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Functionally referential alarm calls in noisy miners communicate about predator behaviour

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Many vertebrates have alarm calls that warn conspecifics about danger, and some species even communicate about the type of predator or its behaviour, allowing for appropriate responses. However, such 'functionally referential' communication has been shown experimentally in only a handful of species, and requires demonstrating that individuals give acoustically distinct calls to different threats, and that the calls alone are sufficient to prompt listeners to behave as if a specific threat is present. We carried out model presentations, acoustic analyses and a playback experiment to test whether the alarm calls of noisy miners, *Manorina melanocephala*, are functionally referential. Miners gave different calls to airborne raptor models compared to terrestrial or perched raptor models, and even switched from 'aerial' alarm calls to 'chur' alarm calls when a hawk glider landed on the ground. They also behaved differently to these two types of threats, showing avoidance to aerial threats, including fleeing or freezing, but deterrent behaviour to terrestrial threats, including vigilance, approach and mobbing. The two alarm call types were acoustically distinct, and consistent with calls to live predators. Blind scoring of video revealed that birds responded appropriately to playbacks of alarm calls alone, typically fleeing to aerial alarm calls yet becoming vigilant, approaching and calling to chur calls. Noisy miners produce alarm calls that therefore meet both criteria for functional reference, and thus become one of the few bird species in which such calls have been confirmed. Many birds appear to give different calls to airborne predators compared to during mobbing of terrestrial or stationary predators, so functionally referential alarms are likely to be common and may often categorize predators by their behaviour and not simply their taxonomic type.

Many birds and mammals give alarm calls that warn others of danger or deter predators (Caro, 2005). Alarm calls can be classified in a variety of ways, including by their sound (e.g. 'bark', 'croak, 'seet', 'whistle'), the context in which they are given (e.g. 'distress', 'general', 'eagle'), or the behaviour of the caller or responders (e.g. 'mobbing', 'flee'). Reflecting the diversity of labels, alarm calls vary greatly in acoustic properties and specific function (Klump & Shalter, 1984; Magrath, Haff, Fallow, & Radford, 2015; Zuberbühler, 2009). Some alarm calls are given in a wide range of circumstances, while others appear restricted to specific contexts. For example, white sifakas, *Propithecus verreauxi verreauxi*, and red-fronted lemurs, *Eulemur fulvus rufus*, both have aerial alarm calls given specifically to raptors, as well as general alarm calls that are given to terrestrial predators and in contexts of surprise or social conflict (Fichtel & Kappeler, 2002). Alarm calls given in specific contexts can convey graded information about a predator's proximity, size or the degree of danger it poses (e.g. Leavesley & Magrath, 2005; Templeton, Greene, & Davis, 2005), categorical information on the type of threat (e.g. Gill & Bierema, 2013), or both graded and categorical information (Manser, 2001; Manser, Bell, & Fletcher, 2001; Sieving, Hetrick, & Avery, 2010). We focus here on communication about the type of threat rather than graded information.

The alarm calls of some species refer to very specific types of threat, allowing appropriate responses by listeners. In perhaps the best known example, vervet monkeys, *Chlorocebus aethiops*, commonly give different alarm calls to leopards, eagles and snakes, allowing listeners to respond in an appropriate way, such as looking down after 'snake' alarms and looking up and fleeing to cover after 'eagle' alarms (Seyfarth, Cheney, & Marler, 1980a, 1980b). Such alarm calls appear to refer to specific external threats, and not simply the presence of a threat or the internal state of the caller, such as degree of fear. These calls were initially interpreted as

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allowing ‘referential’ or ‘semantic’ communication about the world. Such alarm calls are now usually considered to be ‘functionally referential’, which acknowledges that we can observe the use and response to calls, but not the cognitive processes that are implied in communication using symbolic signals (Evans, 1997; Macedonia & Evans, 1993). Some authors also question the concept of functional reference, in part because they challenge the idea that signals are designed to convey information (Rendall, Owren, & Ryan, 2009; Wheeler & Fischer, 2014), but for others information is a central issue in animal communication (Seyfarth et al., 2010); for a range of views, see Stegmann (2013). Overall, many researchers find the concept of functional reference useful, and particularly relevant in the context of alarm calls given to different predators (Gill & Bierema, 2013; Townsend & Manser, 2013).

Demonstrating functional reference requires considering both the production and perception of calls. A functionally referential alarm call must be given primarily to a specific class of threat, and the call itself must prompt responses by listeners that are similar to those prompted by the external threat itself (Macedonia & Evans, 1993). It follows that observational studies of natural interactions with predators cannot show functional reference, because apparent responses to alarm calls might instead rely on direct observation of the predator, the behaviour of the caller, or other contextual information. As a result, playback experiments are essential in isolating the information conveyed by the calls themselves, independent of the context (e.g. Seyfarth et al., 1980a; review: Evans, 1997). Functionally referential calls must therefore be both acoustically distinct, and perceived as distinct by listeners.

