1 **Functionally referential alarm calls in noisy miners communicate about predator**
2 **behaviour**

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16 Running head: Referential alarm calls in a bird
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Abstract 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.

Key words: acoustic communication, alarm calls, anti-predator behaviour, functional reference, mobbing calls

INTRODUCTION

Many birds and mammals give alarm calls that warn others of danger or deter predators (Caro, 2005). Alarm calls can be classified in 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 v. 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

72 to specific external threats, and not simply the presence of a threat or the internal state
73 of the caller, such as degree of fear. These calls were initially interpreted as allowing
74 'referential' or 'semantic' communication about the world. Such alarm calls are now
75 usually considered to be 'functionally referential', which acknowledges that we can
76 observe the use and response to calls, but not the cognitive processes that are implied
77 in communication using symbolic signals (Evans, 1997; Macedonia & Evans, 1993).
78 Some authors also question the concept of functional reference, in part because they
79 challenge the idea that signals are designed to convey information (Rendall, Owren, &
80 Ryan, 2009; Wheeler & Fischer, 2014), but for others information is a central issue in
81 animal communication (Seyfarth et al., 2010); for a range of views, see Stegmann
82 (2013). Overall, many researchers find the concept of functional reference useful, and
83 particularly relevant in the context of alarm calls given to different predators (Gill &
84 Bierema, 2013; Townsend & Manser, 2013).

85 Demonstrating functional reference requires considering both the production
86 and perception of calls. A functionally referential alarm call must be given primarily
87 to a specific class of threat, and the call itself must prompt responses by listeners that
88 are similar to those prompted by the external threat itself (Macedonia & Evans, 1993).
89 It follows that observational studies of natural interactions with predators cannot show
90 functional reference, because apparent responses to alarm calls might instead rely on
91 direct observation of the predator, the behaviour of the caller, or other contextual
92 information. As a result, playback experiments are essential in isolating the
93 information conveyed by the calls themselves, independent of the context (e.g.
94 Seyfarth et al., 1980a; review: Evans, 1997). Functionally referential calls must
95 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-bill anis *Crotophaga ani* and tamarins *Saguinus fuscicollis* and *S. mystax* should also be added (Grieves, Logue, & Quinn, 2014; Kirchhof & Hammerschmidt, 2006). All 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* (Kiriakis & 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 signaling about types of predator, but signaling 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* signaled 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.

143 **METHODS**

144 *Study Species*

145 Noisy miners are medium-sized (c. 60-70 g), highly social honeyeaters (family
146 Meliphagidae) that breed in colonies made of loosely territorial groups (Dow, 1979).
147 Parental care is cooperative, with the breeding female and several males provisioning
148 individual broods (Dow & Whitmore, 1990; Pöldmaa, Montgomerie, & Boag, 1995).
149 Miners are common in eastern Australia and typically live in habitat containing both
150 open areas and trees, particularly eucalypts. They feed primarily on invertebrates and
151 nectar, anywhere from the ground to the canopy (Ashley, Major, & Taylor, 2009). As
152 a result of habitat preference, miners are common in human-altered habitats such as
153 grazing land, urban parks and suburban gardens (Maron, 2007; Sewell & Catterall,
154 1998). They are aggressive to many species, including predators, and miners can
155 exclude smaller species, particularly competitors for food, from their colonies (Dow,
156 1977; Piper & Catterall, 2003; Sewell & Catterall, 1998).

157 Noisy miners are aptly named, as they have a large repertoire of conspicuous
158 vocalizations, including two alarm calls with a putatively distinct function (Holt,
159 2013). Chur alarm calls are given in the wild to potential predators that are on the
160 ground, perched, or being harassed by miners (Higgins et al., 2001; Holt, 2013).
161 Targets include perched raptors, mammals, snakes and large lizards (Dow, 1975).
162 These calls have been prompted experimentally by live dogs *Canis familiaris*, and
163 taxidemic models of foxes *Vulpes vulpes* and cats *Felis catus* (Kennedy et al., 2009;
164 Lowry, Lill, & Wong, 2012). Birds respond to playback of chur calls by approaching
165 the speaker and often also repeating the calls, suggesting that these calls are mobbing
166 alarm calls that alert others and incite them to harass threats (Kennedy et al., 2009). In
167 contrast to chur calls, aerial alarm calls are given in the wild to flying raptors such as

brown goshawks *Accipiter fasciatus* and collared sparrowhawks *A. 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).

