorphs (1 family, pikas, 1 species)	Bird	0	0	0	0	0	0	—
	Mammal (1 family, scuirids, 2 species)	1	0	0	2	0	0	55
Bats (1 family, vesper bats, 3 species)	Bird	0	0	0	0	0	0	—
	Mammal (1 family, vesper bats, 3 species)	3	0	0	6	0	0	56
All mammals (7 orders; 11 families, 30 species)	*Bird (10 families, 14 species)*	*9*	*1*	*1*	*13*	*1*	*1*	—
	Mammal (8 families, 24 species)	*17*	*3*	*2*	*26*	*4*	*2*	—
	Total (18 families, 38 species)	***26***	***4***	***3***	***39***	***5***	***3***	—

Table 2. Continued

Eavesdropper	Caller	(a) Eavesdropping species[a,b] response to playback:			(b) Species pairs[b,c] response to playback:			Sources
		Clear	Weak	None	Clear	Weak	None	
Reptiles	Lizards (3 families, 3 species)	2	1	0	2	1	0	57, 58, 59
	Mammal	0	0	0	0	0	0	—
	Totals (2 families, 2 species)	*2*	*1*	*0*	*2*	*1*	*0*	—
Grand totals	*All eavesdropping species*	46	2	5	58	3	9	—
	Bird (26 families, 39 species)							
	(16 orders; 41 families, 74 species[a]) Mammal (8 families, 25 species)	*19*	*3*	*2*	*29*	*4*	*2*	—
	Totals (34 families, 64 species)	*65*	*5*	*7*	*87*	*7*	*11*	—

[a]One entry per eavesdropping species in body of table, except for three species tested for eavesdropping on both birds and mammals (rodent: woodchuck, *Marmota monax*, and primates: Diana monkeys, *Cercopithecus diana*, and Sahamalaza sportive lemur, *Lepilemur sahamalazensis*). Woodchucks did not respond to the bird alarm, but showed a weak response to the mammal alarm; both primates responded clearly to both the bird and mammal alarms. Therefore the body of the table adds to 77 species.

[b]Sahamalaza sportive lemur responded to aerial but not terrestrial alarm call of the blue-eyed black lemur; it is listed as an eavesdropper on that species.

[c]One entry per species pair. Species pairs are defined both by the eavesdropper and caller, so there are multiple entries if an eavesdropping species responds to the calls of more than one species of caller. Therefore numbers are larger than for eavesdropping species.

[d]The dwarf mongoose, *Helogale parvula*, responded to playback of sentinel calls of fork-tailed drongo, *Dicrurus adsimilis*, but was not tested for response to their alarm calls. Other mongooses do respond to drongo alarm calls, and dwarf mongoose appear to as well.

Sources: 1, Leger & Nelson (1982); 2, Ridley *et al.* (2014); 3, Griffin *et al.* (2005); 4, Sullivan (1984*a*); 5, Nuechterlein (1981); 6, Parejo *et al.* (2012); 7, Rainey *et al.* (2004); 8, Rainey *et al.* (2004); 9, Bell *et al.* (2009); 10, Branch & Freeberg (2012); 11, Fallow & Magrath (2010); 12, Flower (2011); 13, Flower & Gribble (2012); 14, Goodale & Kotagama (2005); 15, Goodale & Kotagama (2008); 16, Hetrick & Sieving (2012); 17, Huang, Seiving & St. Mary (2012); 18, Hurd (1996); 19, Magrath & Bennett (2012); 20, Magrath *et al.* (2007); 21, Magrath *et al.* (2009); 22, Magrath *et al.* (2009); 23, Martínez & Zenil (2012); 24, Møller (1988); 25, Nocera *et al.* (2008); 26, Radford *et al.* (2011); 27, Randler & Förschler (2011); 28, Ridley *et al.* (2010); 29, Ridley *et al.* (2010); 30, Templeton & Greene (2007); 31, Wheatcroft & Price (2013); 32, Müller & Manser (2008); 33, Sharpe, Joustra & Cherry (2010); 34, Seiler *et al.* (2013); 35, Seyfarth & Cheney (1990); 36, Zuberbühler (2000*a*); 37, Eckardt & Zuberbühler (2004); 38, Fichtel (2004); 39, Kirchhof & Hammerschmidt (2006); 40, Oda & Masataka (1996); 41, Ramakrishnan & Coss (2000); 42, Zuberbühler (2000*b*); 43, Zuberbühler (2000*c*); 44, Zuberbühler (2001); 45, Lea *et al.* (2008); 46, Carrasco & Blumstein (2012); 47, Kitchen *et al.* (2010); 48, Lingle *et al.* (2007); 49, Aschemeier & Maher (2011); 50, Getschow *et al.* (2013); 51, Randler (2006); 52, Schmidt *et al.* (2008); 53, Blumstein & Armitage (1997); 54, Shriner (1998); 55, Trefry & Hik (2009); 56, Russ *et al.* (2004); 57, Ito & Mori (2010); 58, Vitousek *et al.* (2007); 59, Ito & Mori (2013).

to Madagascar paradise flycatcher mobbing alarms (Ito & Mori, 2010).

Individuals often approach and mob predators in response to mobbing and sometimes distress alarm calls, which can allow prey to gather information on danger or prompt the predator to depart (Klump & Shalter, 1984). For example, several passerine species approach and give mobbing calls after playback of black-capped chickadee mobbing calls (Hurd, 1996). Active mobbing is reported less often during heterospecific playbacks to mammals, but Diana, *Cercopithecus diana*, and Campbell's monkey, *C. campbelli*, males, or whole groups, approach and give loud calls to the other species' alarm calls (Zuberbühler, Cheney & Seyfarth, 1999; Zuberbühler, 2001, 2000*c*). This behaviour can drive away eagles and leopards.

(*b*) *Discriminating among call types – choosing appropriate responses*

As implied by the diversity of anti-predator responses, individuals of at least some species gain information from heterospecific alarm calls on the type of danger, comparable to information gained from conspecifics. For example, ring-tailed lemurs, *Lemur catta*, respond to the aerial and terrestrial alarm calls of Verreaux's sifaka in the same way as to the corresponding conspecific calls, by looking up to the former but running to trees to the latter (Oda & Masataka, 1996). Birds in general mob in response to heterospecific mobbing calls, yet flee or become vigilant to heterospecific aerial alarm calls, suggesting that individuals discriminate among call types, but there have been surprisingly few playback tests of discrimination. Carolina chickadees respond to aerial alarm calls of tufted titmice, *Baeolophus bicolor*, by freezing and becoming silent, yet approach and call to titmice mobbing calls (Hetrick & Sieving, 2012). Superb fairy-wrens are more likely to flee to cover to aerial compared with mobbing alarm calls of noisy miners, *Manorina melanocephala*, reflecting a difference in the immediacy of danger (Magrath & Bennett, 2012). Similarly, black- and yellow-casqued hornbills, *Ceratogymna atrata* and *C. elata*, approach and call after Diana monkey 'eagle' but not 'leopard' alarm calls, which is appropriate given that only eagles threaten these birds (Rainey, Zuberbühler & Slater, 2004*a,b*).

Individuals can gain information from heterospecific alarm calls on the degree of danger posed by a specific type of predator. This has been shown in three species of birds. Superb fairy-wrens and white-browed scrubwrens each respond more urgently to the other species' aerial calls encoding greater danger (Fallow & Magrath, 2010), and red-breasted nuthatches, *Sitta canadensis,* respond with more vigorous mobbing to playback of black-capped chickadee mobbing calls indicating a more dangerous perched raptor (Templeton & Greene, 2007). Information on current risk can also be gained from heterospecific sentinel calls, as discussed in the next section.

(2) Indirect and longer-term benefits

(*a*) *Increased foraging success and expanded foraging niche*

The ability to eavesdrop on another species' alarm calls means that individuals can reduce vigilance and increase foraging success when that species is present. Furthermore, eavesdropping on sentinel calls allows assessment of the presence and vigilance of that species. For example, pied babblers are able to eavesdrop on the alarm calls of fork-tailed drongos, *Dicrurus adsimilis*, and reduce vigilance and increase foraging success if drongo presence is simulated through playback of sentinel calls (Ridley & Raihani, 2007; Flower, 2011). Heterospecific alarm calls also allow babblers to update their estimate of predation risk, which in turn affects their own sentinel calls and foraging efficiency (Bell *et al.*, 2009). Similarly, scimitarbills, *Rhinopomastus cyanomelas*, eavesdrop on babbler alarm calls, and when in mixed-species groups they reduce vigilance and increase foraging success, in part because they shift from exclusive arboreal feeding to foraging with babblers for larger prey on the ground (Ridley, Wiley & Thompson, 2014).

(*b*) *Gaining spatial information on danger*

Eavesdropping on alarm calls can provide spatial information on predatory risk, and so affect spatial exploration and breeding. Eastern chipmunks, *Tamias striatus*, become more cautious at feeders near broadcasts of tufted titmice alarm calls (Schmidt *et al.*, 2008), which could reduce their longer-term risk of predation by affecting spatial patterns of foraging. Scops owls, *Otus scops*, preferentially occupy safer areas, as indicated by later breeding at sites where little owl, *Athene noctua*, alarm calls were repeatedly broadcast, suggesting that eavesdropping on alarm calls can affect habitat selection and breeding behaviour (Parejo, Avilés & Rodríguez, 2012). Spatial changes in calling over time can track predator movement, at least within species (McGregor & Dabelsteen, 1996; Thompson & Hare, 2010), so that eavesdropping on a whole community might provide dynamic information on spatial risk.