Surprisingly few studies have tested experimentally for functionally referential alarm calls, despite the long history of interest and observational studies suggesting they are common. Recent reviews list eight species of birds and seven species of mammals that show production and perception specificity (Gill & Bierema, 2013; Suzuki, 2016; Townsend & Manser, 2013), although smooth-billed anis, *Crotophaga ani*, and tamarins, *Saguinus fuscicollis* and *Saguinus mystax*, should also be added (Grieves, Logue, & Quinn, 2014; Kirchhof & Hammerschmidt, 2006). All these studies include playbacks to test response independent of context, and either observations or experiments to examine production specificity. For example, fowl, *Gallus gallus*, give acoustically distinct alarm calls to video images of raptors flying overhead compared to raccoons, *Procyon lotor*, on the ground, which are consistent with calls to natural predators, and playbacks prompt appropriate responses, such as moving to cover, crouching and looking upwards to aerial alarm calls, and standing erect and looking around after ‘terrestrial’ alarms (Evans, Evans, & Marler, 1993). Among mammals with evidence of functional reference, seven are primates (e.g. Seyfarth et al., 1980a; Zuberbühler, 2000), but both Gunnison's prairie dogs, *Cynomys gunnisoni* (Kiriazis & Slobodchikoff, 2006) and meerkats, *Suricata suricatta* (Manser, 2001; Manser et al., 2001) also produce distinct calls to different predators that prompt appropriate responses.

Studies of functionally referential alarm calls have almost exclusively focused on signalling about types of predator, but signalling about predator behaviour is also relevant to escape strategy. In the only study of its type, Griesser (2008) showed that the alarm calls of Siberian jays, *Perisoreus infaustus*, signalled about hawk behaviour. Calls given to perched, moving and attacking *Accipiter* hawks differed acoustically, and playbacks prompted appropriate responses. For example, playback of ‘perched hawk alarms’ prompted listeners to search for the threat, without taking cover, which is similar to the behaviour of birds mobbing a perched hawk, whereas playback of ‘attack calls’ led birds to flee immediately to cover, followed by search behaviour. Siberian jays therefore classify predators by their behaviour, not just predator type, which is relevant because appropriate responses depend on predator behaviour. In fact, avian alarm calls are often classified as ‘flee’ (or ‘warning’ or ‘aerial’) alarm calls or ‘mobbing’ alarm calls, suggesting that functionally referential alarm calls in birds, and some mammals, may often classify predators by current behaviour in addition to or instead of the type of predator.

We studied the alarm calls of noisy miners, *Manorina melanocephala*, a species with putatively distinct alarm calls that refer to different threats. ‘Chur’ calls appear to signal about potential terrestrial or perched predators posing little immediate threat, while ‘aerial’ alarm calls appear to warn primarily of raptors in flight (Higgins, Peter, & Steele, 2001). However, there have been no direct experimental contrasts of the context of production and acoustic structure of these calls, and playbacks have so far been limited to chur calls (Kennedy, Evans, & McDonald, 2009). We examined experimentally both the production and perception of these calls by wild birds to test for functional reference. To do so, we used predator models of perched and flying raptors to examine the context of production, compared the acoustic properties of calls, and carried out a playback experiment in which responses were scored blind to ensure our expectations did not influence results.

METHODS

Study Species

Noisy miners are medium-sized (ca. 60–70 g), highly social honeyeaters (family Meliphagidae) that breed in colonies made of loosely territorial groups (Dow, 1979). Parental care is cooperative, with the breeding female and several males provisioning individual broods (Dow & Whitmore, 1990; Pöldmaa, Montgomerie, & Boag, 1995). Miners are common in eastern Australia and typically live in habitat containing both open areas and trees, particularly eucalypts. They feed primarily on invertebrates and nectar, anywhere from the ground to the canopy (Ashley, Major, & Taylor, 2009). As a result of habitat preference, miners are common in human-altered habitats such as grazing land, urban parks and suburban gardens (Maron, 2007; Sewell & Catterall, 1998). They are aggressive to many species, including predators, and miners can exclude smaller species, particularly competitors for food, from their colonies (Dow, 1977; Piper & Catterall, 2003; Sewell & Catterall, 1998).

Noisy miners are aptly named, as they have a large repertoire of conspicuous vocalizations, including two alarm calls with a putatively distinct function (Holt, 2013). Chur alarm calls are given in the wild to potential predators that are on the ground, perched or being harassed by miners (Higgins et al., 2001; Holt, 2013). Targets include perched raptors, mammals, snakes and large lizards (Dow, 1975). These calls have been prompted experimentally by live dogs, *Canis familiaris*, and taxidermic models of foxes, *Vulpes vulpes*, and cats, *Felis catus* (Kennedy et al., 2009; Lowry, Lill, & Wong, 2012). Birds respond to playback of chur calls by approaching the speaker and often also repeating the calls, suggesting that these calls are mobbing alarm calls that alert others and incite them to harass threats (Kennedy et al., 2009). In contrast to chur calls, aerial alarm calls are given in the wild to flying raptors such as brown goshawks, *Accipiter fasciatus*, and collared sparrowhawks, *Accipiter cirrhocephalus*, which attack from the air, and have been prompted in the wild with model sparrowhawks (Magrath & Bennett, 2012) and model planes (Doohan, 2014). There has, however, been no experimental comparison of calls prompted by different threats. Furthermore, the function of aerial alarm calls has not been tested through playback experiments, except that superb fairy-wrens, *Malurus cyaneus*, flee to cover after playback of these calls (Magrath & Bennett, 2012), which is the same response fairy-wrens have to conspecific and other heterospecific aerial alarm calls that warn of flying predators (Magrath, Pitcher, & Gardner, 2007, 2009).