



Birds orient their heads appropriately in response to functionally referential alarm calls of heterospecifics

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Vertebrate alarm calls signal danger and often encode graded or categorical information about predator proximity or type. In addition to allowing communication with conspecifics, alarm calls are a valuable source of information for eavesdropping heterospecifics. However, although eavesdropping has been experimentally demonstrated in over 70 species, we know little about exactly what information eavesdroppers gain from heterospecific alarm calls. Here, we investigated whether Australian magpies, *Cracticus tibicen*, extract relevant information about the type of threat from functionally referential alarm calls given by noisy miners, *Manorina melanocephala*. Miner aerial alarm calls signal a predator in flight, whereas mobbing calls signal a terrestrial or perched predator. We therefore tested whether magpies gain information on the elevation of expected danger. We first confirmed, by measuring bill angles on video, that magpie head orientation changes appropriately with differences in the elevation of a conspicuous moving object. We then conducted a field experiment that measured magpie bill angle in response to playback of miner aerial and mobbing alarm calls. The maximum and mean bill angles were higher in response to aerial than to mobbing calls, suggesting that magpies use information from miner alarms to search visually at appropriate elevations for the specific type of danger. Magpies were also vigilant for longer after aerial alarm calls that followed mobbing calls, implying perception of an escalating threat level. Our work shows that individuals can gain information on the type or location of danger from heterospecific alarm calls, which is likely to increase the effectiveness of antipredator responses.

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Many mammal and bird species give alarm calls to warn others about detected predators (Caro, 2005; Hollén & Radford, 2009; Magrath, Haff, Fallow, & Radford, 2015; Zuberbühler, 2009). Alarm calls often not only signal the presence of danger but also encode additional information about the urgency or the type of threat. This information can be graded (Leavesley & Magrath, 2005; Templeton, Greene, & Davis, 2005) or categorical (Seyfarth, Cheney, & Marler, 1980a; Suzuki, 2016a); in some cases, graded information

can be included in calls also encoding categorical information (Manser, 2001; Sieving, Hetrick, & Avery, 2010). Functionally referential alarm calls, the focus of this paper, are those that are given to specific types of threat and that elicit appropriate responses by receivers (Gill & Bierema, 2013; Suzuki, 2016a; Townsend & Manser, 2013). The earliest experimental demonstration of referential calls came from vervet monkeys, *Chlorocebus aethiops*, which produce different alarm calls on detecting eagles, leopards and snakes, and to which receivers respond appropriately, such as fleeing to cover on hearing 'eagle' alarms and running into trees on hearing 'leopard' alarms (Seyfarth et al., 1980a, Seyfarth, Cheney, & Marler, 1980b). Convincing experimental evidence of functionally referential alarm calling now exists for about 20 species, including 10 bird species that produce and respond appropriately to distinct 'aerial' alarms for airborne predators compared to 'mobbing' alarms to terrestrial or perched predators

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(Cunningham & Magrath, 2017; Farrow, Doohan, & McDonald, 2017; Gill & Bierema, 2013; Grieves, Logue, & Quinn, 2014; Suzuki, 2016a).

In addition to responding to conspecific alarm calls, over 70 species have been experimentally shown to eavesdrop on the alarm calls of other vertebrates (Magrath, Haff, Fallow, et al., 2015). Among birds, many species respond to the acoustic warning signals given by other avian species (e.g. Bell, Radford, Rose, Wade, & Ridley, 2009; Magrath, Pitcher, & Gardner, 2007; Parejo, Avilés, & Rodríguez, 2012), and some even respond to mammalian alarm calls (Rainey, Zuberbühler, & Slater, 2004a, 2004b). However, in comparison to conspecific receivers, much less is known about what information heterospecifics extract from alarm calls (Magrath, Haff, Fallow, et al., 2015). In some cases, heterospecifics can gain graded information on the degree of a threat, such as superb fairy-wrens, *Malurus cyaneus*, and white-browed scrubwrens, *Sericornis frontalis*, which respond to urgency information encoded in each other's aerial alarm calls (Fallow & Magrath, 2010). In other cases, individuals can gain categorical information on the type of threat. For instance, black- and yellow-casqued hornbills, *Ceratogymna atrata* and *Ceratogymna elata*, approach and call after Diana monkey, *Cercopithecus diana*, 'eagle' but not 'leopard' alarm calls, which is appropriate because the hornbills are only threatened by eagles (Rainey et al., 2004a, 2004b). Similarly, Carolina chickadees, *Poecile carolinensis*, freeze and become silent in response to aerial alarm calls of tufted titmice, *Baeolophus bicolor*, but approach and call on hearing titmice mobbing calls (Hetrick & Sieving, 2012).