(*c*) *Learning about predators*

Eavesdropping on other species' alarm calls could facilitate social learning about predators, but surprisingly there has been only one test of this idea. Playback of conspecific mobbing calls or heterospecific mobbing call choruses resulted in common blackbirds, *Turdus merula*, learning to mob models that were previously ignored (Curio, Ernst & Vieth, 1978; Vieth, Curio & Ernst, 1980). This implies that eavesdropping can lead to predator recognition and reduced risk in future.

(3) Information from heterospecifics compared to conspecifics

(a) More individuals to detect danger

Eavesdropping on heterospecific alarm calls could provide similar information to that from conspecifics, but could increase the chance that information is obtained (Goodale & Kotagama, 2005). Conspecifics could be equally capable of detecting and communicating about predators, but eavesdropping effectively increases the number of eyes looking for danger. This is likely to be true among ecologically similar species with comparable sensory and communication systems. For example, white-browed scrubwrens and superb fairy-wrens are both ground-feeding passerines with similar alarm communication that are vulnerable to the same predators, and each responds similarly to the other species' calls and their own (Magrath *et al.*, 2007; Fallow & Magrath, 2010).

(b) Better detection of danger

Eavesdroppers could take advantage of species that are better at detecting all or some threats, by virtue of their foraging niche, social system or sensory ability (Goodale *et al.*, 2010). For example, species that forage higher in vegetation appear better able to detect aerial predators than those feeding lower in the habitat (Morse, 1977; Munn & Terborgh, 1979; Gautier-Hion, Quris & Gautier, 1983; Munn, 1986). Group-living species may be a good source of information because there are more individuals to detect danger (Bshary & Noe, 1997). Similarly, species of birds that feed by catching insects in flight are highly vigilant, and thus good at detecting aerial predators (Munn, 1986; Srinivasan, Raza & Quader, 2010; Martínez & Zenil, 2012). Birds may often be better than mammals at visual detection of predators because of sensory and ecological differences (Rasa, 1983; Lea *et al.*, 2008), which might explain why more species have been shown to eavesdrop on birds than mammals (Section II.2).

Information from heterospecifics will be relatively more valuable when an individual has less personal information (Goodale & Kotagama, 2008; Martínez & Zenil, 2012). This means that information from the same caller can be of variable value for different eavesdropping species. Two studies support this idea by showing that species that forage from substrates, and so have a limited view of the world, are more responsive to heterospecific alarm calls than species that feed on flying insects, which are highly vigilant in search of prey. In mixed-species bird flocks in Sri Lanka, two leaf-gleaning species (ashy-headed laughingthrush, *Garrulax cinereifrons,* and orange-billed babbler, *Turdoides rufescens*) are more responsive to playback of heterospecific alarm calls than are two species that capture insects on the wing (greater racket-tailed drongo, *Dicrurus paradiseus*, and Malabar trogon, *Harpectes fasciatus*; Goodale

& Kotagama, 2008). Similarly, leaf-gleaning Amazonian species, in two different habitats, are more responsive to antshrike alarm calls than are flycatching species (Martínez & Zenil, 2012).

The availability of information from conspecifics could also affect the benefits of eavesdropping on heterospecifics. For example, pied babblers are a ground-feeding, social species with an effective sentinel system and alarm calls (Ridley & Raihani, 2007; Ridley *et al.*, 2010). However, collective vigilance is lower in smaller groups and therefore eavesdropping on fork-tailed drongo sentinel and alarm calls becomes relatively more valuable. Probably as a result, babblers in small groups are more tolerant of nearby drongos, despite their kleptoparasitism (Section VI.1), and respond more strongly to their alarm calls (Ridley & Raihani, 2007). Similarly, perhaps because of their own vigilance and reliable alarm calling, babblers ignore playback of the alarm calls of pair-breeding scimitarbills, which might be less reliable, whereas scimitarbills respond to babbler alarms (Ridley *et al.*, 2014).

(c) Better communication about danger

Species differ in their probability of communicating about danger, once it has been detected, and so eavesdroppers can gain information not readily available from conspecifics (Goodale & Kotagama, 2005; Goodale *et al.*, 2010). Most obviously, some species lack alarm calls. For example, some non-vocal lizards gain information from alarm calls of birds (Vitousek *et al.*, 2007; Ito & Mori, 2010). Differences among species in communication appear to be common, even among species that have alarm calls. Highly social species are more likely to give alarm calls than solitary species, presumably to warn conspecifics (Sridhar, Beauchamp & Shanker, 2009; Srinivasan *et al.*, 2010). For example, downy woodpeckers give alarm calls only when their mate is present, and so often rely on information gained from alarm calls and contact calls of gregarious chickadees and titmice, with whom they form mixed-species flocks (Sullivan, 1985).

(d) Information at reduced cost

Eavesdroppers might gain information from heterospecifics at a lower cost than from conspecifics. Even if conspecifics can detect and communicate detailed information about danger, they are also competitors for resources, such as food and mates. The costs of competition could therefore diminish the net benefit gained from conspecific signals of danger. By contrast, heterospecifics are not necessarily competitors, and therefore any benefit from eavesdropping may not be offset by costs (Seppänen *et al.*, 2007). In some cases, heterospecifics may not be competitors at all. In other cases, dominant species may be able to use

information from subordinate species with minimal cost (Goodale *et al.*, 2010), such as woodpeckers and nuthatches eavesdropping on alarm calls of chickadees, yet often being able to supplant them at sources of food (Sullivan, 1984*b*; Waite & Grubb, 1988). Conversely, subordinate species may pay a greater cost. There appear to have been no direct tests of this idea, but a laboratory experiment shows that blue jays, *Cyanocitta cristata*, are sensitive to the costs of acquiring signals. Jays use artificial signals more when making foraging decisions if the cost of acquiring the signal is low (McLinn & Stephens, 2010).

IV. EAVESDROPPING MECHANISMS

Eavesdropping is widespread and has clear benefits for individuals, yet the mechanisms allowing recognition of other species' alarm calls have only begun to be understood. Understanding response mechanisms is important for predicting how species will respond to unfamiliar alarm calls, as well as for understanding potential constraints on recognition. This section explores the mechanisms underlying both unlearned and learned responses. Unlearned responses can allow individuals to respond to heterospecific alarm calls without prior experience, thus minimizing exposure to predators (Hollén & Radford, 2009). By contrast, learning can allow flexibility but has the disadvantage that individuals require experience before they can respond appropriately (Griffin, 2004).

(1) Unlearned responses

(*a*) *Acoustic similarity to conspecific alarm calls*

Whether through chance, phylogenetic conservation or selection, there can be acoustic similarities in alarm calls among species, and this can allow for heterospecific responses without learning (Marler, 1955, 1957; Randler, 2012). For example, alarm calls given in high-urgency situations such as flee alarms given when a hawk is approaching, are often high-pitched, narrow-band tones or whistles that are difficult to locate, as exemplified by the 'seet' alarm calls of some European passerines (Marler, 1955; Rooke & Knight, 1977; Klump, Kretzschmar & Curio, 1986; Jones & Hill, 2001; Bradbury & Vehrencamp, 2011). Unlearned eavesdropping on acoustically similar calls can occur when response to conspecific alarm calls is innate (Lind & Cresswell, 2005; Hollén & Radford, 2009), and selection for response to conspecific alarm calls results in unlearned generalization to acoustically similar heterospecific alarms (Wiley & Richard, 1982; Ghirlanda & Enquist, 2003; Fallow, Pitcher & Magrath, 2013). This is because animals often rely on one or a few key acoustic features to recognize familiar calls, and treat new sounds that share those features similarly to familiar ones (Ghirlanda & Enquist,

2003; ten Cate & Rowe, 2007). Furthermore, variation in call production both within and between individuals, as well as environmental degradation of sounds, can create selection on receivers for a broad response range to conspecific calls, and this can lead to unlearned generalization to a relatively broad range of heterospecific alarm calls (Blumstein & Munos, 2005; Leavesley & Magrath, 2005; Fallow, Gardner & Magrath, 2011; Fallow *et al.*, 2013). Such broad generalization could be adaptive, as the cost of ignoring alarms is often greater than a mistaken response (review: Searcy & Nowicki, 2005).

There are widespread responses to playback of unfamiliar alarm calls that are acoustically similar to conspecific alarms (Table 3). For example, Australian apostlebirds, *Struthidea cinerea*, respond to the mobbing calls of North American Carolina wrens, *Thryothorus ludovicianus* (Johnson *et al.*, 2003); superb fairy-wrens respond to the aerial alarm calls of some allopatric congeners (Fallow *et al.*, 2011); European great tits, *Parus major*, respond appropriately to the urgency encoded in North American chickadee mobbing alarms (Randler, 2012); and European soprano bats, *Pipistrellus pygmaeus*, respond to the distress calls of four endemic Malagasy bats (Russ *et al.*, 2004). Response is typically enabled through similarities to conspecific calls in one or more acoustic features.