Study Sites

We studied noisy miners from April to September 2015 (primarily autumn and winter) in suburban parks and nature reserves in Canberra, Australia, where miners are common. Chirp and aerial alarm calls are both common throughout the year, including autumn and winter (Doohan, 2014; Holt, 2013; personal observations). Experimental replication was achieved by using 15 study sites that were distributed over an area of 58 km², with a minimum distance of 750 m between sites. Individual miners have a home range size with a diameter of up to about 250 m (Dow, 1979), so the spatial separation of sites was designed to ensure that data collected at different sites were independent, despite the birds not being individually recognizable. All sites had eucalypt trees, open grassy areas, and scattered understory plants. Raptors, including *Accipiter* spp, the Australian hobby *Falco longipennis*, peregrine falcon *F. peregrinus*, and boobook owl *Ninox novaeseelandiae*, are widespread through the Canberra area (Fennell, 2009; Taylor & Group, 1992), and all commonly include birds in their diet (Higgins, Peter, & Cowling, 1999; Marchant & Higgins, 1993). One

or more of these species have been sighted at all 15 experimental sites (<http://canberranaturemap.org>), and have known nest sites within 1 km of all but 4 of the sites (Stuart Rae, pers. comm). Terrestrial predators—such as dogs, foxes, cats and snakes—are also common in the study sites (Cunningham, pers. obs.).

Context of production

We used a matched experimental design, in which miners at each site were presented with all treatments (two models and two controls) in order to test whether different alarm calls are given to airborne compared to stationary threats. Airborne models were shaped and painted to resemble an adult brown goshawk, or an adult or juvenile collared sparrowhawk (details in Magrath, Haff, McLachlan, & Igic, 2015). These life-sized models were made of sculpted foam; the goshawk model was similar in appearance but larger than the adult sparrowhawk. The models were thrown by hand, from a distance of about 10 m, and aimed to pass by the miner within 5 m of its initial position. If thrown correctly, the models glided for 20–40 m, and remained airborne for about 2–4 seconds. Models were covered in green cloth before being used, so they could not be seen before being launched. Failed throwing attempts—when a glider veered immediately into vegetation or to the ground—were repeated as soon as possible. Stationary models were taxidermic mounts of two sparrowhawks and a boobook owl. They were placed on the ground, on a low perch and inside a chicken-wire cage designed to protect the mounts from attack by miners. The cage was covered by a green cloth, which was removed by hand when a miner was within 5 m. The three models of each type were each used five times during presentations at the 15 sites.

217 We used two controls to test whether our activity or the method of
218 presentation itself affected miner calls. The control for the airborne raptor models
219 involved an observer walking to within 10 m of a miner and miming the action of
220 throwing a glider model. The control for the stationary taxidermic mounts involved
221 presenting the empty chicken-wire cage in the same way as the mounts were
222 presented. The covered cage was placed on the ground, and then the cloth was
223 removed when a miner was nearby. These controls were designed to assess whether
224 miner alarm calls were given to the models themselves, independently of our presence
225 or activity during presentation. The key prediction of functional reference is that the
226 alarm calls should differ according to the type of threat, in this case airborne versus
227 stationary models.

228 All presentations were videoed and audio-recorded during model presentation
229 to allow scoring of behaviour, and preceded by an observation period to ensure there
230 were no alarm calls or predators seen for at least 5 min before a model or control was
231 presented. Audio recordings were made from a mean distance of 13 m (median 15 m,
232 range 8–26 m), using a Sennheiser ME66 directional microphone with Marantz 670
233 recorder, saving uncompressed wave files at 16 bits and 44.1 kHz. Birds were videoed
234 from a similar distance by a second person using a Digital Canon XA20 video
235 camera. There was a minimum of 1 h between different treatments at each site, during
236 which time the observers left the site. Presentations were usually carried out over two
237 or more days, to avoid rain and wind, and to allow scheduling of presentations at
238 multiple sites (median 28 h between first and last presentations at a site, range 5–133
239 h). The order of presentation of models and controls was randomized, given that we
240 could not include all 24 orders of four treatments, but constrained so that no type of
241 presentation occurred more than five times in a specific order. If a random order led to

that outcome, the order was re-randomized. Later analyses revealed no affect of order of presentation on miner behaviour or any carry-over effects (Results).

It was not possible to score the videos of model presentations blind, because the predator models or observer were usually shown in the videos. However, recordings and spectrograms of audio-recordings allowed unambiguous classification by ear and eye into aerial and chur alarm calls, and detailed acoustic analyses showed that the call types are discrete (Results). Scoring the response to hawk gliders started when the model was thrown, and continued until 5 min after the model had landed. Furthermore, we used the video and audio recordings to subdivide the response into the period when the model was airborne compared with the period after it had landed. The response to stationary mounts was scored from the time a miner first showed any response to the model, including giving any type of alarm call, or approached within 2 m of the model. Behavioural sampling then continued for 5 min, while the model remained visible, after which sampling stopped and the model was covered and removed. A 5-min period was also used to score behaviour after control presentations, timed from the action of throwing the glider or uncovering the cage.

