

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

Francesca S. E. Dawson Pell ^{a,2}, Dominique A. Potvin ^{b,1}, Chaminda P. Ratnayake ^b, Esteban Fernández-Juricic ^c, Robert D. Magrath ^b, Andrew N. Radford ^{a,*}

^a School of Biological Sciences, University of Bristol, Bristol, U.K.

^b Division of Ecology & Evolution, Research School of Biology, Australian National University, Canberra, Australia

^c Department of Biological Sciences, Purdue University, West Lafayette, IN, U.S.A.

ARTICLE INFO

Article history:

Received 17 January 2018

Initial acceptance 12 February 2018

Final acceptance 28 March 2018

MS. number: 18-00047

Keywords:

alarm calls
communication
eavesdropping
functionally referential
information
predation
vigilance

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.

Crown Copyright © 2018 Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. All rights reserved.

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

* Correspondence: A.N. Radford, School of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, U.K.

E-mail address: andy.radford@bristol.ac.uk (A. N. Radford).

¹ Dominique A. Potvin is now at the School of Science and Engineering, University of the Sunshine Coast, Queensland, Australia.

² Francesca S.E. Dawson Pell is now at the Department of Animal and Plant Sciences, University of Sheffield, Sheffield, U.K.

(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

adjacent areas where Australian magpies and noisy miners were sympatric and accustomed to the presence of people: the Australian National University campus, Black Mountain Peninsula, Acton Peninsula and parks in Turner. All areas include native and exotic shrubs and trees, lawn and buildings, providing a combination of cover and open ground. Aerial and terrestrial predators are present throughout the study area. Aerial predators include brown goshawks, *Accipiter fasciatus*, collared sparrowhawks, *Accipiter cirrocephalus*, Australian hobbies, *Falco longipennis*, peregrine falcons, *Falco peregrinus*, and boobook owls, *Ninox novaeseelandiae* (Taylor, 1992), all of which include birds in their diet (Higgins, 1999) and are mobbed by both miners and magpies (Higgins, Peter, & Steele, 2001, 2006). Terrestrial predators include foxes, *Vulpes vulpes*, cats, *Felis catus*, dogs, *Canis lupus familiaris*, and snakes (Cunningham & Magrath, 2017).

Australian magpies are large endemic passerines (ca. 220–350 g), distributed throughout Australia (Higgins et al., 2006). They live in groups of varying size where there is a mix of open areas and trees (Brown, Farabaugh, & Veltman, 1988; Robinson, 1956). Noisy miners are medium-sized (ca. 60–70 g) colonial honeyeaters (Meliphagidae), distributed throughout eastern and southeastern Australia (Higgins et al., 2001). Colonies reside in distinct territories in open eucalypt woodland and urban areas (Higgins et al., 2001). Miners possess an extensive vocal repertoire that includes two distinct, functionally referential alarm calls (Cunningham & Magrath, 2017; Farrow et al., 2017; Holt, Barati, & McDonald, 2017). A broad-frequency ‘mobbing’ call is given to ground predators such as foxes, feral cats and perched large birds, while a high-

pitched ‘aerial’ alarm call is given to aerial predators in flight (Fig. 1).

Identification of Individual Magpies

As the study population of Australian magpies was unbanded, we identified individuals through a combination of age, sex, location and plumage variation. We used only adults in this study; juveniles can be distinguished from adults by their brown-tinged plumage, dark bill and dark iris (Higgins et al., 2006). Adult males have contrasting areas of black and pure white plumage, while the light plumage areas of adult females show gradients from white to grey feathers (Higgins et al., 2006). Groups defend permanent territories, so individuals are usually located in predictable areas (Brown et al., 1988; Robinson, 1956). The eight subspecies show large variation in various characteristics, including plumage patterns (Schodde & Mason, 1999). Canberra lies within a hybrid zone between white-backed and black-backed subspecies, leading to a range of plumage containing both pure and intermediate colour morphs (Burton & Martin, 1976). We therefore took photographs of the dorsal plumage of the birds, using a DMC-TZ60 Panasonic Lumix digital camera (Osaka, Japan), to facilitate reliable recognition of focal individuals.

We conducted two tests to assess our ability to identify correctly adult individuals of the same sex from their plumage. One test mimicked the field scenario of selecting a focal bird for an experimental trial from a group of individuals present at the same time. The researcher had to select which one of four photographs of different local birds contained the same individual shown in a different photograph of a focal bird. The second test mimicked the field scenario in which a decision was made about whether a bird was the correct subject for an experimental trial. The researcher had to decide whether a photograph of a single test bird of the same sex was the same individual as shown in a photograph of a focal bird. Different photographs were used if the focal bird was shown in both photographs (10 of 24 cases). We carried out these tests on both researchers (F.D.P., D.P.) responsible for recognition of magpies in the field. The two researchers both scored 12/12 (100%) in the first test and 24/24 (100%) and 22/24 (91.7%) in the second test, indicating reliable identification of individual birds.

Experimental Overview and General Methods

In this section, we give general field and video-analysis methods applicable to both experiments, and then follow with methods specific to each experiment.

Field methods

We lured focal adult magpies with grated cheese to an open, flat location with no immediate tree cover, and recorded their subsequent behaviour at the food source with two video cameras (Panasonic, HC-V770, Osaka, Japan) placed perpendicular to each other on the ground. We set the video cameras on tripods, 6 m horizontally from the cheese, and levelled them using the internal electronic system. The lens height was set at 26 cm above ground level, which we estimated as the average adult magpie eye height when standing. The similar height of the lens and magpie head was to reduce parallax error when measuring the vertical angle of the bill from video stills (below). We set the camera shutter speed to 1/2000 to capture sharp images, and the lens to about 4x optical zoom (the camera did not permit a fixed focal length). We used two video cameras for two reasons. First, if the view of a bird’s bill from one camera was obscured by grass or another bird, we could use video from the other camera. Second, if a bird was facing away from one camera, its bill would be visible from the other camera.