In addition to affecting response to allopatric alarms, acoustic similarity to conspecific alarms appears to influence the likelihood of responding to sympatric heterospecific alarm calls. For example, sympatric swamp and song sparrows, *Melospiza georgiana* and *M. melodia*, have acoustically similar distress calls, and both respond to each other's distress calls but ignore the acoustically distinct distress calls of sympatric white-throated sparrows, *Zonotrichia albicollis* (Stefanski & Falls, 1972). Similarly, 5 day-old nestling white-browed scrubwrens reduce calling to brown thornbill mobbing alarms, which are structurally similar to parental alarm calls, but ignore the acoustically distinct mobbing alarms of two other sympatric species vulnerable to similar predators (Haff & Magrath, 2012).

Acoustic similarity to conspecific alarm calls can allow for mutual response in some sympatric species (e.g. Stefanski & Falls, 1972), but this is not always the case, as species may differ in recognition rules for conspecific alarms. Female mule deer, for example, respond to the distress calls of young white-tailed deer, *Odocoileus virginianus*, but not *vice versa* (Teichroeb *et al.*, 2013). Similarly, common starlings, *Sturnus vulgaris*, ignore the distress calls of herring gulls, *Larus argentatus*, and black headed gulls, *L. ridibundus*, as well as those of common lapwings, *Vanellus vanellus* (Aubin & Brémond, 1989), while those species do respond to starling distress calls (Aubin & Brémond, 1989; Brémond & Aubin, 1990; Aubin, 1991).

Table 3. Mechanisms for eavesdropping on heterospecific alarm calls

Mechanism	Alarm type	Eavesdropper	Caller	Evidence	Sources
Birds					
Acoustic similarity	Distress	Song sparrow *Melospiza melodia*	Swamp sparrow *Melospiza georgiana*	Conspecific similarity	1
	Distress	Swamp sparrow *Melospiza georgiana*	Song sparrow *Melospiza melodia*	Conspecific similarity	1
	Flee	Superb fairy-wren *Malurus cyaneus*	Splendid fairy-wren *Malurus splendens*	Allopatric	2
	Flee	Superb fairy-wren *Malurus cyaneus*	Variegated fairy-wren *Malurus lamberti*	Allopatric	2
	Flee	Superb fairy-wren *Malurus cyaneus*	White-winged fairy-wren *Malurus leucopterus*	Allopatric	2
	Mob	Apostlebird *Struthidea cinera*	Carolina wren *Thryothorus ludovicianus*	Allopatric	3
	Mob	Great tit *Parus major*	Black-capped chickadee *Poecile atricapillus*	Allopatric	4
	Mob	White-browed scrubwren *Sericornis frontalis*	Brown thornbill *Acanthiza pusilla*	Conspecific similarity, Temporal	5
	Nest[a]	Brown-headed cowbird *Molothrus ater*	Red-winged blackbird *Agelaius phoeniceus*	Cross-foster	6
	Synthetic	Apostlebird *Struthidea cinera*	Synthetic	Direct test	3
	Synthetic	Black-headed gull *Larus ridibundus*	Synthetic	Direct test	7
	Synthetic	Common starling *Sturno vulgaris*	Synthetic	Direct test	7 to 9
	Synthetic	Herring gull *Larus argentatus*	Synthetic	Direct test	7, 9
	Synthetic	Superb fairy-wren *Malurus cyaneus*	Synthetic	Direct test	10
	Synthetic	Northern lapwing *Vanellus vanellus*	Synthetic	Direct test	7
	Synthetic	Rook *Corvus frugilegus*	Synthetic	Direct test	7
	Synthetic	Song sparrow *Melospiza melodia*	Synthetic	Direct test	7
	Synthetic	Swamp sparrow *Melospiza georgiana*	Synthetic	Direct test	1
	Synthetic	White-throated sparrow *Zonotrichia albicollis*	Synthetic	Direct test	1
Frightening & attention capturing	Mobbing	Superb fairy-wren *Malurus cyaneus*	Noisy miner *Manoria melanocephala*	Allopatric	11
	Synthetic	Great-tailed grackles *Quiscalus mexicanus*	Synthetic	Direct test	12
Innate, species-specific	Nest[b]	Cuckoo, reed warbler host race *Cuculus canorus*	Reed warbler *Acrocephalus scirpaceus*	Cross-foster	13
Learned generalization	Synthetic	Superb fairy-wren *Malurus cyaneus*	Synthetic	Direct test	10
Learning	Flee	Superb fairy-wren *Malurus cyaneus*	Noisy miner *Manoria melanocephala*	Geographic	11
	Flee	Superb fairy-wren *Malurus cyaneus*	White-browed scrubwren *Sericornis frontalis*	Geographic	14
	Flee, Mob	White-browed scrubwren *Sericornis frontalis*	New Holland honeyeater *Phylidonyris novaehollandiae*	Temporal, Geographic	15
	Flee, mob	White-browed scrubwren *Sericornis frontalis*	Superb fairy-wren *Malurus cyaneus*	Temporal	15
	Mob	22 species across 3 communities	22 species across 3 communities	Geographic	16
	Unknown	Western grebe *Aechmophorus occidentalis*	Eared grebe *Podiceps nigricolli*	Cross-foster	17
Mammals					
Acoustic similarity	Distress	Common pipistrelle *Pipistrellus pipistrellus*	Nathusius's pipistrelle *Pipistrellus nathusii*	Conspecific similarity	18
	Distress	Common pipistrelle *Pipistrellus pipistrellus*	Soprano pipistrelle *Pipistrellus pygmaeus*	Conspecific similarity	18
	Distress	Mule deer *Odocoileus hemionus*	White-tailed deer *Odocoileus virginianus*	Conspecific similarity	19
	Distress	Nathusius's pipistrelle *Pipistrellus nathusii*	Common pipistrelle *Pipistrellus pipistrellus*	Conspecific similarity	18
	Distress	Nathusius's pipistrelle *Pipistrellus nathusii*	Soprano pipistrelle *Pipistrellus pygmaeus*	Conspecific similarity	18
	Distress	Soprano pipistrelle *Pipistrellus pygmaeus*	Common pipistrelle *Pipistrellus pipistrellus*	Conspecific similarity	18
	Distress	Soprano pipistrelle *Pipistrellus pygmaeus*	Major's long-fingered bat *Miniopterus majori*	Conspecific similarity	18

Table 3. Continued

Mechanism	Alarm type	Eavesdropper	Caller	Evidence	Sources
	Distress	Soprano pipistrelle *Pipistrellus pygmaeus*	Malagasy mouse-eared bat *Myotis goudoti*	Conspecific similarity	18
	Distress	Soprano pipistrelle *Pipistrellus pygmaeus*	Manavi long-fingered bat *Miniopterus manavi*	Conspecific similarity	18
	Distress	Soprano pipistrelle *Pipistrellus pygmaeus*	Nathusius's pipistrelle *Pipistrellus nathusii*	Conspecific similarity	18
	Distress	Soprano pipistrelle *Pipistrellus pygmaeus*	Peters's sheath-tailed bat *Emballonura atrata*	Conspecific similarity	18
	General	Yellow-bellied marmot *Marmota flaviventris*		Geographic	20
	Synthetic	Mule deer *Odocoileus hemionus*	Synthetic	Direct test	19
	Synthetic	Soprano pipistrelle *Pipistrellus pygmaeus*	Synthetic	Direct test	21
Learning	Flee, mob	Ringtailed lemur *Lemur catta*	Verreaux's sifaka *Propithecus verreauxi*	Geographic	22
	Mob	Bonnet macaque *Macaca radiata*	Hanuman langur *Semnopithecus entellus*	Geographic	23
	Mob	Bonnet macaque *Macaca radiata*	Nilgiri langur *Trachypithecus johnii*	Geographic	23
	Mob	Bonnet macaque *Macaca radiata*	Sambar deer *Cervus unicolor*	Geographic	23
	Mob	Diana monkey *Cercopithecus diana*	Chimpanzee *Pan troglodytes*	Geographic	24
	Mob	Vervet monkey *Chlorocebus pygerythrus*	Superb starling *Spreo superbus*	Temporal, Geographic	25
	Synthetic	Golden-mantled ground squirrel *Spermophilus lateralis*	Synthetic	Direct test	26

The evidence column presents six different types of evidence supporting mechanism type: allopatric = response without overlap in species ranges; conspecific similarity = alarm call acoustic structure similar to conspecific alarms; species sympatric; cross-foster = response tested after nestling birds raised in heterospecific nest; direct test = response to specific acoustic properties of alarm calls tested through playback of synthetic sounds; geographic = appropriate response only in locations where species overlap; temporal = appropriate response develops over time.

[a]These nestling blackbird alarm calls are given when a predator is near the nest, but the behaviour of adults is not described.

[b]These 'churr' alarms are given by parent reed warblers when a predator is near the nest, and cause nestling warblers to go silent.