Miners did not call to every predator presentation, especially taxidermic models, so we gathered additional recordings of alarm calls to enable fully replicated playback experiments (below). These supplementary presentations were used solely to gather recordings for playback, and not to score behavioural responses to different models or test statistical hypotheses about call structure. In these presentations, we repeated the glider presentation to one group of miners to gather an additional call in an aerial context. Lack of calling was more common to stationary taxidermic mounts (Results), perhaps because their lack of movement made them less like live predators. Therefore, to increase realism, we combined presentation of taxidermic models with 4

s playback of the Australian magpie-lark's *Grallina cyanoleuca* general alarm call ('rapid' call), which is given during aggressive encounters with conspecifics as well as to predators (Higgins, Peter, & Cowling, 2006). We used magpie-lark calls because this species is abundant in Canberra (Taylor & Group, 1992), also prefers habitat with open areas and trees, and is common at all our experimental sites. Furthermore, because rapid calls are used in a variety of social and predator contexts, we expected them to draw attention to the stationary model while giving no specific information on the type of threat. Miners always gave alarm calls in this context, so we used these calls in the playback experiment. While playback of magpie-lark alarm calls increased the probability of miners calling, they still produced the same type of calls (Results).

Acoustic structure

We measured the acoustic structure from spectrograms of alarm calls in Raven Pro 1.4. Spectrograms used a custom pre-set that determined both the length of time shown on the screen (1.4 s) and the spectrogram settings (Hann window function, size 10.2 ms, 3 dB filter bandwidth 141 Hz; DFT size 512; hop size 0.522 ms). Individual alarm calls were made of a sequence of discrete elements, and we measured the fundamental (first harmonic) from a random element for each individual caller (**Fig. 1**). We placed the selection box around the harmonic, from which we recorded: (1) duration (ms), the duration containing 90% of the energy; (2) peak frequency (Hz), the frequency at where amplitude is maximum; (3) low frequency (Hz), the frequency above which 95% of energy occurs; (4) high frequency (Hz), the frequency below which 95% of energy occurs; (5) frequency bandwidth (Hz), the frequency range containing 90% of the energy. We used these automated percentage values to minimize errors introduced by manual placement of selection boxes. In addition to

these temporal and frequency measures of the fundamental, we measured (6) the relative amplitude of the fundamental compared with the mean of the second and third harmonics. To do this we measured the average power of the first three harmonics, and then we calculated the difference in dB between the fundamental and the mean of harmonics 2 and 3. Positive values meant that the fundamental was of higher amplitude than the mean of harmonics 2 and 3. We used this value because previous work on miners suggested that the fundamental is loudest in aerial alarms, but that harmonic 2 or 3 is loudest in chur calls (Holt, 2013; Jurisevic & Sanderson, 1994b; Kennedy et al., 2009; Magrath & Bennett, 2012). We did not measure amplitude (dB SPL) itself because we could not control for distance and bird orientation, and were interested specifically in the difference in structure between alarm-call types. Overall, for the context of production experiment, we measured 14 alarm calls when a raptor glider was airborne, 14 after a raptor glider had landed on the ground, and 7 when there was a stationary taxonomic raptor (Results). These calls were recorded from 15 sites, following the matched sampling procedure (above), with only one sample from a given context at each site. There was a minimum of 15 individuals, from 15 different social groups, included in the sample, but because birds could not be identified individually (above), there could have been more individuals sampled across the three contexts within the 15 social groups. To place these recordings in a broader context, we also measured the acoustic properties of alarm calls produced to natural predators ($n = 9$), and to calls produced during the supplemental presentation of taxidermic raptors accompanied by magpie-lark alarm calls ($n = 15$). Again, each recording in a given context was taken from a different location.

316 *Response to alarm calls*

317 We carried out a playback experiment to determine if miners respond
318 appropriately to the different putative alarm calls in the absence of any cues about
319 predator type. Again, we used a matched experimental design in which unique
320 exemplars of all four treatments were broadcast to focal individuals at each of the 15
321 experimental sites. Playback treatments were designed to encapsulate natural
322 variation: (1) an aerial alarm call; (2) a short chur alarm call; (3) a long sequence of
323 chur alarm calls; and a (4) control contact call of a harmless parrot (Supplementary
324 Audio S1–S4). The aerial alarm, short chur call and control call were all about 2 s
325 long, while the long chur alarm sequence was 15 s long. Aerial alarm calls are
326 typically short, while chur calls are variable in length, and individuals can continue
327 calling for long periods if a predator remains nearby (pers. obs.; Holt, 2013; Kennedy
328 et al., 2009). In our sample of responses to raptor glider models, the mean aerial alarm
329 call length was 1.7 s, with 1–2 calls being given over a period of 1–4 s. In response to
330 taxidermic raptor models, chur calls were a mean length of 2.4 s, with calling lasting
331 for between 6 s and 5 min (when the model was removed). Short chur call playbacks
332 were designed to enable a direct contrast with aerial calls, while holding duration
333 constant at 2 s, which is between the means of the two call types. We included a long
334 sequence of chur calls to determine if the duration of calling changes response. This
335 sequence consisted of a series of individual calls, following a natural timing. Control
336 calls were contact piping calls of crimson rosellas, *Platycercus e. elegans*, locally
337 abundant, harmless parrots, that occur at all study sites. *Platycercus* spp are medium-
338 sized parrots (c. 100–130 g) that are not excluded from miner colonies (Cunningham,
339 pers. obs; Maron, 2007; Sewell & Catterall, 1998). If miners communicate about the
340 type of predator, then individuals should behave as if that type of predator is present,

and so flee or freeze to aerial alarm calls, but become vigilant, approach or call to chur calls. We expected that a long sequence of chur calls would prompt a longer or stronger response, as it implies a predator present for longer.