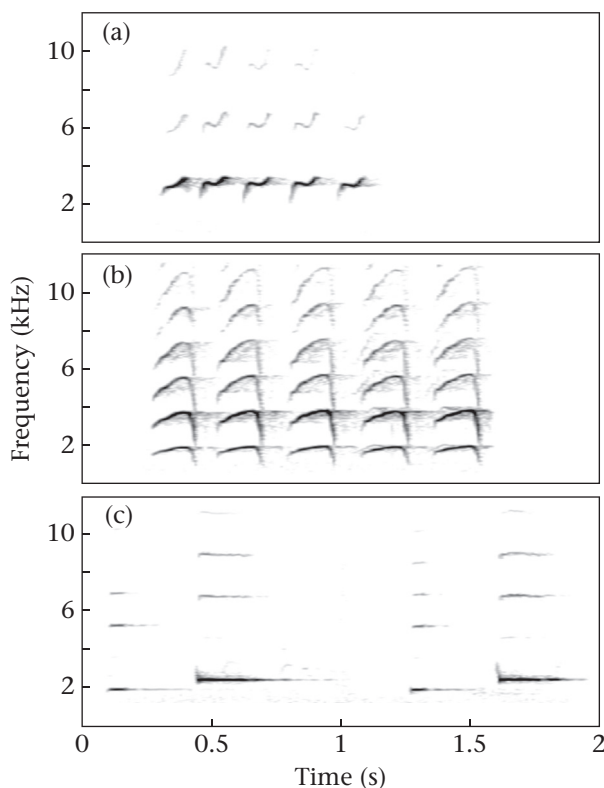


Figure 1. Spectrograms of examples of playbacks used in experiment 2. (a) Miner aerial alarm call, (b) miner mobbing alarm call and (c) rosella contact call, used as a control. Each magpie received a unique set of playbacks. Alarm call playbacks always had five elements, while rosella playbacks varied between four and eight elements because calls naturally varied in element duration and tempo. Spectrograms were prepared in Raven Pro 1.5, using a Blackman window function, size of 23.8 ms and 3 dB filter bandwidth of 68.9 Hz.

Experiments were based on a matched design, in which individual magpies received all treatments in an experiment during a single day. We conducted experiments on dry days with little wind, no overt disturbances (e.g. due to territorial disputes or human activities), and no nearby predators or noisy miners. We used identification photographs (above) to identify focal birds; one individual per location was tested. After setting up the equipment and attracting the magpie with cheese, we exposed the focal individual to the first treatment after a minimum of 1 min of normal foraging behaviour. Treatments were presented in a balanced order within each experiment. For each trial, we recorded group size and juvenile presence as potential confounding variables; birds were considered 'present' when within 5 m of the focal bird.

Video analysis

One researcher (C.R.) cut and temporally aligned video from the cameras in Adobe Premier Pro CC (Adobe Systems Software, Ireland), so that each trial had its own video file from each camera (in H.264 format). C.R. then gave files code names that did not include information about the treatment or individual and saved the video without the audio track. These de-identified videos were subsequently watched (50 fps, 1920 × 1080 pixels) using Adobe Media encoder, and scored blind by D.P. for experiment 1, and D.P. and F.D.P. for experiment 2.

We used bill angle as a proxy of head orientation. We estimated bill angle in the vertical plane from measurements of bill position in multiple frames from each video. For each frame in the analysis, we recorded x, y coordinates (in pixels) of the position of the tip and base of the bill using Tracker V.4.92 software (Fig. 2). Coordinates were measured every 200 ms to gain data on head orientation throughout the period of response. In the second experiment, we also measured additional frames in the first 3 s after the start of a playback, to gain a higher resolution of one sample each 100 ms. We calculated bill angle, measured as degrees above the horizontal, for each measured frame using the equation:

$$\text{bill angle(degrees)} = \arcsin((y_t - y_b)/\text{bill length}),$$

where y_t and y_b represent the y coordinates for bill tip and bill base, respectively.

We calculated bill length, in pixels, as the distance between the bill tip and bill base coordinates when the bill was side-on to the camera, where:

$$\text{bill length} = \sqrt{((x_t - x_b)^2 + (y_t - y_b)^2)}.$$

We also used this formula to measure the 'apparent' bill length in every frame, as a criterion for video selection (below). We did not

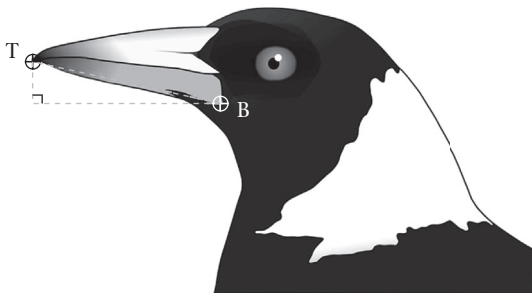


Figure 2. Measurement of bill angle. Tracker software was used to obtain x, y coordinates at the base (B, x_b, y_b) and tip (T, x_t, y_t) of the bill for every selected video frame during the magpie's response. Bill length was then calculated as the distance from B to T (the hypotenuse), using the formula $\sqrt{((x_t - x_b)^2 + (y_t - y_b)^2)}$ on a frame when the bill was side-on to the camera. Subsequently, the angle of the bill to horizontal (degrees) was calculated as $\arcsin((y_t - y_b)/\text{bill length})$. Image drawn by Branislav Ijic.

calibrate our measures to absolute lengths because we were interested in bill angle and not bill size.

After measuring bill position coordinates in videos from both cameras, we excluded videos that did not permit calculation of bill angle and chose the camera with the best view of the bill for use in analysis. Videos were discarded if (1) there was no side-on view to measure bill length in any frame, as that meant we could not calculate bill angle, or (2) the bird was obscured or facing away from the camera for all or most of the sample period, because we could not measure x, y coordinates. Next, if the videos from both cameras were suitable for analysis, we used two criteria to choose which provided the most reliable bill angles. (1) We chose the camera with the fewest 'missing' frames in which the bill's tip and base coordinates could not be measured. Missing measurements happened if a bird moved temporarily out of the frame or faced away from the camera, or if an object, such as grass or another bird, obscured either the bill's tip or base. (2) If both cameras had clear images of the bill, we chose the camera that had on average the most side-on view of the bill because this provided the clearest image of tip and base 'landmarks'. To do this, we chose the camera with the greatest mean 'apparent' bill length during the period of response, relative to the actual bill length (measured in a frame when it was side-on); apparent bill length is shorter if a bird faces further away from the camera.

Experiment 1: Head Orientation in Response to Objects at Different Elevations

In this experiment, we tested whether head orientation of Australian magpies (as measured by bill angle) was sensitive to an object moving at different elevations. Specifically, we used an underarm motion to roll an orange ball (diameter: 16 cm) along flat ground or to throw it into the air, so that it passed about 4 m in horizontal distance from the focal bird. The ball rolled smoothly about 15–20 m along the ground. The thrown ball travelled a similar horizontal distance and followed a trajectory with a maximum height of about 5 m, landing 5–10 m beyond the magpie. For a magpie 4 m away, and given an eye height of 26 cm, the centre of the ball would be about 1 degree below the horizontal when rolling along the ground; when thrown, it would be a maximum of about 50 degrees above the horizontal if its highest point was when closest to the magpie (the angle would be lower at all other times). A quiet vocal cue, captured on video camera, was given to indicate the start of the roll or throw. We alternated the order of treatments between focal individuals, and each bird received both treatments, with a minimum of 30 s of normal foraging between trials.