Sources: 1, Stefanski & Falls (1972); 2, Fallow *et al.* (2011); 3, Johnson *et al.* (2003); 4, Randler (2012); 5, Haff & Magrath (2012); 6, Madden *et al.* (2005*a,b*); 7, Aubin (1991); 8, Aubin (1989); 9, Aubin & Brémond (1989); 10, Fallow *et al.* (2013); 11, Magrath & Bennett (2012); 12, Slaughter *et al.* (2013); 13, Davies *et al.* (2006); 14, Magrath *et al.* (2009*b*); 15, Haff & Magrath (2013); 16, Wheatcroft & Price (2013); 17, Buitron & Nuechterlein (1993); 18, Russ *et al.* (2004); 19, Teichroeb *et al.* (2013); 20, Blumstein & Armitage (1997); 21, Russ, Jones & Racey (2005); 22, Oda & Masataka (1996); 23, Ramakrishnan & Coss (2000); 24, Zuberbühler (2000*b*); 25, Hauser (1988); 26, Shriner (1999).

(*b*) *Frightening or attention-capturing sounds*

Some alarm calls may lend themselves to innate recognition by heterospecifics even without detailed acoustic similarity, if they contain characteristics that are inherently frightening or arousing. For example, mobbing alarm calls, distress calls or general alarms in response to terrestrial predators are often harsh, abrupt and broadband (Hirth & McCullough, 1977; Morton, 1977; Rendall, Owren & Ryan, 2009; Bradbury & Vehrencamp, 2011; Seiler *et al.*, 2013), and some alarm calls appear to have been selected to capture listener attention through inclusion of nonlinear features (Owings & Morton, 1998; Owren & Rendall, 2001; Rendall *et al.*, 2009). Nonlinear properties of alarm calls include aperiodic broadband vibrations (deterministic chaos) that make a call harsh or noisy, subharmonics, and abrupt onset or transitions (Fitch, Neubauer & Herzel, 2002). These features are partly uncontrollable because they result from the 'blow out' of caller sound production systems, and are therefore thought to be honest signals of fear or arousal (Fitch *et al.*, 2002; Riede, Owren & Arcadi, 2004; Blumstein & Chi, 2012). Because of the strong link between nonlinear call structure and fear or arousal, calls containing such properties are predicted to be generally evocative, and less prone to habituation (Fitch *et al.*, 2002; Blumstein *et al.*, 2008; Blumstein & Récapet, 2009; Blumstein, Davitian & Kaye, 2010; Townsend & Manser, 2011; Slaughter *et al.*, 2013; Karp *et al.*, 2014). The inclusion of nonlinear properties in conspecific alarm calls and synthetic sounds increases receiver response, demonstrating the potential effectiveness of these sounds in facilitating response to heterospecific alarm calls (Manser, 2001; Blumstein & Récapet, 2009; Haff & Magrath, 2010; Biedenweg *et al.*, 2011; Townsend & Manser, 2011; Slaughter *et al.*, 2013). Overall, therefore, it is probable that alarm calls containing nonlinearities will affect response by heterospecifics, at least by prompting attention.

(*c*) *Novelty*

Novelty alone might prompt wariness of other species' alarm calls. An innate fear of novel sounds would prompt individuals to respond to unfamiliar alarm calls upon first response. More importantly, such a response would be useful if combined with learning, such as habituation to calls that do not indicate threats, or associative learning of calls that do (Guilford & Dawkins, 1991). However, while neophobia to visual stimuli is well documented (Curio, Ernst & Vieth, 1978; Bomford & O'Brien, 1990; Hemmi & Merkle, 2009), there is no strong evidence that novelty alone affects response to unfamiliar sounds, including alarm calls (Rydén, 1978; Talling *et al.*, 1998; Johnson *et al.*, 2003; Blumstein & Récapet, 2009; Haff & Magrath, 2010; Biedenweg *et al.*, 2011). For example, nestling white-browed scrubwrens suppress calling to novel synthetic broadband calls, but not to novel synthetic tonal calls (Haff & Magrath, 2010); nestling great tits ignore parental 'seet' alarm calls slowed to half speed (Rydén, 1978); and apostlebirds ignore novel birdsong (Johnson *et al.*, 2003). Western grey kangaroos, *Macropus fuliginosus,* respond more strongly to playback of novel synthetic sounds with nonlinearities than to those without (Biedenweg *et al.*, 2011), suggesting that nonlinear properties of sounds, but not novelty alone, prompted alarm responses. Neophobia to acoustic stimuli may not be widespread because responding to every new sound with an alarm response could be costly by significantly reducing time available for other activities.

(*d*) *Innate species-specific response*

Close association with another species could lead to selection for an innate response to its alarm calls. The most likely example comes from the response of brood-parasitic common cuckoos, *Cuculus canorus*, to common reed warbler, *Acrocephalus scirpaceus*, alarm calls given near the nest (Table 3). The two species do not share a recent phylogenetic history, and cuckoos do not give alarm calls, yet nestling cuckoos parasitizing reed warblers suppress calling after hearing host alarm calls (Davies *et al.*, 2006). Furthermore, even 'warbler' cuckoo nestlings cross-fostered into other species' nests respond to playback of reed warbler alarms, suggesting that cuckoos have a neural template for recognizing reed warbler alarms. However, these cross-fostered cuckoos actually increase begging to warbler alarms, demonstrating that cuckoo nestlings also require experience with reed warbler alarm calls in the appropriate context to respond with call suppression (Davies *et al.*, 2006). More work is required to test for recognition of the calls of particular heterospecifics, and to elucidate how widespread it is within brood parasites and possibly in other contexts. Close association could also lead to deception and communication, not merely eavesdropping or exploitation, as discussed in Section VII.

(2) **Learned responses**

(*a*) *Diversity of alarm call structure*

Although acoustic structure alone can enable interspecific eavesdropping, there is substantial variation among alarm calls of different species, even for calls of similar meaning, which may limit the possibilities for innate responses. For example, the aerial alarm calls of species in the Australian bird superfamily Meliphagoidea range widely in mean frequency, frequency modulation and frequency sweeps (Rooke & Knight, 1977; Juresivic & Sanderson, 1994; Fallow *et al.*, 2011), there is great variation in aerial alarms among members of Sri Lankan mixed-species bird flocks (Goodale & Kotagama, 2005), and none of these aerial alarms have the classic 'seet' structure characteristic of European passerines (Marler,

1955). Further, there is substantial diversity in mobbing call structure in both North American and Himalayan passerines (Ficken & Popp, 1996; Wheatcroft & Price, 2013), and the high-urgency alarm calls of mammals such as ground squirrels, primates and meerkats can vary widely (Manser, 2001; Fichtel, 2008). Little is known about the reasons for diversity of alarm calls among species, but some alarm calls can be used in intra-specific social interactions, and this could select for divergence among species (Wheatcroft & Price, 2013). Overall, acoustic structure alone often does not provide information about call type or meaning (Seiler *et al.*, 2013), strongly suggesting that learning frequently plays an important role in facilitating heterospecific eavesdropping on alarm calls.

(b) Benefits of learning

There are several clear benefits of learning to eavesdrop on heterospecific alarm calls. Learning could enable response to a broader range of alarm calls than unlearned mechanisms alone, which is important considering the wide range of variation in alarm call structure across taxa (see above). Learning could allow individuals to keep abreast of changes in local community composition (Griffin, 2004), which can occur during events such as migration or shifts in species' ranges (Nocera & Ratcliffe, 2010). Further, learning could tailor responses specifically to sounds that reliably indicate danger relevant to the receiver (Seppänen & Forsman, 2007; Magrath, Pitcher & Gardner, 2009; Nocera & Ratcliffe, 2010), or could allow individuals to interpret the semantics of heterospecific alarm calls (Rainey *et al.*, 2004a; Fichtel, 2008; Lea *et al.*, 2008; Seiler *et al.*, 2013). For example, learning can help individuals discriminate between alarms and other calls that are acoustically similar but that do not indicate danger (Ghirlanda & Enquist, 2003; Magrath *et al.*, 2009b; Shettleworth, 2010; Magrath & Bennett, 2012; Seiler *et al.*, 2013). Despite its clear advantages, however, the evidence for learning to recognize alarm calls is so far primarily indirect.

(c) Geographic evidence for learning

Geographic patterns of interspecific eavesdropping suggest that individuals can learn to recognize heterospecific alarm calls (Table 3; Oda & Masataka, 1996; Ramakrishnan & Coss, 2000; Magrath *et al.*, 2009b; Magrath & Bennett, 2012; Haff & Magrath, 2013; Wheatcroft & Price, 2013). For example, bonnet macaques flee after playback of terrestrial alarm calls of Nilgiri langurs, *Trachypithecus johnii*, or Hanuman langurs, *Semnopithecus entellus*, only at locations where the heterospecific is common (Ramakrishnan & Coss, 2000). This suggests that macaques must learn to recognize langur alarm calls. Similarly, superb fairy-wrens respond to white-browed scrubwren alarms only at sites where the two species are sympatric (Magrath *et al.*,

2009b). In the Himalayas, entire community assemblages of birds at three sites respond more strongly to familiar heterospecific alarm calls, despite substantial divergence in call structure among species, than to unfamiliar alarm calls that are acoustically more similar to conspecific calls (Wheatcroft & Price, 2013).