Playbacks were prepared from recordings of miner alarm calls prompted by models in the context experiment, or in supplementary presentations of the models (above). All 15 experimental sites received unique examples of aerial, chur and control calls, so the experiment was fully replicated. Aerial and chur calls were recorded at the experimental site at which they were used, and control calls recorded in Canberra. We chose high quality recordings with no distinct background sounds, and filtered at 0.75 kHz to remove sound below the frequency of all call types. Calls were standardized for duration by removing or repeating elements at the end of calls if necessary, and the long chur sequence was made of multiple calls with natural intervals. All calls were broadcast so that the loudest element had a mean element amplitude of 69 dB SPL at 10 m, the mean amplitude of chur elements at that distance and within the natural range of both alarm call types (mean $\pm$ SD: aerial 73.4 ± 3.3 dB, chur 69.3 ± 3.9 dB; Magrath & Bennett, 2012).

During experiments, calls were broadcast from a distance of about 10 m to the bird, using a Roland Edirol R-09 HR player, a custom amplifier and a Peerless 810921 tweeter speaker, all mounted on the observer's waist. The focal bird's response was videoed by a second person. Playbacks were only carried out after a 5-minute period during which there were no alarm calls heard or predators seen. During this 5-minute period, the observers followed an individual miner (the focal bird) that became the target of playback. Playbacks were then carried out when the bird was feeding (or occasionally preening) at a height of 2.5–8 m, and videos continued until the focal bird had resumed feeding for about 30 s or had left the area. Playbacks at a

given site were all carried out within 24 h, with a minimum of 15 min between playbacks. A pilot project using only short alarm playbacks carried out in 2014 found no obvious order effects with a minimum 5-minute interval between playbacks, so we assumed that a 15-minute period would avoid substantial order effects, even with a long-chur sequence included. Like the model presentation experiment, which also had four treatments, the order of treatments was randomized but within the constraint that each playback type occurred approximately equally at all orders. We also tested for effects of playback order on miner response, or carry-over effects, and found none (Results).

The focal bird's immediate response to playback was scored blind from video recordings, while vocal responses were scored directly in the field. Examples of videos are given in Supplementary Videos S1-S3. To enable blind scoring, Adobe Premier Pro CC (2015) was used to remove sound from the file, and a visual marker was added to mark the start of playback. The file was then given an arbitrary name by someone uninvolved in the study, and then passed to the person (SC) who scored responses by viewing footage at half-speed using VLC 2.2.1. It was possible to score only the first 5 s from the start of playback on the video, because the birds often left the camera frame after that period. Responses were scored as flee (fly from the feeding site, but not towards the speaker), freeze (remain totally still), vigilance (stop feeding and look around), approach (leave the feeding site and move towards the speaker), or none (continue feeding or preening). The categories of response therefore included avoidance (flee or freeze) and monitoring or harassment (vigilance and approach, which are typical responses to mobbing calls in birds). After blind scoring of behavioural responses, the complete video including audio track was checked to

confirm field scoring of aerial and chur calls. Aerial and chur call types are distinct (below), so categorization was unambiguous and always consistent with field scoring.

Statistical analyses

Analyses of experiments were based on their matched design, where each site received all treatments. We used McNemar tests, appropriate for paired dichotomous data (Agresti, 2007; Siegel & Castellan, 1988), to compare the probability of giving aerial versus chur calls to gliding versus stationary models. Paired t-tests were used to compare specific acoustic properties of calls prompted by raptor models in the matched ‘context of production’ experiment. Analyses of the playback experiment also entailed paired dichotomous response variables, so analyses were carried out using McNemar tests, when comparing two treatments, and Cochran Q tests, when comparing more than two treatments (Siegel & Castellan, 1988). We used exact rather than asymptotic probabilities in these tests and in contingency tests for carry-over effects (Fisher’s exact test and extensions; Field, 2013). Separate from statistical tests of hypotheses, that were comparisons within the planned experiment using a matched sampling design and randomized order, Principal Components Analysis (PCA) was carried out simply to visualize overall variation in acoustic properties of calls recorded in all contexts (Tabachnick & Fidell, 2007), including supplementary model presentations and serendipitous recordings of calls to natural predators. These PCA analyses including peak frequency, frequency bandwidth, duration and relative amplitude of the fundamental, because they measured attributes of calls that can vary independently. Low and high frequency were excluded because they were both strongly correlated with and are intrinsically related to peak frequency (which must lie between the two). Statistical tests and PCA were conducted in IBM SPSS Statistics

415 Version 22 (Field, 2013).

416

417 *Ethical note*

418 All work was approved by the Australian National University Ethics
419 Committee, and was designed to minimize disturbance or stress to the birds. We used
420 model predators to measure responses to different types of predator and to prompt
421 birds to give alarm calls. Birds were therefore never exposed to real threat, and we
422 minimized sample sizes by using matched experimental designs. Furthermore,
423 experiments were distributed over 15 separate sites, and any one site received at most
424 two model presentations in an experiment. Similarly, playbacks used a matched
425 design and entailed only three alarm broadcasts at each of 15 sites. Overall, birds did
426 display anti-predator behaviour to both models and playbacks, but individuals
427 returned to apparently normal behaviour quickly, usually within a few minutes.