We carried out trials on 30 focal birds (15 of each sex) in different locations across the study area. Trials were repeated twice whenever possible (27 of 30 cases), and we used the first pair of trials where the bird did not run or fly away before the ball had landed or rolled past. In 25 cases, we were able to get clear video of responses to both treatments from the first or second set of trials. The measure of response was the maximum bill angle during each type of ball presentation. We used the maximum bill angle because the angular height of the thrown ball, and to a much lesser extent the rolled ball, changed over time.

Experiment 2: Response to Playback of Noisy Miner Alarm Calls

In this experiment, we tested whether Australian magpie head orientation (as measured by bill angle) differed when individuals were exposed to playback of aerial compared to mobbing noisy miner alarm calls. Such a difference in bill angle would suggest magpies are visually searching at different elevations for the source of threat indicated by information obtained from the miner alarm calls. The playback experiment had three treatments: miner aerial

alarm calls, miner mobbing alarm calls and, as a control, the contact calls of crimson rosellas, *Platycercus elegans* (Fig. 1). Rosellas are locally abundant, harmless parrots posing no threat to magpies. We chose rosella calls to ensure that the control was a neutral stimulus that did not imply threat of any kind, but that controlled for playback of a sudden call of the same amplitude as the alarm calls. Playbacks to other local species have shown that rosella contact calls ('bell' or 'piping' calls) do not provoke antipredator behaviour (e.g. Cunningham & Magrath, 2017; Leavesley & Magrath, 2005; Magrath et al., 2007, 2009).

We recorded all calls in or near the study sites, to avoid geographical variation affecting the response during playback experiments. We prompted noisy miner alarm calls with life-sized, gliding, model collared sparrowhawks (details in Magrath, Haff, McLachlan, & Ijic, 2015). Models were thrown by hand when approximately 10 m from the bird and directed so they glided past the bird about 5–10 m away, before landing on the ground. Noisy miners produce aerial alarms to hawk models when airborne, and switch to mobbing calls once they have landed (Cunningham & Magrath, 2017). We collected recordings throughout the study sites, with each recording separated by at least 100 m, to minimize the risk of getting repeated recordings from individual birds. Recordings were made by a second person, who was 5–15 m from the bird, using a Sennheiser ME66 directional microphone and a Marantz 670 or 661 digital recorder, sampling wave files at 44.1 kHz and 16 bits. We used 30 unique recordings of each alarm call type in the playback experiment, with 21 of each type recorded as part of this study, and the remaining nine of each type recorded in 2009 within the same area and using the same equipment and techniques (Magrath & Bennett, 2012). Crimson rosella contact calls were recorded in previous years, using similar equipment, from spontaneously calling birds.

We prepared audio files for playback from high-quality field recordings with no distinct background sounds and filtered to remove sound below 300 Hz. The playback experiment was fully replicated, with each focal bird receiving a unique set of playbacks. We used Raven Pro 1.5 software (<http://www.birds.cornell.edu/brp/raven/ravenversions.html>) to standardize alarm call playbacks so that all contained five elements given by a single bird, removing elements from longer calls or replicating elements from shorter calls if necessary; a five-element call lies within the natural range for both alarm call types (Cunningham & Magrath, 2017; Holt et al., 2017; Kennedy, Evans, & McDonald, 2009). We prepared and filtered rosella calls in a similar way and matched them by duration to alarm calls (playbacks therefore contained four to eight elements). We then adjusted all playbacks on computer so that they were broadcast at an amplitude of 63 ± 1 dB (mean amplitude of the loudest element) at 10 m, which was the distance of broadcast to magpies. To do this, sounds were broadcast from the equipment used in the playback experiment, re-recorded at 10 m using the field recording equipment set at a constant gain, and iteratively adjusted on computer to achieve the target amplitude. We broadcast sounds from a Roland R-05 digital recorder (Hamamatsu, Japan), via a Kemo Electronics integrated amplifier (20–25000 Hz, Geestland, Germany) to a full-range speaker (Scan Speak, Discovery 10F/4424G00, Videbæk, Denmark). We calibrated amplitude by recording a continuous tone and simultaneously measuring its amplitude at 10 m with a Brüel & Kjær 2240 sound-level meter. Playback at 63 dB was chosen to be clearly audible, yet equivalent to the amplitude of miners calling from about 20–30 m away, assuming mean amplitude at 10 m of aerial alarm calls of 73 dB and mobbing of 69 dB (Magrath & Bennett, 2012). We used short and relatively low-amplitude playbacks to mimic a nearby but not imminent threat, so magpies would be more likely to look for danger rather than flee, allowing measurement of bill angle.

We broadcast playbacks from the speaker at a height of 1 m, placed 10 m from the focal magpie. Miners can call from a variety of locations, from the ground to the treetops, but we kept the playback height and distance constant so that any differences in response must be due to playback type and not speaker location. Playback order was perfectly balanced, with each of the six possible orders of the three treatments presented five times during the experiment. Furthermore, only one individual was used as a focal individual in any one group. This design ensures that playback order and carryover effects do not confound responses to playback within or between individuals. We left at least 1 min of normal feeding between each playback. Once birds returned to normal feeding, they did not revert to further vigilance, and by keeping the interval short we could increase the chance of getting matched responses from individual birds while holding environmental conditions as similar as possible. Long intervals are likely to reduce any order effects, but at the cost of carrying out playbacks under potentially different conditions, such as how recently a natural predator was nearby. If a bird flew away or startled to one or more of the playbacks, it was not possible to measure bill angle for all treatments, and so we excluded that bird. In such cases, another focal bird, in a different location, received that playback set and order of playback. Similarly, once playbacks were completed successfully on a focal bird, we moved to a different location. Overall, we carried out playbacks on 39 individuals, of which nine were excluded, leaving the final sample of 30, with 15 of each sex.

We calculated four response variables from the blind scoring of video frames: (1) whether the bird responded to the playback or not; (2) the maximum bill angle (degrees) during the period of response; (3) the mean bill angle (degrees) during the period of response; and (4) the duration of response (s). A bird was scored as responding if it stopped feeding and became vigilant, during which it stood with its bill approximately horizontal or elevated; if it continued feeding, when the bill was typically pointed downwards to the food source, it was scored as not responding. The maximum bill angle was the same measure as used for experiment 1. The mean bill angle gives an estimate of the overall head orientation during each treatment. As described above, mean and maximum angles were calculated over all video samples for the duration of response (i.e. each 100 ms for the first 3 s, and each 200 ms thereafter). The duration is an estimate of the period over which birds searched visually and was timed from 200 ms after the initiation of playback until the bird ceased to be vigilant and resumed feeding or started another behaviour not specific to alarm calling, such as singing. We started the sample at 200 ms because, across all birds and treatments, there was never any evidence of response until that frame. Individual videos were excluded from analysis if the bird left the field of view before the response had ended. Occasionally, one camera had a better side view of the bird overall, and therefore was chosen for analysis (above), but had a few missing frames. In these cases, we substituted measures from the second camera if the missing frames happened when the bird briefly faced away from the best camera and so was side-on for the other camera. Example videos of all three experimental treatment are available as Supplementary Material.