Eavesdropping patterns at finer spatial scales help to rule out response through genetic adaptation. For example, Diana monkeys that live within the core home range of chimpanzees, *Pan troglodytes,* respond with their own leopard alarm calls to chimpanzee 'leopard' terrestrial alarms, whereas nearby monkeys that do not overlap with chimpanzee core home ranges do not (Zuberbühler, 2000b). This implies that experience is required to recognize chimpanzee alarm calls. Similarly, superb fairy-wrens respond to the aerial alarm calls of noisy miners only where their territories overlap with miner colonies, suggesting that fairy-wrens must learn about miner alarms (Magrath & Bennett, 2012). Thus, fine-scale geographic patterns of eavesdropping provide strong evidence that learning can be necessary to interpret the alarm calls of other species.

(d) Temporal evidence for learning

Learning involves a change in the behaviour of an individual as the result of experience, and so an appropriate response takes time to develop. By contrast, the rate of development for unlearned responses is independent of experience, and can occur on first exposure. This difference in response acquisition means that the relative speed and timing of development can indirectly test for learning (Hollén & Radford, 2009). Young animals have proved useful in testing this prediction, as they initially have little exposure to heterospecifics, and evidence suggests that young can learn to eavesdrop on heterospecific alarm calls (Hauser, 1988; Fichtel, 2008; Haff & Magrath, 2012, 2013). For example, 5-day-old nestling white-browed scrubwrens ignore sympatric superb fairy-wren and New Holland honeyeater, *Phylidonyris novaehollandiae,* mobbing calls, which are acoustically distinct from parental alarms, but do respond by the time they are 10 days old (Haff & Magrath, 2012). The temporal change in response is not simply due to hearing constraints, as young nestlings respond appropriately to conspecific mobbing calls, as well as the structurally similar mobbing alarms of brown thornbills (Haff & Magrath, 2012; Section IV.1a). These patterns suggest that exposure to fairy-wren and honeyeater alarm calls allows learning. Surprisingly, although learning about conspecific calls can occur very early on (Colombelli-Negrel *et al.*, 2012), tests of learning about heterospecific alarm calls using cross-fostering reveal little or no learning (Buitron & Nuechterlein, 1993; Davies, Madden & Butchart, 2004; Madden, Kilner & Davies, 2005), suggesting that young may require a parental 'demonstrator' to learn to recognize other species' alarms (Section IV.2e).

Correlations between the rate of response development and the magnitude of exposure to heterospecific alarm calls provide stronger evidence for learning than temporal changes alone. In a classic example, infant vervet monkeys develop adult-like responses to superb starling, *Lamprotornis superbus*, mobbing alarm calls more quickly on territories where starlings are common, suggesting that those young have more opportunities to learn about the alarms than young on territories where starlings are less abundant (Hauser, 1988). Similarly, fledgling white-browed scrubwrens develop a response to New Holland honeyeater aerial alarm calls more quickly on territories where the honeyeaters are more common. By contrast, fairy-wrens are common throughout the study site, and fledgling scrubwrens quickly and uniformly acquire an appropriate response to fairy-wren alarm calls (Haff & Magrath, 2013).

(*e*) *Mechanisms of learning*

One way that individuals could learn to eavesdrop is through personal experience, whereby individuals form direct associations between predators and heterospecific alarm signals (Shettleworth, 2010). Learning through direct experience can be advantageous because it avoids errors from copying the behaviour of others, and because it may be relatively easy to form direct associations between predators and other cues of danger (Hurd, 1996; Seppänen *et al.*, 2007; Kendal *et al.*, 2009; Rendell *et al.*, 2010). Learning about heterospecific alarm calls from personal experience can be risky, however, if it involves exposure to predators. Because of its inherent risks, direct learning may be most common in low-risk situations, such as predator mobbing (Caro, 2005), which combines predator presence with repetitive, easily locatable calls (Vieth *et al.*, 1980; Klump & Shalter, 1984; Hurd, 1996; Griffin, 2004; Goodale & Kotagama, 2006; Magrath *et al.*, 2009*b*; Nocera & Ratcliffe, 2010; Bradbury & Vehrencamp, 2011). Observational evidence suggests that young vervet monkeys learn to associate starling mobbing alarms directly with predators (Hauser, 1988). There has been only one experimental test of direct learning about unfamiliar alarm calls. Wild golden-mantled ground squirrels learned to associate a computer-generated alarm call with the presence of a model hawk gliding down a wire (Shriner, 1999). This response appeared to be independent of the behaviour of neighbouring squirrels.

A second way that individuals could learn to eavesdrop is by associating heterospecific alarms with the fearful responses of demonstrators. This is known as observational conditioning, and is a type of social learning (Griffin, 2004; Kendal *et al.*, 2009; Hoppitt & Laland, 2013). Social learning should be selected for when the cost of direct learning is high, as in situations involving direct encounters with predators (Griffin, 2004; Seppänen & Forsman, 2007; Kendal *et al.*, 2009; Rendell *et al.*, 2010; Hoppitt & Laland, 2013). Mobbing events

or other low-urgency situations that involve repetitive, conspicuous alarm calling from multiple callers probably provide easy opportunities for individuals to learn to pair unfamiliar calls with alarms and anti-predator behaviour from conspecifics or known heterospecifics (Curio *et al.*, 1978*a*; Galef & Laland, 2005; Nocera, Taylor & Ratcliffe, 2008; Davies & Welbergen, 2009; Wheatcroft & Price, 2013). Aerial or high-urgency alarm calls probably also offer opportunities for social learning, as intense demonstrator responses, such as fleeing to cover, can enhance social learning (Griffin, 2004). Indirect evidence from lemurs suggests that social learning is important in developing appropriate responses to heterospecific alarm calls (Fichtel, 2008). Young Verreaux's sifakas look towards parents before responding to playback of both general and aerial alarm calls of red-fronted lemurs, suggesting that young learn appropriate responses by watching adults. To our knowledge there have been no direct tests of social learning about heterospecific alarm calls.

Generalization from learned responses could also enable response to novel alarm calls (Ghirlanda & Enquist, 2003; ten Cate & Rowe, 2007; Getschow *et al.*, 2013). Such generalization could be from learned responses to either heterospecific or conspecific alarm calls. For example, superb fairy-wrens respond similarly at first exposure to unfamiliar alarm calls and to synthetic sounds that have similar peak frequencies to heterospecific calls, to which they have probably learned to respond (Fallow *et al.*, 2011, 2013). Generalization that simply prompts attention could also facilitate learning by causing individuals to attend to unfamiliar alarms, thus promoting reinforcement through experience (Fichtel, 2004; Wheatcroft & Price, 2013). Potentially, generalization from multiple learned alarms might explain the breadth of responses by some species to sounds that are intermediate between real alarms (Fallow *et al.*, 2013). Furthermore, peak shift, wherein individuals develop biases towards more extreme versions of signals that emphasize the aspect of the signal used for recognition (Ghirlanda & Enquist, 2003; ten Cate & Rowe, 2007; Shettleworth, 2010), could enable strong response to sounds with 'exaggerated' alarm-like features. Finally, some alarm calls might simply be easier to remember and thus learn about than others (Guilford & Dawkins, 1991), because they are similar to known alarms, or because they have evocative properties that are characteristic of alarm calls in general (Section IV.1).

V. CONSTRAINTS ON EAVESDROPPING

Eavesdropping on other species' alarm calls has a variety of potential benefits, as discussed in Section III, but there are also constraints on the reception and use of information. Here we consider limitations on

eavesdropping imposed by signal reception, recognition and value. Reception entails detecting and discriminating among different calls, which then need to be recognized as alarm calls. Once recognized, alarm calls will vary greatly in value depending on their relevance and reliability. Such limitations are important because they affect the flow of information and interactions among species, and so will affect information networks, and community function and structure, as discussed in Section VI.

(1) Reception and recognition in a noisy world

The basic constraint on communication and eavesdropping is that calls must be detected and discriminated from other signals and sounds, which in turn relies on sensory systems and neural processing (Dooling, 2004; Bradbury & Vehrencamp, 2011; Stephens, 2013). In the ecological context, acoustic signals attenuate and become degraded as they travel from sender to receiver, setting limits to the distance over which communication or eavesdropping can occur (the active space; Wiley & Richard, 1982; Slabbekoorn, 2004). Studies in the quiet of a laboratory can establish absolute hearing abilities, but in natural environments the ability to detect sounds will often be determined by the level of natural or anthropogenic background noise of similar acoustic frequency to that of the signal (Wiley & Richard, 1982; Brumm & Slabbekoorn, 2005). Noise of similar frequency masks the signal if it exceeds a critical ratio compared to the signal (Langemann & Klump, 2005), and can make it difficult perceptually to isolate meaningful sounds from a continuous auditory stream ('information masking': Hulse, 2002; Gutschalk, Micheyl & Oxenham, 2008). The issue of masking is of pressing interest because anthropogenic noise is a growing global problem (reviews: Barber, Crooks & Fristrup, 2010; Brumm, 2013; Morley, Jones & Radford, 2014).