428

429 **RESULTS**

430 *Context of production*

431 Miners produced different alarm calls to different types of threats. Raptor
432 gliders in flight prompted only aerial alarm calls in the 14 trials in which birds gave
433 calls, whereas taxidermic models of perched raptors prompted only chur calls in the 7
434 trials in which birds gave any calls (**Table 1a**; McNemar test, alarm call type, $n = 7$
435 birds calling to both type of prompt, 2-tailed exact $p = 0.016$). The different call types
436 were related to model behaviour, not whether the model was prepared from a
437 taxidermic skin or artificial material, because all 13 birds that called to both the glider
438 in flight and landed switched from giving aerial to chur calls after the model landed
439 (**Table 1a**; McNemar, 2-tailed exact $p = 0.00024$). The calls were prompted by the

models themselves, and not by the way the models were presented: birds never called to the action of throwing itself, and never when revealing an empty the cage (**Table 1a**). There was no affect of the order of model presentation on call type (McNemar, $n = 7$ that called to both models; 2-tailed exact $p = 0.45$). Furthermore, if a bird called to either model, it always gave an aerial call to the airborne model and a chur call to the perched taxidermic model. There could be no carry-over effect on call type since it was invariant according to the model, and we found no effect even on the probability of giving a call. The probability was not affected by whether a model was preceded by the other model or not (perched model, Fisher 2-tailed exact $p = 0.31$; glider model, Fisher 2-tailed exact $p = 1.0$).

In addition to prompting different alarm calls, the different types of model predator prompted different anti-predator responses. Raptor gliders in flight most commonly caused birds to flee, whereas perched models most commonly provoked attack, with the birds ‘dive-bombing’ the models (**Table 1b**; McNemar, 2-tailed exact $p = 0.0078$; comparing fleeing and freezing versus attack, approach and vigilance). Similarly, the miners changed from avoidance to attack after a gliding model hawk landed (**Table 1b**; McNemar, $n = 13$ cases with a response at each stage, 2-tailed exact $p = 0.016$). Similar to the vocal responses, neither the act of throwing nor revealing an empty cage prompted any responses. There was also no effect of the order of presentation of perched and gliding models on the type of response (McNemar, avoidance versus attack, 2-tailed exact $p = 1.0$). Similarly we found no carry-over effect; the response to the perched or gliding model did not differ according to whether it was preceded by the other model or not (Fisher test, 2-tailed exact $p = 1.0$ for each model).

Alarm call acoustic structure

Aerial and chur alarm calls were acoustically distinct, with no overlap in some acoustic measurements. The fundamental was shorter and of higher frequency by all measures in aerial compared to chur calls (**Fig. 1; Table 2**; data from experimental presentation of models). The fundamental was also much louder than the mean of second and third harmonics within aerial alarm calls, but similar or of lower amplitude in chur calls (delta amplitude means for gliding model hawk versus taxonomic raptor: 27.4 and -5.4 dB respectively; **Table 2**). Indeed, there was no overlap in measurements for delta amplitude or low, high or peak frequency for calls to gliding models hawks versus perched taxonomic raptors (**Table 2**).

Alarm calls given to different specific prompts, including from natural observations and supplemental recordings, grouped into either aerial or chur calls based on Principle Component Analysis of acoustic properties (**Fig. 2**). For example, chur calls given to a hawk glider after it had landed were similar to those given to stationary taxidermic mounts, and calls to natural predators grouped with aerial or chur calls depending on whether the predator was flying or stationary. The first two principal components explained over 90% of the variance: PC1 68.0% and PC2 23.2%. Aerial calls had higher PC1 values, which were associated with a higher peak frequency (component weighting 0.96), shorter duration (-0.82) and greater relative amplitude of the fundamental (0.95). Chur calls tended to have higher PC2 values, which were primarily associated with a greater bandwidth (0.87).