Statistical Analysis

In both experiments, each individual received all treatments, so we used linear mixed models (LMMs) with focal individual as the random term. We conducted LMMs using the 'lmer' function in the 'lme4' package (Bates, Maechler, Bolker, & Walker, 2012) in R version 3.3.1 (R Development Core Team, 2016). We checked model assumptions and transformed data when necessary. The maximal model included treatment, treatment order and their interaction, as

well as the potential confounding effects of juvenile presence (yes/no), group size (1–4), sex and, for experiment 2, the identity of the researcher scoring the video. We achieved model simplification through stepwise backwards elimination (Crawley, 2005); terms were removed by order of least significance and comparisons of models were conducted using likelihood ratio tests. We obtained significance values for retained terms by comparing the minimal model with a model from which the term was removed. We individually returned terms removed during model selection to the minimal model to assess significance, and we present information on terms in the final model and those removed. Terms were considered significant at $P < 0.05$.

For experiment 1, we tested specifically the effect on bill angle of ball treatment (roll or throw), treatment order and their interaction. In experiment 2, there was little response to control playbacks, but universal response to both aerial and mobbing alarm calls (see Results), so we restricted LMMs to a comparison of alarm calls. We used separate LMMs for maximum bill angle, mean bill angle and log (response duration) to examine the effects of alarm call type, playback order and the interaction between playback type and order.

Ethical Note

All work was conducted with the approval of the Australian National University Ethics Committee (Protocol number: A2015/67) and was designed to minimize disturbance and stress. We minimized sample sizes by using matched experimental designs, to control for individual variation, and we distributed experiments over multiple separate sites. We used model predators to prompt alarm calls and thus never exposed birds to real threats. While birds responded with antipredator behaviour to the playback of alarm calls, individuals returned to apparently normal behaviour quickly; most returned to feeding in less than 30 s, and the few birds that flew off usually returned to feed within minutes.

RESULTS

In experiment 1, birds had a greater maximum bill angle when the ball was thrown through the air than when it was rolled along the ground (Table 1, Fig. 3), showing that head orientation was affected by the elevation of objects. The mean maximum bill angle when the ball was thrown through the air was about 29 degrees, which was 20 degrees higher than the mean maximum bill angle when the ball rolled along the ground. Maximum bill angle was not significantly affected by treatment order, the interaction between treatment order and treatment, or by juvenile presence, sex or group size (Table 1).

Table 1
Linear mixed model examining factors affecting maximum bill angle in experiment 1

	Fixed effect	df	Effect \pm SE	χ^2	P
Minimal model	(Intercept)		9.221 \pm 1.862		
	Treatment	1	20.442 \pm 2.512	39.740	<0.001
Dropped terms	Juvenile presence	1		0.083	0.773
	Sex	1		1.882	0.170
	Group size	1		0.188	0.665
	Treatment order	1		1.402	0.236
	Treatment*Order	1		0.172	0.679
Random term	Individual ID		7.812 \pm 2.795		

Significant term is indicated in bold. Effect sizes (\pm SE) for fixed effects were obtained from the minimal model; variance (\pm SD) given for the random term is in italics. $N = 25$ focal birds, each receiving both treatments.

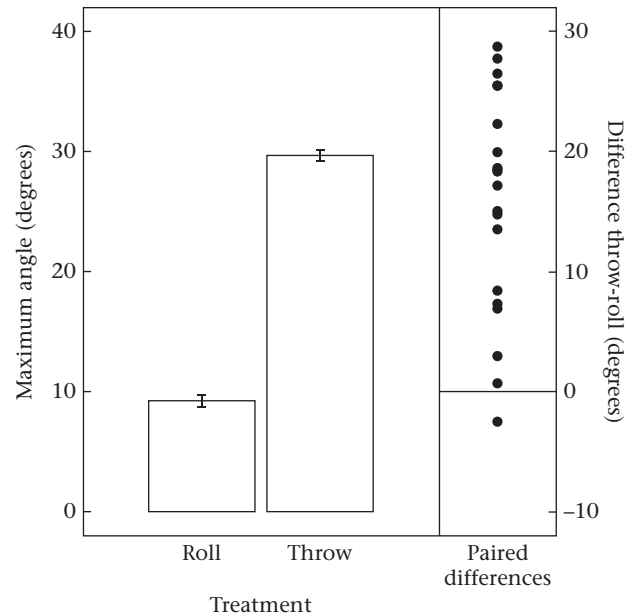


Figure 3. Maximum bill angle of a magpie when a ball was either rolled or thrown past. Columns show predicted means and 95% confidence limits for these means; scatterplot shows the difference in maximum bill angle according to treatment for each bird. $N = 25$ magpies with data from both treatments.

In experiment 2, birds rarely responded to control calls but always did so to miner alarm calls, and bill angles were higher in response to aerial than to mobbing alarm calls. All 30 magpies responded to the playback of both alarm calls, yet only seven did so to the control rosella contact calls (Cochran's Q test: $Q_2 = 46.0$, $P < 0.0001$), so we restricted subsequent analyses to the comparison of responses to aerial and mobbing alarm calls. Aerial alarm calls prompted a mean maximum bill angle of 31 degrees, which was 7 degrees higher than that to mobbing alarm calls (Table 2, Fig. 4a). Aerial alarm calls also prompted a greater mean bill angle of 21 degrees, which was 6 degrees greater than that to mobbing alarms (Table 2, Fig. 4b). There was no significant effect on maximum or mean bill angle of playback order, the interaction between playback type and order, juvenile presence, group size, sex or the identity of the video scorer (Table 2).

The duration of response to alarm call playback was significantly affected by the interaction between playback type and order of presentation (Table 2, Fig. 5). While the response duration to a mobbing call was not affected by whether it came before or after an aerial call, the response duration to an aerial call was greater if it followed a mobbing call compared to when it came before. Response duration was not significantly affected by juvenile presence, group size, sex or the identity of the video scorer (Table 2).