The detection and discrimination of acoustic signals could be more difficult for heterospecific eavesdroppers than for an intended, conspecific receiver, although this has not yet been tested. (*i*) An eavesdropper will not benefit from species-specific perceptual adaptations for recognizing conspecific calls (Dooling, 2004), a problem that could be exacerbated for degraded or masked calls. (*ii*) Heterospecific calls could come from unpredictable species, directions and distances, rather than from a known location of within-group conspecifics, which could make reception more difficult. (*iii*) By definition eavesdroppers are not intended receivers of a signal, and so they do not benefit from calling that addresses an intended receiver, as occurs in communication. Senders often use orientation, location, timing and signal amplitude to maximize the chance that the call reaches the intended receiver (Brumm & Slabbekoorn, 2005; Dabelsteen, 2005; Yorzinski & Patricelli, 2010). In the case of alarm calls, individuals have limited choice about when and where to call, so at least some alarms

might be 'broadcast' rather than directed to specific receivers, and the magnitude of eavesdropper disadvantage could therefore be less than for some other signals. Despite the potential challenges of eavesdropping, and the likelihood that environmental noise affects alarm call reception (Barber *et al.*, 2010), there has been almost no study of the challenges of reception of alarm calls from heterospecifics compared to conspecifics, except to show that sparrowhawks, *Accipiter nisus*, have relatively poor hearing compared to great tits at the frequency of alarm calls given to hawks (Klump *et al.*, 1986). Furthermore, this sole example relates to predator–prey interactions, and not the challenges of eavesdropping among prey species.

In addition to constraints on the interception of heterospecific alarm calls, there could be limitations on their recognition. Several species show limited or no response to playback of the alarm calls of sympatric species (Table 2). This might be because they are of low value (see below), and so there is no selection to respond, but in other cases there could be constraints on recognition. Playbacks are usually directed to the potential eavesdropper, so that signal reception is unlikely to be a constraint unless hearing is sensitive to a different range of frequencies, but there could be variation in learning abilities among species. Species' learning abilities are often related to their ecological circumstances (Shettleworth, 2010), so that species can have biases towards learning about conspecific communication signals. This can be true of alarm calls (Rydén, 1980; Davies *et al.*, 2004; Endres, Widmann & Fendt, 2007), which can constrain learning about heterospecific alarm calls (Buitron & Nuechterlein, 1993; Davies *et al.*, 2004; Madden, Kilner & Davies, 2005; Madden *et al.*, 2005). More broadly, social species or other species with a repertoire of different alarm calls, might be better able to learn to recognize heterospecific calls (Lea *et al.*, 2008). However, the diversity of species that eavesdrop on other species includes solitary and even non-vocal species, providing no evidence of such a constraint (Lea *et al.*, 2008). Clearly the possibility of learning constraints needs to be tested further.

(2) Relevance and reliability of heterospecific alarm calls

(*a*) *Value of eavesdropping*

The value of eavesdropping on heterospecific alarm calls depends partly on the constraints of reception and availability of alternative information, but it also critically depends on the relevance and reliability of those alarm calls. A source of information has net value if its use leads to an increase in fitness (Dall *et al.*, 2005). An alarm call type is relevant if it is given to threats that endanger the eavesdropper (Magrath *et al.*, 2009*a*), and it is reliable if it is given when those threats are present but not when they are absent (Searcy & Nowicki,

2005). Relevance and reliability are related for heterospecific alarm calls, because from a listener's perspective alarm calls are increasingly unreliable with an increasing proportion that are given to predators that are not relevant to the eavesdropper, even if the alarms are relevant to the calling species. Relevance and reliability will affect learning, by changing the association between the call and danger, which thereby provides a mechanism to tailor responses to informative heterospecific alarm calls (Section IV). Here we consider the importance of call relevance and reliability in constraining information available to eavesdroppers, but treat deception – another source of unreliability – in Section VII.

(b) Relevance

Eavesdroppers face the problem of assessing the relevance of heterospecific alarm calls. While members of the same species – at least of similar age and sex – are vulnerable to the same suite of predators, and so their alarm calls are relevant, heterospecific alarm calls vary greatly in relevance. Alarm calls are relevant if the calling species shares all predators with the eavesdropping species, partly relevant if they share a subset of predators, and irrelevant if they are vulnerable to completely different predators. Furthermore, only a subset of alarm call types may be relevant, such as those indicating aerial rather than terrestrial predators for an arboreal animal (Rainey *et al.*, 2004*a*), and so an eavesdropper cannot simply classify all calls by one species as relevant. Ecological differences among species will therefore impose constraints on the value of eavesdropping on heterospecific alarm calls (Seppänen *et al.*, 2007; Goodale *et al.*, 2010).

The importance of alarm call relevance on eavesdropper response has rarely been tested, despite its plausibility, and there is strong evidence from only two species of birds. Yellow-casqued hornbills, which are vulnerable to eagles but not leopards, respond to playback of 'eagle' but not 'leopard' alarm calls given by Diana monkeys (Rainey *et al.*, 2004*a*). Furthermore, the hornbill's response is the same as to playback of the predators' own calls – they approach and call after eagle calls but ignore leopard calls. Black-casqued hornbills similarly respond to eagle but not leopard alarm calls by both Diana and Campbell's monkeys (Rainey *et al.*, 2004*b*). There is equivocal evidence from other species. New Holland honeyeaters usually flee to white-browed scrubwren but not superb fairy-wren aerial alarm calls, which from a honeyeater's perspective are less relevant. In total 52% of fairy-wren and 18% of scrubwren aerial alarms are to species that do not threaten honeyeaters (Magrath *et al.*, 2009*a*). However, most fairy-wren alarm calls are to aggressive species that threaten conspecifics and scrubwrens, so scrubwrens flee to fairy-wren calls, which from their perspective are almost always relevant. Similarly, consistent with their greater vulnerability

to leopards, impala are more likely than larger ungulates to respond to baboon alarm calls, given to both leopards and lions (Kitchen *et al.*, 2010). However, the greater response by impala might reflect a greater familiarity with baboon alarm calls, as impala at the study site associate more closely with baboons than do the larger species (Kitchen *et al.*, 2010).

(c) Reliability

One component of reliability is the probability of giving 'false alarms', which we define as the probability of giving an alarm call when there is no predator. Here we focus on 'mistaken' false alarms that appear not to entail active deception, which we consider in Section VII. Individuals usually respond to alarm calls of conspecifics despite the fact that false alarms can be quite common, presumably because the cost of ignoring alarm calls is higher than that of responding unnecessarily (review: Searcy & Nowicki, 2005). Nevertheless, playback experiments show that individuals could learn to identify unreliable conspecific individuals (Hare & Atkins, 2001; Blumstein, Verneyre & Daniel, 2004). There have been few tests of whether the probability of heterospecific false alarms affects eavesdropper response, aside from the related issue of call relevance (see above). Ashy-headed laughingthrushes tend to respond more strongly to racket-tailed drongo alarm calls than orange-billed babbler alarm calls, which are often given mistakenly to non-predators, but the difference is small and statistically non-significant (Goodale & Kotagama, 2005, 2008). Given that there will be selection for reliability – on average – within communication systems (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005), it seems probable that alarm call relevance will have a greater effect on heterospecific eavesdroppers than mistaken false alarms.

The second component of reliability is the probability of giving a detectable alarm call if a predator is present. This, in turn, will be affected by the probability of the signaller detecting and calling when a predator is present, and the probability of the eavesdropper detecting and identifying the signal (Goodale *et al.*, 2010). These attributes are likely to vary greatly among species, with highly vigilant species that give conspicuous alarm calls being the most reliable source of information (Goodale *et al.*, 2010). Ecological differences will contribute to predator detection; for example, birds that feed higher in vegetation or on flying insects are likely to be better at detecting approaching hawks than those feeding lower or gleaning prey off substrates, as discussed in Section III.3. Similarly, ecological and social differences are likely to contribute to communication about danger, with group-living species, and sometimes those with kin nearby, more likely to give calls if danger is detected (Section III.3).

VI. EAVESDROPPING NETWORKS AND COMMUNITY FUNCTION

Constraints on eavesdropping, including variation in the value of eavesdropping on different species, will affect the way that information flows among species, and so will affect 'information networks' and community structure (Holt, 2007; Seppänen *et al.*, 2007; Goodale *et al.*, 2010; Schmidt *et al.*, 2010). At one extreme, some species could produce information while others merely seek it, while at the other extreme all species might produce information in signals and seek information by eavesdropping. Understanding the role of species in an information network is important because it could affect species' ecology, including the benefits of group living, and community resilience. Eavesdropping on other species' calls could exacerbate the problem of false alarms, but using information from multiple callers, including those of different species, could increase the accuracy of information about danger. Finally, we consider the potential for social network analysis to enhance understanding of interspecific eavesdropping.

(1) Keystone information producers

Some species are particularly valuable sources of information for eavesdroppers. In the framework of social and ecological network theory, a species with links to many others can be a 'keystone' species with a disproportionate influence on community function (Flack *et al.*, 2006; Holt, 2007; Croft, James & Krause, 2008; Sih, Hanser & McHugh, 2009). Such links could include the flow of information from key species that produce information to those seeking it (Goodale *et al.*, 2010). As discussed in Section III.3, some species are better at detecting or communicating about danger, and so loss of these keystone species, and therefore the information available to eavesdroppers, could have serious ecological consequences. In addition to losing a species, the same principle applies if there is any disruption in information flow from keystone species, such as natural or anthropogenic noise masking their calls (Holt, 2007) or inciting them to change call structure or use (Read, Jones & Radford, 2014).