Most previous studies of responses to heterospecific alarm calls have focused on gross motor behaviour, such as fleeing (Magrath & Bennett, 2012), startle (Carlile, Peters, & Evans, 2006) or mobbing (Templeton et al., 2005), which in some cases could indicate the degree rather than the type of danger. However, more subtle reactions, such as changes in head orientation, can reveal whether eavesdroppers extract location information about danger from heterospecific alarm calls. The rationale is based on the orienting response, whereby animals are expected to move their heads to align their centres of acute vision with the direction from which they need to collect high-quality visual information (Sokolov, Nezlina, Polyanskii, & Evtikhin, 2002). Changes in head orientation in response to heterospecific alarm calls have been examined in primates (Kirchhof & Hammerschmidt, 2006; Seyfarth & Cheney, 1990). For example, saddleback and moustached tamarins, *Saguinus fuscicollis* and *Saguinus mystax*, faced upwards for longer when hearing heterospecific aerial alarm calls and faced downwards for longer when hearing heterospecific terrestrial calls (Kirchhof & Hammerschmidt, 2006). This difference in head orientation indicates that the monkeys gain information on the type of predator and so search at the appropriate elevation. Among birds, some heterospecifics respond to playback of 'jar' alarm calls of Japanese tits, *Parus minor*, given specifically to snakes, by pointing their bills towards the ground (Suzuki, 2016b). This is the same orienting response of Japanese great tits to their own 'jar' calls, suggesting that these heterospecifics might gain information on snake presence from the calls (Suzuki, 2016b), although the relevant information may also have been obtained by watching the response of the great tits that were present during playbacks. To the best of our knowledge, there has been no other study of avian head orientation in response to functionally referential alarm calls of heterospecifics, and none in which head orientation was quantified.

Head orientation of birds is not as simply related to the direction of visual attention as in primates but can still provide a useful indicator of search direction. Primates have forward-facing eyes, so that head orientation gives a strong indication of the direction of visual attention (Treves, 2000). However, the more lateral

placement of avian eyes makes studying the direction of visual attention more challenging, because the retinal centres of acute vision and visual attention often project laterally in birds (Davidson, Butler, Fernández-Juricic, Thornton, & Clayton, 2014; Fernández-Juricic, 2012). As a result, birds move their heads rapidly to align their centres of acute vision with objects of interest (Dawkins, 2002; Moore, Tyrrell, Pita, Bininda-Emonds, & Fernández-Juricic, 2017). None the less, changes in the head orientation of birds can be indicative of visual exploration and visual fixation behaviours (Butler, Hosinski, Lucas, & Fernández-Juricic, 2016; Dawkins, 1995; Fernández-Juricic et al., 2011), and a few avian studies have used qualitative scoring of head orientation to assess the response to conspecific alarm signals. On hearing an alarm call indicating a predatory threat overhead, domestic hens, *Gallus gallus domesticus*, rotated their heads, probably to make use of their lateral vision (Evans, Evans, & Marler, 1993). Three studies of passerines have shown that individuals point their bills in the expected direction of a threat. Japanese great tits perched in trees pointed their bills at the ground when hearing a call indicating a predatory snake, while they moved their heads horizontally in response to an alarm indicating an aerial predator (Suzuki, 2012). Australian magpies, *Cracticus tibicen*, on the ground responded to aerial alarms by pointing their bills more vertically compared to their response to generic alarm call and mixed alarm call presentations (Kaplan & Rogers, 2013). Finally, perched noisy miners, *Manorina melanoccephala*, spent most time with their bill upwards after playback of aerial alarm calls, but horizontally after playback of mobbing alarm calls (Farrow et al., 2017). However, there has been no quantitative scoring of head orientation in response to alarm calls.

We investigated the head orientation of wild Australian magpies in response to the functionally referential alarm calls of noisy miners. Magpies are vulnerable to a range of aerial and terrestrial predators and are large passerines that forage predominantly on the ground (Higgins, Peter, & Cowling, 2006; Kaplan, Johnson, Koboroff, & Rogers, 2009), making them ideal for playback experiments and video recording. Within our study site, magpie territories overlap with those of noisy miners, which are vulnerable to many of the same predators (see *Methods*) and which produce distinct, functionally referential aerial and mobbing alarm calls to appropriate predatory threats; miner aerial alarm calls signal a predator in flight, whereas mobbing calls signal a terrestrial or perched predator (Cunningham & Magrath, 2017; Farrow et al., 2017). We used two field experiments, combined with video analysis and blind scoring, in which we measured head orientation. First, to validate that magpies alter their head orientation to objects at different elevations, suggesting different visual search strategies, we quantified the angle of the bill relative to the horizontal when individuals were exposed to an object moving through the air or on the ground. Second, to examine the response of magpies to functionally referential heterospecific alarm calls, we quantified bill angle relative to the horizontal in response to playback of noisy miner aerial and mobbing alarm calls. If magpies can extract relevant information on the type of danger from these heterospecific vocalizations, we predicted that individuals would have higher bill angles in response to aerial than to mobbing alarm calls. This prediction follows from the higher bill angle shown by both miners and magpies when responding to conspecific aerial compared to mobbing calls (Farrow et al., 2017; Kaplan & Rogers, 2013).

METHODS

Study Site and Species

The study took place from February to April 2016 in Canberra (−35°28'S, 149°13'E), Australia. We collected data from four

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