DISCUSSION

Australian magpies had higher maximum and mean bill angles, and at times longer responses, after playback of noisy miner aerial than mobbing alarm calls. Given the different head orientations that the birds displayed in response to these two alarms, they appeared to gain information about the specific type of threat indicated by those heterospecific alarm calls. While some studies have documented qualitatively appropriate head orientation responses of birds to different conspecific alarms (Evans et al., 1993; Farrow et al., 2017; Kaplan & Rogers, 2013; Suzuki, 2012), and possibly one heterospecific alarm (Suzuki, 2016b), our study

Table 2

Linear mixed models examining factors affecting maximum bill angle, mean bill angle and response duration (log transformed) in experiment 2

	Fixed effect	df	Effect \pm SE	χ^2	P
Maximum bill angle					
Minimal model	(Intercept)		17.636 \pm 2.937		
	Playback treatment	1	6.884 \pm 1.610	14.272	0.001
Dropped terms	Juvenile presence	1		3.342	0.068
	Sex	1		0.328	0.567
	Group size	1		3.418	0.064
	Playback order	1		0.624	0.430
	Scorer	1		0.377	0.539
	Playback treatment*Order	1		0.710	0.399
Random term	Individual ID		64.35 \pm 8.022		
Mean bill angle					
Minimal model	(Intercept)		8.816 \pm 2.843		
	Playback treatment	1	5.906 \pm 1.705	10.091	0.001
Dropped terms	Juvenile presence	1		0.873	0.350
	Sex	1		0.916	0.339
	Group size	1		0.136	0.713
	Playback order	1		1.323	0.250
	Scorer	1		1.123	0.289
	Playback treatment*Order	1		0.841	0.359
Random term	Individual ID		24.340 \pm 4.934		
Response duration					
Minimal model	(Intercept)		0.828 \pm 0.311		
	Playback treatment*Order	1	0.294 \pm 0.125	5.050	0.025
	Playback treatment	1		1.511	0.219
	Playback order	1		3.025	0.082
Dropped terms	Juvenile presence	1		2.342	0.126
	Sex	1		1.863	0.172
	Group size	1		1.020	0.313
	Scorer	1		0.397	0.529
Random term	Individual ID		0.002 \pm 0.048		

Significant terms are indicated in bold. Effect sizes (\pm SE) for fixed effects were obtained from the minimal model; variance (\pm SD) for the random term is in italics. $N = 30$ birds, each receiving all treatments.

provides the first quantitative evidence of eavesdropping on functionally referential heterospecific alarm calls.

Our playback experiment, combined with blind scoring of bill angles, indicated that magpies exhibited a different visual search strategy in response to miner aerial than mobbing alarm calls, which provides strong evidence for detailed understanding of another species' referential alarm calls. The differences in head orientation occurred despite the playback speaker being at a constant height, so call origin provided no cue about the elevation of the threat. Noisy miner aerial alarms indicate a threat from above, often a predatory bird in flight (Cunningham & Magrath, 2017; Farrow et al., 2017), so magpies adjusting their visual search to higher elevations may be more likely to detect the threat and thus make appropriate decisions about evasive action. The similar maximum bill angles found in response to the thrown ball (experiment 1) and the aerial alarm call playback (experiment 2) implies that the alarm call prompts searching well above the ground, given that the ball was up to 50 degrees above horizontal for the bird. Mobbing alarm calls indicate a terrestrial threat or a perched predator (Cunningham & Magrath, 2017; Farrow et al., 2017), so that the threat will usually be at a lower elevation than that indicated by aerial calls. Thus, adjusting the visual search strategy to lower elevations in response to mobbing calls could lead to more rapid detection of the predator. The higher bill angle in response to the mobbing calls (experiment 2) than to the ball rolling on the ground (experiment 1) is expected because mobbing calls could indicate a predator on or above the ground, whereas the ball rolling was unambiguously on the ground.

The differences in head orientation following eavesdropping on heterospecific aerial and mobbing calls are consistent with findings on conspecific communication, in which individuals responded to different types of alarm calls with appropriate changes in head

orientation (see above; Evans et al., 1993; Farrow et al., 2017; Kaplan & Rogers, 2013; Suzuki, 2012). Furthermore, changes in response to different alarm calls can increase the chance of detecting specific predators; Japanese great tits were more likely to detect snake-like objects after 'jar' alarm calls, given to snakes, than after 'chicka' alarm calls, given in other circumstances (Suzuki, 2018). Just as in such communication about predator type within species, one benefit of eavesdropping is gaining information on how best to detect and avoid a specific type of threat. Our conclusions would also hold if changing bill angle is in part a defensive posture, with the bill directed towards the expected origin of danger. This seems a possibility in Australian magpies, which are large, aggressive birds that use their bills in attacks on other species, including humans (Higgins et al., 2006; Jones, 2002). Birds have also been shown to engage in gaze following (Butler & Fernández-Juricic, 2014), so the orientation of the bill could be a cue to others about the source of risk. Indeed, Australian magpies appear to use their bills to point towards known danger (Kaplan, 2011), although the benefit of pointing seems limited if birds are responding solely to alarm calls and have not yet seen a threat.

The duration of vigilance to aerial and mobbing alarms was generally similar, except that response to an aerial alarm increased if it was played second. A greater response to aerial alarm calls might be expected given that they indicate more immediate danger (a fast-moving predator) than mobbing calls. The longer response when an aerial alarm call followed a mobbing call could be because the threat appears to have escalated. Conversely, if a mobbing alarm follows an aerial alarm, any threat may appear to have subsided, so that there is no increase in vigilance, despite the call also indicating that a predator remains in the vicinity. Another possibility is that a lower angle of searching visually in response to previous mobbing calls might not detect predators in flight,