Response to alarm calls

The miners' immediate responses to playback were appropriate to the type of playback, in the absence of any other cues about danger (**Fig. 3**). Blind scoring

490 revealed that each type of alarm-call playback prompted anti-predator behaviour in at
 491 least 14/15 cases (93%), yet did so in only two of 15 control playbacks (14%;
 492 Cochran Q, all treatments, response or not: Cochran's Q, 2-tailed exact $p < 0.001$).
 493 We therefore restricted analyses of response to among alarm calls, for which we
 494 compared avoidance responses (flee or freeze) with mobbing responses (vigilance or
 495 approach). Miners always either fled or froze after playback of aerial alarm calls, yet
 496 all but two approached or became vigilant after playback of chur alarm calls of similar
 497 duration, with only one bird fleeing and another showing no response (McNemar,
 498 avoidance versus mobbing response: $n = 14$ with a response to both, 2-tailed exact $p =$
 499 0.00024). The long chur playbacks prompted a very similar response to short chur
 500 calls, with 14 individuals showing a mobbing response, and one having no response
 501 (McNemar: long chur compared to aerial, 2-tailed exact $p = 0.00012$; long chur
 502 compared to short chur, 2-tailed exact $p = 1.0$). There was no effect of playback order
 503 on the type of response, as the responses to each playback type were almost invariant
 504 (Cochran Q, three playback types excluding the control, $n = 14$, 2-tailed exact $p =$
 505 1.0). Given the almost invariant response to a given type of playback, there was also
 506 no evidence of a carry-over effect (contingency table with response to playbacks
 507 according to which alarm call type had preceded it or neither had preceded it: aerial, p
 508 $= 1.0$; short chur, $p = 0.43$; long chur, $p = 0.53$; all 2-tailed exact p values).

509 In addition to the different physical responses, miners had different vocal
 510 responses to the different types of playback. Birds never gave aerial alarm calls after
 511 any playback, yet they were more likely to give chur calls to chur call playbacks: none
 512 gave a chur call after the control playback, one after aerial playback, five after short
 513 chur call playbacks and 11 after long chur call playbacks (probability of giving a chur
 514 call among alarm call treatments: Cochran Q, exact $p = 0.001$). The difference was

only clear in a contrast of aerial versus long chur not short chur playbacks (McNemar 2-tailed exact $p = 0.002$ and 0.2 respectively). There was no affect of the order of playback on the probability of giving a chur call, either considering all four playback types (Cochran Q, $n = 15$, 2-tailed exact $p = 0.93$) or restricting to short and long chur playbacks (McNemar, $n = 15$, 2-tailed exact $p = 0.74$). Similarly, there were no carry-over effects; the probability of giving a chur call in response to playback did not depend which alarm call type, if any, had preceded it (contingency table, including chur or aerial or neither before: short chur, 2-tailed exact $p = 1.0$; long chur, 2-tailed exact $p = 0.77$; birds never called to aerial playbacks).

DISCUSSION

Noisy miner aerial and chur alarm calls meet both the production and perception criteria for functional reference. Acoustically distinct aerial calls were given specifically to airborne raptor models, while chur calls were given to perched raptor models and stationary glider models, with birds switching from aerial to chur calls when a gliding model raptor model landed. Furthermore, playback of these calls led to appropriate responses, in the absence of any contextual information. Noisy miners therefore join the small list of birds and mammals with experimental evidence for functionally referential communication about predators (reviews: Gill & Bierema, 2013; Suzuki, 2016; Townsend & Manser, 2013). Our results also support Greisser's (2008) finding that these calls can categorize threats by current predator behaviour, not simply taxonomic differences, and so convey additional information relevant to predator avoidance.

The two alarm-call types were used consistently in our study regardless of the specific model or context, and consistent with previous descriptions of these calls.

Chur calls were given regardless of whether the prompt was a silent, taxidermic raptor, a taxidermic raptor accompanied by magpie-lark alarm calls, a gliding foam raptor after it had landed, or natural calls to live dogs or perched birds. Similarly, aerial alarms were given to gliding models or live, flying birds. These two call types are also consistent with previous spectrographic and quantitative descriptions of aerial and chur calls (Doohan, 2014; Holt, 2013; Jurisevic & Sanderson, 1994a, 1994b; Lowry et al., 2012; Magrath & Bennett, 2012; Wood, Sanderson, & Evans, 2000).

In addition to being acoustically distinct, aerial and chur alarm calls were given in specific experimental contexts, and accompanied by different anti-predator behaviour. Aerial alarm calls were given exclusively to the gliding model raptors, while only chur calls were given to the perched, taxidermic raptors, and to gliding raptors after landing. At the same time, airborne raptor models most commonly prompted birds to flee to cover, while stationary models most commonly provoked attack; the exceptions entailed birds become vigilant but not fleeing or attacking. The results from our experimental contexts are similar to previous reports on the context of production of aerial and chur calls. Aerial alarms have primarily followed airborne prompts, including model planes, and flying raptors and other large birds, while chur calls primarily follow stationary or terrestrial prompts including taxidermic cats, foxes and raptors, and live cats, dogs, humans, and large perched birds including raptors (Doohan, 2014; Holt, 2013; Jurisevic & Sanderson, 1994a, 1994b; Lowry et al., 2012; Wood et al., 2000). Overall, the context of alarm call production and associated anti-predator responses are related to predator behaviour and not predator type: airborne threats prompt aerial alarms and evasion, while those perched or landed prompt chur calls and attack.