The ecological importance of keystone species for eavesdroppers is exemplified by mixed-species avian flocks. For example, experimental removal of tufted titmice, a common nuclear species of mixed flocks in North America that regularly gives alarm calls, leads to increased vigilance in downy woodpeckers and white-breasted nuthatches, *Sitta carolinensis*, and reduced condition and possibly reduced survival in the nuthatches (Dolby & Grubb, 1998). Nuthatches also visit exposed feeders less frequently when titmice are removed (Dolby & Grubb, 2000), showing that nuthatches take into account the presence of titmice when making foraging decisions, which could affect condition and survival. These effects on behaviour and condition are plausibly related to loss of information from eavesdropping, not simply to changes in group size, because downy woodpeckers increase vigilance and freeze after playback of aerial alarm calls of titmice, and then resume foraging after playback of their contact calls (Sullivan, 1984*a*). The nuthatches also probably respond to titmice alarm calls, as has been confirmed by playback of parid calls to a congener (Templeton & Greene, 2007). Experimental studies of other species confirm that eavesdropping on flock sentinel species can reduce vigilance, increase foraging success and even result in a change in foraging niche (Section III.2; Bell *et al.*, 2009; Ridley *et al.*, 2010, 2014; Radford *et al.*, 2011).

More broadly, eavesdroppers can gain information from sympatric species even if they do not form mixed-species groups, and again there are differences in which species produce and seek information. For example superb fairy-wrens, which feed on the ground, respond to the alarm calls of two species of highly vigilant honeyeaters that forage in trees and give conspicuous alarm calls (Magrath *et al.*, 2009*b*; Magrath & Bennett, 2012). Similarly, several honeyeater species appear to be 'community sentinels' because of their high vigilance and conspicuous alarm calls (Juresivic & Sanderson, 1994; Taylor & Paul, 2006). Overall, information gained from eavesdropping on heterospecifics could affect survival and population viability. Loss of keystone information producers, in particular, could have major effects on community function and structure.

(2) Information from multiple species

Eavesdroppers potentially have multiple sources of heterospecific information in any natural community, and their combined importance depends in part on whether alarm calls convey similar or complementary information. If different species produce similar information, then one species can substitute for another, which will minimize loss of information if one species is absent. However, this is not true if information is complementary. For example, saddle-back tamarins, *Saguinus fuscicollis*, form mixed-species groups with congeners, including moustached tamarins, *Saguinus mystax*. Saddle-backs occur lower in the forest strata and warn particularly of terrestrial predators, whereas congeners occur higher and warn of raptors (Heymann & Buchanan-Smith, 2000). Furthermore, both saddle-back and moustached tamarins respond to playback of the other's alarm calls (Kirchhof & Hammerschmidt, 2006), so that information is known to be a valuable resource. Therefore, loss of either species means a qualitative decline of information available to each species and any third-party eavesdroppers also vulnerable to eagles and terrestrial predators, such as other monkeys that can also join these groups (Heymann & Buchanan-Smith, 2000). Overall, community resilience is likely to be

affected by whether heterospecific information is redundant or complementary.

Although individuals may benefit from eavesdropping on multiple heterospecific species, they are also likely to face the problem of information unreliability. Multiple informant species could reduce the risk of predators going unnoticed, but exacerbate the problem of false alarms, because a single false alarm from an individual of any species might lead to 'information cascades' and mass flight (Giraldeau, Valone & Templeton, 2002; Sirot, 2006). One solution to this problem is to balance information from alarm calls – of conspecifics or heterospecifics – with alternative sources of information, such as from personal vigilance (Giraldeau *et al.*, 2002), or from other social cues, such as sentinel calls (Bell *et al.*, 2009). Another solution is to use a 'quorum' rule, by only responding if a threshold proportion of individuals give alarm calls (Wolf *et al.*, 2013). Both solutions reduce the probability of responses to false alarms, and the quorum rule, at least, can also increase the probability of correct detections (Wolf *et al.*, 2013). We are aware of no evidence that individuals use such rules when eavesdropping on heterospecifics, although they can do with conspecifics (Bell *et al.*, 2009). Quorum decisions seem possible in mixed-species bird flocks in Sri Lanka, because multiple species call when a predator is present (Goodale & Kotagama, 2005), but playback studies reveal no difference in response to single-species compared to multi-species alarm calls (Goodale & Kotagama, 2008). Overall, it is unclear how individuals manage the risk of false alarms from heterospecifics.

Eavesdroppers could potentially increase the relevance and reliability of total information by integrating overlapping information from the alarm calls of different calling species. Imagine an individual that eavesdrops on two common heterospecific species, one of which is primarily vulnerable to smaller predators than the eavesdropping species, and the other primarily to larger predators. Suppose that in each case 80% of calls by either heterospecific species are to predators that are too small or large to be a threat to the eavesdropping species, so that the information is usually irrelevant; from the perspective of the eavesdropper 80% are false alarms. The relevance and reliability of information is dramatically changed if the eavesdropper bases decisions on the combined calling of these species, rather than each species alone or in sum. If both call to a predator, then the predator is always a threat to the eavesdropper as well, while if one species calls, but not the other, then the predator is not a threat. The listener could therefore reduce 'false alarms' by integrating information from two different sources, although in this case it must also know that both species are present and always call to predators that are relevant to themselves. This idea has never been tested, but is plausible given that putty-nosed monkeys, *Cercopithecus nictitans*,

can use acoustic contextual cues to attribute an 'alarm' meaning to a call given in multiple contexts (Arnold & Zuberbühler, 2013). This contrasts with a 'quorum rule' which counts the number of individuals giving the same information, and the use of complementary information from heterospecifics, which is merely additive across species giving different information. Overall, there needs to be more work on the value of eavesdropping on multiple species.

(3) Social network analysis

Social network analysis promises new insights into information flow and eavesdropping. Social network theory is based around analyses of links – such as spatial associations or behavioural interactions – among individuals within species (Croft *et al.*, 2008), but this approach is also likely to be valuable when applied to information flow among individuals of different species (Aplin *et al.*, 2012; Farine, Garroway & Sheldon, 2012). The recent use of this approach has found differences among individuals in association with particular heterospecifics, just as there can be differences among individuals in behaviour in social systems within species (Farine *et al.*, 2012; Farine & Milburn, 2013). In some cases the strongest associations are between individuals of different species within mixed flocks (Farine & Milburn, 2013). Such associations might facilitate eavesdropping or communication, by allowing assessment of individual caller reliability, a key issue in information gathering. The net cost of association with heterospecifics also varies among individuals. Subordinate rather than dominant individuals of one species, for example, could benefit more from associating with another species over which they are dominant and therefore suffer a lower cost of competition (Farine *et al.*, 2012). This could change the net value of eavesdropping on others, by reducing the competition costs of acquiring information (Section III.3). This 'bottom-up' approach of using interactions between individuals has been important in understanding social systems within species, and will contribute to understanding social organization and information flow among species.

VII. DECEPTION AND COMMUNICATION

Eavesdropping by our definition involves individuals intercepting alarm calls intended for others, but eavesdropping can set the stage for the evolution of deliberate calling to the listener (Kostan, 2002). If the caller is unaffected by an eavesdropper's response, then there will be no selection for deliberate signalling. However if the caller benefits from the eavesdropper's response, there could be selection for calling directed to the listener, while if the caller suffers a cost then there could be selection to thwart eavesdropping (Dabelsteen,

2005). Eavesdropping could also have consequences for communication within species, if such communication enhances eavesdropping. We do not aim to cover the full range of potential evolutionary consequences here, but merely to illustrate a range of possibilities.

(1) Interspecific deception

Some species use alarm calls to deceive heterospecific eavesdroppers, and take advantage of their response to steal food (Munn, 1986; Møller, 1988; Goodale & Kotagama, 2005; Flower, 2011). For example, white-winged shrike-tanagers, *Lanio versicolor*, and bluish-slate antshrikes, *Thamnomanes schistogyns*, are 'sentinel' species in mixed-species Amazonian flocks. They are usually the first to spot danger from flying raptors, and give loud alarm calls to which other flock members respond. However, they also give alarm calls when no predator is present and they are competing to capture a flying insect, suggesting that deceptive calls are actively directed to the victim. These deceptive alarm calls are acoustically similar to alarm calls given when predators appear, and playbacks prompt similar anti-predator responses to true alarm calls given to predators (Munn, 1986). Similarly, fork-tailed drongos use deceptive alarm calls to steal food from both pied babblers and meerkats (Ridley & Raihani, 2007; Flower, 2011). These deceptive alarms are acoustically identical to true alarm calls and playbacks of either cause victims to abandon food and flee to cover (Flower, 2011). In addition to using false alarms specifically when following potential victims rather than when alone (Flower, 2011), drongos use false alarms strategically according to the intended target: they preferentially use them, rather than a simple aggressive attack, when targeting larger animals that could better defend their prey items (Flower & Gribble, 2012).