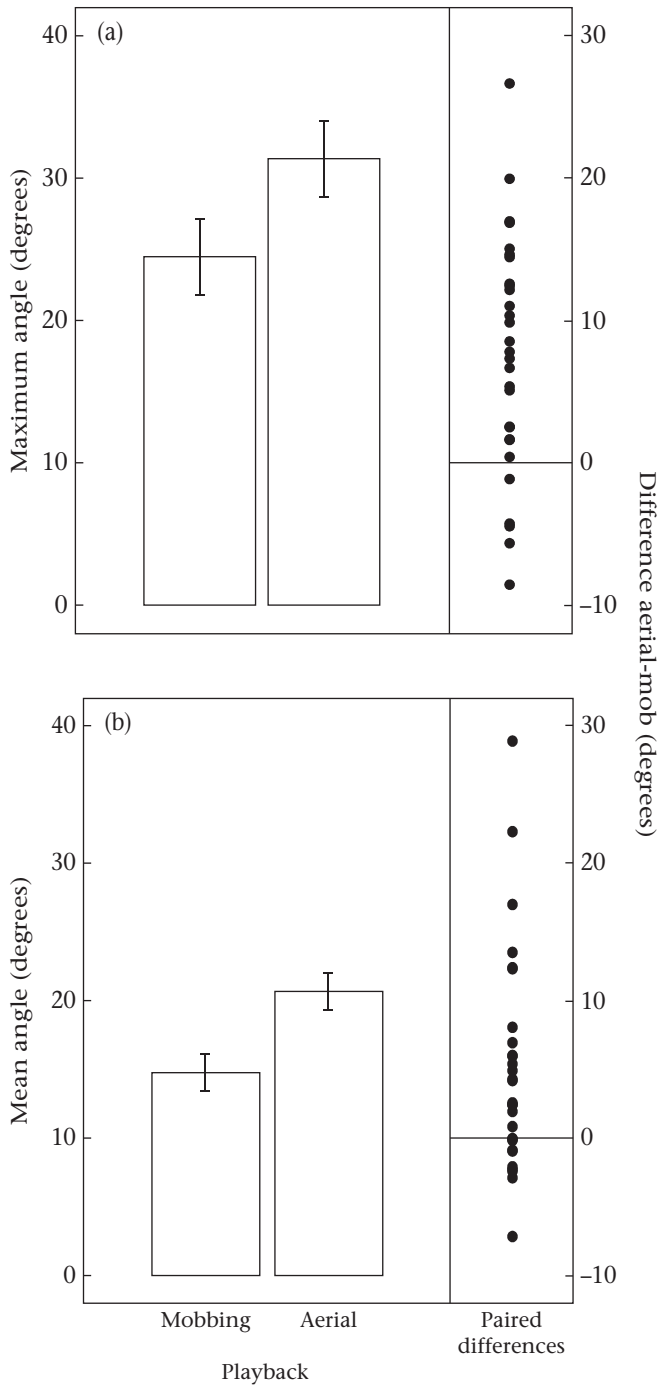


Figure 4. (a) Maximum and (b) mean bill angles of magpies in response to playback of noisy miner mobbing alarm calls and aerial alarm calls. Columns show predicted means and 95% confidence limits for these means; scatterplot shows the difference in bill angle according to treatment for each bird. $N = 30$ magpies with data from both treatments.

whereas a greater angle of searching visually to previous aerial alarms might also mean detection of predators at lower elevation. If so, prior searching area might affect current response. Whatever the specific explanation for Australian magpies, prior information about levels of risk is known to influence alarm call responses in other species: when information from pied babbler, *Turdoides bicolor*, sentinels suggested increased levels of risk, group members were more likely to flee to nearby cover in response to an

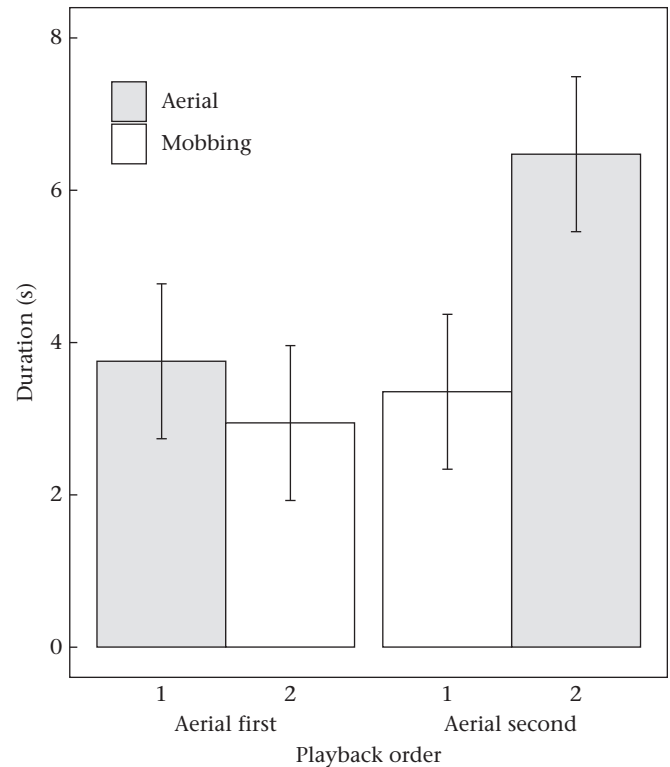


Figure 5. Duration of response according to playback order and whether the playback was a noisy miner mobbing alarm call or aerial alarm call. Columns show predicted means and 95% confidence intervals for these means; scatterplot shows the difference in bill angle according to treatment for each bird. $N = 30$ magpies in total, with 15 receiving each playback order.

alarm call than when a sentinel indicated lower levels of risk (Bell et al., 2009). In general, responses to current information are likely to be influenced by prior information, with that most recently acquired of most relevance.

Changes in avian head orientation provide an indication of general visual search directions, sufficient in our study when considering the signalling of threats that are most likely to be present at very different elevations. To associate changes in head orientation with more specific changes in gaze direction, it is necessary to know the position of the centres of acute vision (e.g. foveae) in the retina to project them into the visual space (Butler et al., 2016). This is important because of large interspecific variation in the position of the centres of acute vision in birds (Moore et al., 2012), even between closely related species (Moore, Pita, Tyrrell, & Fernández-Juricic, 2015). A recent study concluded that the centres of acute vision project on average to the frontolateral sides of the head (Moore et al., 2017). If we assume that the projection of the Australian magpie centres of acute vision falls into a similar range, changes in the vertical orientation of the eye will change the projection of the centres of acute vision. However, detailed visual studies are needed to specify gaze direction in this species; various additional approaches could be adopted in the future, including eye-tracking technology (Tyrrell, Butler, Yorzinski, & Fernández-Juricic, 2014), top-view videos of head movements in conjunction with anatomical estimates of the positioning of the retinal centre of acute vision (Butler, Templeton, & Fernández-Juricic, 2018), and cognitive tests (Suzuki, 2018).

Overall, we conclude that Australian magpies gain information on the type or location of predatory threat by eavesdropping on noisy miner alarm calls. Our quantitative work on head orientation

therefore supports and extends previous studies finding that eavesdropping on heterospecific alarm calls can provide valuable information on danger (review: Magrath, Haff, Fallow, et al., 2015). The ability to use specific information on danger by eavesdropping on heterospecific vocalizations is likely to be adaptive by complementing both personal information and information from conspecific alarm calls (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Magrath, Haff, Fallow, et al., 2015; Schmidt, Dall, & Van Gils, 2010; Seppänen, Forsman, Mönkkönen, & Thomson, 2007). Gathering information allows animals to reduce uncertainty and to choose appropriate responses to present conditions (Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Danchin, Giraldeau, Valone, & Wagner, 2004). Relying solely on personal information, gained through vigilance and other activities, is time consuming and reduces time for other activities (Danchin et al., 2004; Seppänen et al., 2007). Social information that arises from the cues and signals of others, including heterospecifics, can therefore be valuable (Danchin et al., 2004). Since heterospecifics usually constitute most of any given community and are not necessarily competitors, they have the potential to provide a wealth of information at little cost (Goodale et al., 2010; Seppänen et al., 2007). Individuals are likely to gain the greatest benefit when they respond to the detailed information from heterospecific alarm calls, as Australian magpies do to noisy miner alarms, rather than merely the presence or magnitude of a threat.