Miners responded appropriately to playback of the different types of alarm call, which fulfills the second, perception criterion for functional reference (Evans, 1997; Macedonia & Evans, 1993). Playback of aerial calls prompted avoidance behaviour, while chur calls prompted birds to become vigilant or approach the speaker. These responses to playback were similar to their behaviour to the original prompts, and appropriate to the type of threat, showing that the calls themselves convey information about the type of threat. The responses were not identical to those to the original prompts, probably because there was no physical model that provided information on location of danger. For example, an even greater proportion of birds fled after playback of aerial calls than during presentation of the gliding model, which they sometimes just observed, perhaps because an unseen predator is more dangerous (Huang, Seiving, & St. Mary, 2012). Similarly, while birds became vigilant and approached the speaker during playback of chur calls, they never actually attacked, presumably because they could not see the threat. Given that viewing a predator directly will provide slightly different information from that conveyed by alarm calls, and different opportunities for anti-predator behaviour, the key issue for functional reference is that listeners should select ‘appropriate’ responses for the type of threat (Evans, 1997). Responses to playback will usually also be ‘similar’ to responses to the predator itself (Gill & Bierema, 2013), but not necessarily the same, as sometimes implied (Townsend & Manser, 2013).

Our results provide strong evidence of functional reference, by combining an experimental approach to both production and response specificity, along with acoustic analyses of calls and blind scoring of responses to playback. Observations of natural call production, including in miners, are important in establishing call context, but it can be difficult to get large sample sizes and to score the anti-predator

behaviour that accompanies calling (Grieves et al., 2014; Holt, 2013; Jurisevic & Sanderson, 1994a, 1994b; Manser et al., 2001; Zuberbühler, Cheney, & Seyfarth, 1999). Experimental prompting of alarm calls allows full control of context independent of location, comparable samples for acoustic analysis, and facilitates scoring of behavioural responses, which can then be compared to the responses to playback alone (e.g. Evans et al., 1993). Functional reference implies that individuals respond to calls as if the prompt was present (Evans, 1997; Macedonia & Evans, 1993), so it is desirable to directly compare anti-predator behaviour in the two situations. Blind scoring of response to playback is desirable, if possible, because it reduces the risk that scoring could be influenced by expectation (for another example of blind-scoring of response to referential alarm calls, see Grieves et al., 2014). In practice blind scoring is often difficult in studies of wild animals, but this may not be a problem in the literature on referential alarm calls. This is because responses to different types of predators and alarm calls are often distinct and unambiguous, such as approach or flee, and so easy to score in the field.

Our study supports Greisser's (2008) conclusion that referential alarm calls in birds, and perhaps mammals, may often refer to predator behaviour and not just taxonomic categories. Specifically, avian 'flee' and 'mobbing' calls may often refer to 'airborne' versus 'non-airborne' predators, rather than specifically to aerial and terrestrial predators, as is often stated (e.g. Evans et al., 1993; Grieves et al., 2014). This being the case, it would be interesting to assess whether alarm calls can simultaneously convey information about both predator type and behaviour, as is the case for predator type and degree of danger in meerkats (Manser, 2001; Manser et al., 2001; Manser, Seyfarth, & Cheney, 2002) and some birds (e.g. Fallow & Magrath, 2010; Leavesley & Magrath, 2005; Sieving et al., 2010; Templeton et al., 2005).

614 Combining call types may prove a flexible method of encoding subtle information
615 about different threats, as is the case in, for example, tufted titmice *Baeolophus*
616 *bicolor* (Sieving et al., 2010) and Japanese great tits *Parus minor* (Suzuki,
617 Wheatcroft, & Griesser, 2016).

618 Despite the long history of interest and research, there is ample scope for
619 further studies of functional reference in animal communication, and alarm calls
620 provide an excellent model because different threats predict different adaptive
621 responses. First, we need further research on how contextual information could
622 influence the response to alarm calls. Even if calls convey information about predator
623 type, it does not mean that individuals ignore other sources of information to refine
624 responses (Evans, 1997), and recent research on vervet monkeys implies that context
625 is important. Although vervets produce different alarm calls to different predators,
626 these calls are not always acoustically distinct from other calls in the repertoire,
627 suggesting that contextual information is important in a listener's response (Price et
628 al., 2015). For example, 'rraup' calls are given to eagles but also during within-group
629 aggression, so that monkeys might use the absence of fighting within the group to
630 judge that a 'rraup' call warns of an eagle. Similarly, group size and caller distance
631 might both affect the response to playback of different vervet alarm calls.