  Deception in general becomes less successful if used too frequently (Ruxton *et al.*, 2004), so that mimicry of multiple different alarm calls could increase the effectiveness of deception (Flower, 2011). Indeed, fork-tailed drongos mimic the alarm calls of heterospecifics, in addition to using their species-specific alarm calls, when stealing food from other species (Flower, 2011; Flower, Gribble & Ridley, 2014). These mimetic alarm calls are as effective as the alarm calls of the mimicked species in prompting victims to abandon food. In this case, drongos are exploiting the response of eavesdroppers to multiple species, and so reducing the frequency of deception by any specific alarm call type. Furthermore, merely imitating the victim's own alarm call can increase the success of stealing food, without necessarily exploiting heterospecific eavesdropping (Flower *et al.*, 2014). More generally, deceptive false alarm calls may be more successful than other potentially deceptive signals because of the high cost of not responding when a predator is present (Section V.2; Munn, 1986; Searcy & Nowicki, 2005). Indeed, even within-species false alarm calls – often apparently mistaken false alarms – can be as common as true alarms and yet still prompt a response by conspecifics (review: Searcy & Nowicki, 2005).

(2) Interspecific mutualism

Eavesdropping could evolve towards mutualism and active communication if both the listener and caller benefit (Kostan, 2002). The interactions between fork-tailed drongos and pied babblers suggest possible evolution towards mutualism. While drongos benefit by stealing some food by direct attack or giving occasional deceptive alarm calls (see above), it is possible that babblers gain a net benefit from drongo presence. Drongos spend little time on the ground and rarely give alarms to terrestrial predators when foraging alone, but commonly do so when following groups of pied babblers, thereby alerting babblers to relevant danger (Ridley & Raihani, 2007). Drongos also give sentinel calls, and babblers respond to these calls by foraging more in the open and spending less time vigilant, and as a result have a higher food intake (Radford *et al.*, 2011). Although alarm calls to terrestrial predators and sentinel calling by drongos may originally have arisen to create more kleptoparasitism opportunities, the resulting benefits to babblers could reduce selection for the evolution of defences against drongos (Ridley & Raihani, 2007; Radford *et al.*, 2011). Indeed, babblers in small groups are more tolerant than those in large groups to drongo presence, and more responsive to their calls, probably because their own sentinel system is less effective when they are in small groups (Ridley & Raihani, 2007). Overall, both parties appear to be active participants: drongos direct alarm calls to babblers and announce their presence when nearby, and babblers are facultatively tolerant of drongos according to their own group size. Further work is needed to determine the full costs and benefits for both parties, but the interaction is clearly not merely eavesdropping on calls intended for others.

  Alarm call acoustic structure or use might evolve to increase heterospecific response, which could represent manipulation of eavesdroppers or evolution of mutualism, depending on whether the listener also benefits. For example, although the structure of 'seet' aerial alarm calls in several bird species appears to have evolved at least partly to thwart eavesdropping by sparrowhawks (Marler, 1955; Klump *et al.*, 1986), structural similarity with sympatric species might have been selected to prompt unlearned responses by heterospecifics (Marler, 1957). Listeners benefit from being warned of danger, while callers would benefit if heterospecific prey are less likely to betray the presence of mixed-species flocks to predators, or mass flight reduces the caller's own risk. Such possibilities have not been tested, but mass flight of conspecifics can decrease a caller's risk (Sherman, 1985). Mobbing alarm calls

could also be selected to prompt listener response, and could also be of mutual benefit if they enhance collective monitoring and harassment of predators. Indeed, there is some evidence that mobbing could entail reciprocity among familiar but unrelated conspecifics or heterospecifics (Krams & Krama, 2002; Krams, Krama & Igaune, 2006*a,b*), and that mimicry of other species' mobbing calls could prompt a heterospecific response (review: Dalziell *et al.*, in press; Goodale, Ratnayake & Kotagama, 2014). For example, greenish warblers, *Phylloscopus trochiloides*, prompt more intense mobbing from buff-barred warblers, *P. pulcher*, by imitating that species' mobbing calls (Wheatcroft & Price, 2013). Given that most species in the community do respond to mobbing calls if they have had the opportunity to learn to recognize them, this is likely to be a case of mutualism rather than manipulation. Mutualism in this case occurs in a species-poor location, and so targeting individual species may be selected.

(3) Intraspecific communication

Surprisingly, communication within a species might evolve to facilitate heterospecific eavesdropping. First, parents might use vocal mimicry to 'teach' young to recognize heterospecific alarm calls (Oatley, 1970). In support of this possibility, parent Sri Lanka drongos, *Dicrurus paradiseus lophorhinus*, with young commonly imitate heterospecific alarm calls at the same time as predator sounds and conspecific alarm calls (Goodale, Ratnayake & Kotagama, 2014). This might allow young to associate heterospecific alarm calls with danger and so facilitate later eavesdropping. Second, acoustic similarity with conspecific alarm calls can prompt response to heterospecific alarm calls (Fallow *et al.*, 2013), so there could be evolutionary convergence of call structure towards that of heterospecifics. Given that recognition of conspecific alarm calls is often unlearned or learned very early (Section IV), this would facilitate eavesdropping on heterospecifics. Finally, signal design and use in conspecific communication will be under selection to be private if eavesdropper response imposes a cost on callers. Eavesdropping by predators does appear to affect the evolution of alarm call design (Marler, 1955; Klump *et al.*, 1986), but we are aware of no example showing that eavesdroppers at the same trophic level as the caller select for cryptic communication. These and other possible effects of eavesdropping on intraspecific communication remain to be tested.

VIII. CONCLUSIONS

(1) Eavesdropping on heterospecific alarm calls is widespread. Most examples include birds eavesdropping on birds, or mammals on mammals, but birds can eavesdrop on mammals, and mammals or lizards eavesdrop on birds. Eavesdroppers include social and solitary species, and those that give or lack alarm calls, but there has been no systematic study of the extent of eavesdropping in any community.

(2) Eavesdropping brings immediate, indirect and longer-term benefits. Individuals usually respond with anti-predator behaviour, such as becoming cryptic, fleeing to cover, increasing vigilance or mobbing the predator. These responses are similar to those prompted by conspecific alarm calls, and some species respond appropriately to different types of heterospecific alarm calls, such as those given to different predators. Eavesdropping can bring benefits greater than from conspecifics alone, such as more rapid detection of danger, better detection of specific predators, or detection of danger with reduced costs of competition. The ability to eavesdrop can also increase foraging success, provide spatial information on danger, and facilitate social learning about predators. There still remains the challenge of measuring changes in fitness as a consequence of eavesdropping.

(3) Response to heterospecific alarm calls can be unlearned or learned. Unlearned responses occur when heterospecific calls are acoustically similar to conspecific calls. This implies generalization from an innate or learned recognition template. Species-specific recognition might also evolve when there is a close association with another species, such as a brood parasite's host. Generic acoustic features, such as those associated with arousal or fear, might prompt appropriate responses to alarm calls as they can capture attention, but this has not yet been demonstrated for heterospecific alarms. Individuals often do not respond to playback of heterospecific alarm calls at times or in places where those species are absent, implying that recognition is often learned. The diversity of acoustic structure in alarm calls among species also implies that learning is essential for widespread recognition, yet there has been only one direct demonstration of learning.

(4) There are constraints on the reception, recognition and value of heterospecific alarm calls. There may be constraints on detection and discrimination in part because sensory systems can be tuned to conspecific signals, and because the alarm calls are not directed to the eavesdropper. Recognition is likely to be constrained by acoustic structure and opportunities for learning. Unlike conspecific alarm signals, heterospecific alarm calls vary greatly in relevance, in part depending on the whether the caller is vulnerable to the same predators as the eavesdropper. Heterospecifics also vary in the reliability with which predators are discriminated and detected, and alarm calls given. These constraints affect the value of eavesdropping on different species, and may be predictable based in part on species differences in foraging ecology and sociality.

(5) Constraints on eavesdropping affect information networks and community function. Some species,

particularly in mixed-species groups, appear to be 'keystone' information producers, from which other species seek information. Loss of such species could have a major effect on community function. Individuals can also eavesdrop on multiple species, which can provide similar or complementary information. It is likely that eavesdroppers integrate information from multiple sources, which could reduce the problem of 'false alarms' and provide more detailed information on danger. Social network analysis is now being applied to understand interactions among members of different species, and could be extended to quantify information flow. There are many opportunities for research on information networks and their effect on species' ecology.

(6) Eavesdropping presents the opportunity for the evolution of active deception or communication, if callers benefit from eavesdropper responses. Several species use alarm calls deceptively to enable them to steal food, and some even mimic heterospecific alarm calls, which can increase the effectiveness of such deception. There is some evidence of cooperative communication about danger, where one species produces alarm calls relevant to the listener. A net benefit to the eavesdropper might occur even in interactions also involving deception. Eavesdropping could even lead to changes in within-species communication. Adults might 'teach' young to recognize heterospecific alarm calls, or call structure could evolve to facilitate eavesdropping. Quantifying the costs and benefits of species interactions, and the role of heterospecific alarm calls, remains an exciting challenge.

IX. ACKNOWLEDGEMENTS

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