Acknowledgments

We thank Branislav Igic for compiling Fig. 2 and for comments on the manuscript; two anonymous referees also provided useful comments on the manuscript. The work was funded by the Research School of Biology and an Australian Research Council Discovery grant (DP150102632) awarded to R.D.M., A.N.R. and E.F.J.

Supplementary material

Supplementary material related to this article can be found at <https://doi.org/10.1016/j.anbehav.2018.04.010>

References

- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2012). *Linear mixed-effects models using Eigen and S4*. <https://cran.r-project.org/web/packages/lme4/index.html>. (Accessed 14 October 2016).
- Bell, M. B. V., Radford, A. N., Rose, R., Wade, H. M., & Ridley, A. R. (2009). The value of constant surveillance in a risky environment. *Proceedings of the Royal Society B: Biological Sciences*, 276, 2997–3005.
- Brown, E. D., Farabaugh, S. M., & Veltman, C. J. (1988). Song sharing in a group-living songbird, the Australian magpie, *Gymnorhina tibicen*. Part I. Vocal sharing within and among social groups. *Behaviour*, 104, 1–27.
- Burton, T., & Martin, A. A. (1976). Analysis of hybridization between black-backed and white-backed magpies in south-eastern Australia. *Emu*, 76, 30–36.
- Butler, S. R., & Fernández-Juricic, E. (2014). European starlings recognize the location of robotic conspecific attention. *Biology Letters*, 10, 20140665.
- Butler, S. R., Hosinski, E. C., Lucas, J. R., & Fernández-Juricic, E. (2016). Social birds copy each other's lateral scans while monitoring group mates with low-acuity vision. *Animal Behaviour*, 121, 21–31.
- Butler, S. R., Templeton, J. J., & Fernández-Juricic, E. (2018). How do birds look at their world? A novel avian visual fixation strategy. *Behavioral Ecology and Sociobiology*, 72, 38.
- Carlile, P. A., Peters, R. A., & Evans, C. S. (2006). Detection of a looming stimulus by the Jacky dragon: Selective sensitivity to characteristics of an aerial predator. *Animal Behaviour*, 72, 553–562.
- Caro, T. (2005). *Antipredator defenses in birds and mammals*. Chicago, IL: University of Chicago Press.
- Crawley, M. J. (2005). *Statistics: An introduction using R*. Chichester, U.K.: Wiley.
- Cunningham, S., & Magrath, R. D. (2017). Functionally referential alarm calls in noisy miners communicate about predator behaviour. *Animal Behaviour*, 129, 171–179.
- Dall, S. R. X., Giraldeau, L.-A., Olsson, O., McNamara, J. M., & Stephens, D. W. (2005). Information and its use by animals in evolutionary ecology. *Trends in Ecology & Evolution*, 20, 187–193.
- Danchin, É., Giraldeau, L.-A., Valone, T. J., & Wagner, R. H. (2004). Public information: From nosy neighbors to cultural evolution. *Science*, 305, 487–491.
- Davidson, G. L., Butler, S., Fernández-Juricic, E., Thornton, A., & Clayton, N. S. (2014). Gaze sensitivity: Function and mechanisms from sensory and cognitive perspectives. *Animal Behaviour*, 87, 3–15.
- Dawkins, M. S. (1995). How do hens view other hens? The use of lateral and binocular visual fields in social recognition. *Behaviour*, 132, 591–606.
- Dawkins, M. S. (2002). What are birds looking at? Head movements and eye use in chickens. *Animal Behaviour*, 63, 991–998.
- Evans, C. S., Evans, L., & Marler, P. (1993). On the meaning of alarm calls: Functional reference in an avian vocal system. *Animal Behaviour*, 46, 23–38.
- Fallow, P. M., & Magrath, R. D. (2010). Eavesdropping on other species: Mutual interspecific understanding of urgency information in avian alarm calls. *Animal Behaviour*, 79, 411–417.
- Farrow, L. F., Doohan, S. J., & McDonald, P. G. (2017). Alarm calls of a cooperative bird are referential and elicit context-specific antipredator behavior. *Behavioral Ecology*, 28, 724–731.
- Fernández-Juricic, E. (2012). Sensory basis of vigilance behavior in birds: Synthesis and future prospects. *Behavioural Processes*, 89, 143–152.
- Fernández-Juricic, E., Gall, M. D., Dolan, T., O'Rourke, C., Thomas, S., & Lynch, J. R. (2011). Visual systems and vigilance behaviour of two ground-foraging avian prey species: White-crowned sparrows and California towhees. *Animal Behaviour*, 81, 705–713.
- Gill, S. A., & Bierema, A. M. K. (2013). On the meaning of alarm calls: A review of functional reference in avian alarm calling. *Ethology*, 119, 449–461.
- Goodale, E., Beauchamp, G., Magrath, R. D., Nieh, J. C., & Ruxton, G. D. (2010). Interspecific information transfer influences animal community structure. *Trends in Ecology & Evolution*, 25, 354–361.
- Grieves, L. A., Logue, D. M., & Quinn, J. S. (2014). Joint-nesting smooth-billed anis, *Crotophaga ani*, use a functionally referential alarm call system. *Animal Behaviour*, 89, 215–221.
- Hetrick, S. A., & Sieving, K. E. (2012). Antipredator calls of tufted titmice and interspecific transfer of encoded threat information. *Behavioral Ecology*, 23, 83–92.
- Higgins, P. J. (1999). *Handbook of Australian, New Zealand and Antarctic birds*. Melbourne, Australia: Oxford University Press.
- Higgins, P. J., Peter, J. M., & Cowling, S. J. (2006). *Handbook of Australian, New Zealand and Antarctic Birds*. Melbourne, Australia: Oxford University Press.
- Higgins, P. J., Peter, J. M., & Steele, W. K. (2001). *Handbook of Australian, New Zealand and Antarctic Birds*. Melbourne, Australia: Oxford University Press.
- Hollén, L. I., & Radford, A. N. (2009). The development of alarm call behaviour in mammals and birds. *Animal Behaviour*, 78, 791–800.
- Holt, J., Barati, A., & McDonald, P. G. (2017). The complex acoustic repertoire of a highly social species, the noisy miner, *Manorina melanocephala*. *Emu*, 117, 19–30.
- Jones, D. (2002). *Magpie alert: Learning to live with a wild neighbour*. Kensington, Australia: UNSW Press.
- Kaplan, G. (2011). Pointing gesture in a bird—merely instrumental or a cognitively complex behavior? *Current Zoology*, 57, 453–467.
- Kaplan, G., Johnson, G., Koboroff, A., & Rogers, L. J. (2009). Alarm calls of the Australian magpie (*Gymnorhina tibicen*): Predators elicit complex vocal responses and mobbing behaviour. *Open Ornithology Journal*, 2, 7–16.
- Kaplan, G., & Rogers, L. J. (2013). Stability of referential signalling across time and locations: Testing alarm calls of Australian magpies (*Gymnorhina tibicen*) in urban and rural Australia and in Fiji. *PeerJ*, 1, e112.
- Kennedy, R. A. W., Evans, C. S., & McDonald, P. G. (2009). Individual distinctiveness in the mobbing call of a cooperative bird, the noisy miner *Manorina melanocephala*. *Journal of Avian Biology*, 40, 481–490.
- Kirchhof, J., & Hammerschmidt, K. (2006). Functionally referential alarm calls in tamarins (*Saguinus fuscicollis* and *Saguinus mystax*)—evidence from playback experiments. *Ethology*, 112, 346–354.
- Leavesley, A. J., & Magrath, R. D. (2005). Communicating about danger: Urgency alarm calling in a bird. *Animal Behaviour*, 70, 365–373.
- Magrath, R. D., & Bennett, T. H. (2012). A micro-geography of fear: Learning to eavesdrop on alarm calls of neighbouring heterospecifics. *Proceedings of the Royal Society B: Biological Sciences*, 279, 902–909.
- Magrath, R. D., Haff, T. M., Fallow, P. M., & Radford, A. N. (2015). Eavesdropping on heterospecific alarm calls: From mechanisms to consequences. *Biological Reviews*, 90, 560–586.
- Magrath, R. D., Haff, T. M., McLachlan, J. R., & Igic, B. (2015). Wild birds learn to eavesdrop on heterospecific alarm calls. *Current Biology*, 25, 2047–2050.
- Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2007). A mutual understanding? Interspecific responses by birds to each other's aerial alarm calls. *Behavioral Ecology*, 18, 944–951.
- Magrath, R. D., Pitcher, B. J., & Gardner, J. L. (2009). An avian eavesdropping network: Alarm signal reliability and heterospecific response. *Behavioral Ecology*, 20, 745–752.
- Manser, M. B. (2001). The acoustic structure of suricates' alarm calls varies with predator type and the level of response urgency. *Proceedings of the Royal Society B: Biological Sciences*, 268, 2315–2324.
- Moore, B. A., Baumhardt, P., Doppler, M., Randolet, J., Blackwell, B. F., DeVault, T. L., et al. (2012). Oblique color vision in an open-habitat bird: Spectral sensitivity,