632 Ducheminsky, Henzi, & Barrett (2014) found no clear evidence that different alarm
633 calls prompted appropriate responses. The authors suggest that the large groups at
634 their study site may mean more false alarms, so that individuals respond by seeking
635 more information rather than taking immediate action. Larger, dispersed groups also
636 meant that playbacks were from greater distances, perhaps implying lower risk and
637 again prompting individuals to seek further information. Clearly, even this classic
638 example of referential communication will repay further study. Second, although the

term ‘functional reference’ was coined in part to avoid inference about cognition, it would nonetheless be interesting to assess cognitive processes underpinning communication about predator categories (Suzuki, 2016). For example, at one extreme alarm calls might prompt appropriate responses merely because of call acoustic properties (Rendall et al., 2009), while at the other extreme individuals might associate call types with specific predators and respond appropriately according to the predator, not the type of sound (Seyfarth et al., 2010; Zuberbühler et al., 1999). Referential alarm calls provide an excellent model to address animal cognition because of the clear differences in response to playback of different calls.

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Supplementary Material

664 Supplementary material associated with this article can be found, in the online version, at

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830 **Table 1**

831 The number of noisy miner (a) alarm call responses, and (b) non-vocal responses,
832 according to the model presentation treatments.

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	Gliding hawk airborne	Gliding control	Gliding hawk landed	Perched model	Perched control
(a) Call type					
Aerial	14	0	0	0	0
Chur	0	0	14	7	0
No call	1	15	1	8	15
(b) Behaviour					
Flee	8	0	0	0	0
Freeze	1	0	0	0	0
Vigilance	6	0	5	3	0
Attack	0	0	8	10	0
No response	0	15	2	2	15

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Table 2

Acoustic differences between noisy miner aerial alarm calls, given to gliding hawk models in the air, and chur calls, given to landed gliding models and perched taxidermic raptor models. See the text for explanation of measurements. Values show means $\pm$ SD and range for all calls recorded; statistical analyses show paired t-tests with 2-tailed probability estimates for paired data.

Model type	Low frequency 5% (Hz)	High frequency 95% (Hz)	Peak frequency (Hz)	Band width 90% (Hz)	Duration 90% (s)	Delta amplitude (dB)
Model type						
Glider airborne (n = 14)	2805.6 $\pm$ 199.0 2497.9–3273.0	3359.2 $\pm$ 236.5 2756.2–3703.7	3168.5 $\pm$ 229.6 2584.0–3445.3	553.7 $\pm$ 199.0 258.4–861.3	0.083 $\pm$ 0.021 0.053–0.127	27.44 $\pm$ 4.55 18.95–36.25
Glider landed (n = 14)	1381.2 $\pm$ 340.5 947.5–2411.7	1855.9 $\pm$ 358.5 1550.4–2928.5	1756.5 $\pm$ 364.7 1378.1–2842.4	473.7 $\pm$ 240.7 172.3–1033.6	0.156 $\pm$ 0.026 0.115–0.185	-3.89 $\pm$ 2.46 -8.50–1.00
Perched model (n = 7)	1328.9 $\pm$ 109.6 1205.9–1464.3	1710.4 $\pm$ 168.1 1550.4–1981.1	1624.2 $\pm$ 168.1 1464.3–1894.9	381.5 $\pm$ 130.2 172.3–516.8	0.131 $\pm$ 0.030 0.100–0.184	-5.42 $\pm$ 2.23 -8.10– -2.25
Paired t-tests^a						
Glider airborne versus landed	t ₀ = 12.43 p < 0.001	t ₀ = 13.91 p < 0.001	t ₀ = 13.42 p < 0.001	t ₀ = 1.51 p = 0.16	t ₀ = 9.75 P < 0.001	t ₀ = 34.74 p < 0.001
Glider airborne versus perched	t ₀ = 12.51 P < 0.001	t ₀ = 16.74 P < 0.001	t ₀ = 14.07, P < 0.001	t ₀ = 1.47, P = 0.19	t ₀ = -3.59, df = 6 P = 0.01	t ₀ = 15.43, P < 0.001

1. Paired differences followed normal distributions for all variables (Shapiro-Wilk test, p > 0.05).

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Figure 1. Spectrograms of noisy miner (A) aerial alarm calls, and (B) chur alarm calls. Spectrograms were prepared in Raven Pro 1.4, using a Hann window function, size 10.2 ms, with a 3dB filter bandwidth of 141 Hz. Selections boxes were drawn over the first three harmonics (1, 2 and 3) as shown. Automated measures of frequency, duration and amplitude were then made for the first harmonic, and amplitude alone from second and third harmonics. See text for further details of measurements.

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Figure 2. Principal Components plot of the acoustic properties of noisy miner aerial alarm calls and chur calls given to different prompts, showing that these calls are acoustically discrete. The acoustic properties of aerial alarm calls given to the airborne model hawk gliders or to natural flying predators group together, as do the chur calls given to taxidermic perched raptors with or without accompanying playback of magpie-lark ‘rapid’ alarm calls, landed glider hawk models, and perched real predators.

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Figure 3. Noisy miner responses to playback of alarm and control calls. The y-axis shows the number of individuals (out of 15) having that immediate response. Aerial alarm calls and short chur call playbacks were 2 s in duration, while long chur calls were 15 s in length. The control call was a 2 s contact call of a harmless parrot.