- photoreceptor distribution and behavioral implications. *Journal of Experimental Biology*, 215, 3442–3452.
- Moore, B. A., Pita, D., Tyrrell, L. P., & Fernández-Juricic, E. (2015). Vision in avian emberizid foragers: Maximizing both binocular vision and fronto-lateral visual acuity. *Journal of Experimental Biology*, 218, 1347–1358.
- Moore, B. A., Tyrrell, L. P., Pita, D., Bininda-Emonds, O. R. P., & Fernández-Juricic, E. (2017). Does retinal configuration make the head and eyes of foveate birds move? *Scientific Reports*, 7, 38406.
- Parejo, D., Avilés, J. M., & Rodríguez, J. (2012). Alarm calls modulate the spatial structure of a breeding owl community. *Proceedings of the Royal Society B: Biological Sciences*, 279, 2135–2141.
- Rainey, H., Zuberbühler, K., & Slater, P. (2004a). The responses of black-casqued hornbills to predator vocalisations and primate alarm calls. *Behaviour*, 141, 1263–1277.
- Rainey, H. J., Zuberbühler, K., & Slater, P. J. B. (2004b). Hornbills can distinguish between primate alarm calls. *Proceedings of the Royal Society B: Biological Sciences*, 271, 755–759.
- Robinson, A. (1956). The annual reproductive cycle of the magpie, *Gymnorhina dorsalis* Campbell, in south-western Australia. *Emu*, 56, 233–336.
- Schmidt, K. A., Dall, S. R. X., & Van Gils, J. A. (2010). The ecology of information: An overview on the ecological significance of making informed decisions. *Oikos*, 119, 304–316.
- Schodde, R., & Mason, I. J. (1999). *The directory of Australian birds: Passerines*. Canberra, Australia: CSIRO Publishing.
- Seppänen, J.-T., Forsman, J. T., Mönkkönen, M., & Thomson, R. L. (2007). Social information use is a process across time, space and ecology, reaching hetero-specifics. *Ecology*, 88, 1622–1633.
- Seyfarth, R., & Cheney, D. (1990). The assessment by vervet monkeys of their own and another species' alarm calls. *Animal Behaviour*, 40, 754–764.
- Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980a). Monkey responses to three different alarm calls: Evidence of predator classification and semantic communication. *Science*, 210, 801–803.
- Seyfarth, R. M., Cheney, D. L., & Marler, P. (1980b). Vervet monkey alarm calls: Semantic communication in a free-ranging primate. *Animal Behaviour*, 28, 1070–1094.
- Sieving, K. E., Hetrick, S. A., & Avery, M. L. (2010). The versatility of graded acoustic measures in classification of predation threats by the tufted titmouse *Baeolophus bicolor*: Exploring a mixed framework for threat communication. *Oikos*, 119, 264–276.
- Sokolov, E. N., Nezlina, N. I., Polyanskii, V. B., & Evtikhin, D. V. (2002). The orientating reflex: The “Targeting Reaction” and “Searchlight of Attention”. *Neuroscience and Behavioral Physiology*, 32, 347–362.
- Suzuki, T. N. (2012). Referential mobbing calls elicit different predator-searching behaviours in Japanese great tits. *Animal Behaviour*, 84, 53–57.
- Suzuki, T. N. (2016a). Semantic communication in birds: Evidence from field research over the past two decades. *Ecological Research*, 31, 307–319.
- Suzuki, T. N. (2016b). Referential calls coordinate multi-species mobbing in a forest bird community. *Journal of Ethology*, 34, 79–84.
- Suzuki, T. N. (2018). Alarm calls evoke a visual search image of a predator in birds. *Proceedings of the National Academy of Sciences U.S.A.*, 115, 1541–1545.
- Taylor, M. (1992). *Birds of the Australian capital territory: An atlas Canberra*. Canberra, Australia: Canberra Ornithologists Group.
- Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science*, 308, 1934–1937.
- Townsend, S. W., & Manser, M. B. (2013). Functionally referential communication in mammals: The past, present and the future. *Ethology*, 119, 1–11.
- Treves, A. (2000). Theory and method in studies of vigilance and aggregation. *Animal Behaviour*, 60, 711–722.
- Tyrrell, L. P., Butler, S. R., Yorzinski, J. L., & Fernández-Juricic, E. (2014). A novel system for bi-ocular eye-tracking in vertebrates with laterally placed eyes. *Methods in Ecology and Evolution*, 5, 1070–1077.
- Zuberbühler, K. (2009). Survivor signals: The biology and psychology of animal alarm calling. *Advances in the Study of Behavior*, 40, 277–322.