



## Eavesdropping magpies respond to the number of heterospecifics giving alarm calls but not the number of species calling

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Social information varies in its reliability and relevance, requiring individuals to use rules to avoid inappropriate responses to false information. A simple rule is to respond only when a certain number of individuals provide similar information. Although individuals within social groups can use such numerical rules to assess conspecific information and make consensus decisions, it is unknown whether individuals apply similar rules when assessing the value of heterospecific information. We consider the case of individuals eavesdropping on heterospecific alarm calls. Eavesdroppers may be particularly vulnerable to false alarms because of the large pool of potential callers and variability in the specific threats to which they call. Individuals might therefore value alarm calls more if they come from multiple callers or multiple species than from a single caller or a single species. We tested these predictions using field playback experiments on wild Australian magpies, *Gymnorhina tibicen*. Magpies responded more strongly to alarm calls coming from two callers versus one caller of the same heterospecific species. However, in contrast to our prediction, magpies responded similarly to alarm calls from two individuals of different species as they did to alarm calls from two individuals of the same species. We conclude that the number of calling individuals does affect response, probably because information from multiple callers is more reliable, but that the value or reliability of information from multiple species may depend on the types of alarm calls and combination of species involved.

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Organisms require information about the environment to make adaptive decisions. Information, such as about resources, mates and predators, can be obtained directly through personal experience (personal information) or indirectly through the signals and cues produced by other individuals (social information; Caro, 2005; Dall, Giraldeau, Olsson, McNamara, & Stephens, 2005; Dittus, 1984; Evans & Evans, 1999). When available, personal information is generally more accurate, and thus valued more greatly, than social information (van Bergen, Coolan, & Laland, 2004). However, gathering personal information carries costs, such as spending more time looking out for predators or sampling food (Hollén, Bell, & Radford, 2008; Templeton & Giraldeau, 1995, 1996; Ward & Zahavi, 1973), and these costs can favour the use of social information (Dall et al., 2005). Here we focus on the gathering of

information about predators from alarm calls, as this provides a good context to examine the use of personal and social information.

Social information from alarm calls varies in its reliability as not all signals are accurate or honest (Koops, 2004; Searcy & Nowicki, 2005; Semple & McComb, 1996). For example, individuals sometimes produce alarm calls by mistake in the absence of predators due to errors in predator detection (Beauchamp, 2010; Beauchamp & Ruxton, 2007), or produce 'deceptive' alarm calls intentionally to steal resources (Møller, 1988) or increase mating success (Bro-Jørgensen & Pangle, 2010; Møller, 1989). Responding to such false alarms can carry costs (Beauchamp & Ruxton, 2007; Ridley & Raihani, 2007), but not responding to true alarm calls can result in death or injury; individuals must therefore balance these costs. The problem of unreliable alarm calls is worsened when there are multiple potential informants. Although more individuals being on the lookout for danger increases the likelihood that predators are detected, it potentially also increases the number of false alarms as there are more individuals to make mistakes (Wolf, Kurvers, Ward, Krause, & Krause, 2013). Responding to false alarms can in turn lead to information cascades spreading misinformation (Giraldeau,

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Valone, & Templeton, 2002; Sirot, 2006). Therefore, although ignoring alarm calls could be lethal, the reliability of alarm calls varies, and individuals must assess the likelihood of predation against the costs of unnecessary responses.

Individuals can reduce unnecessary responses to false alarms by evaluating the reliability of social information. One strategy is to learn to distinguish between reliable and unreliable informants (Hare & Atkins, 2001; Kern, Sumner, & Radford, 2016; Ramakrishnan & Coss, 2000; although see ; Blumstein, Verneyre, & Daniel, 2004). When it is difficult to discriminate true alarm calls from false ones, individuals can apply numerical rules and integrate information from several sources to help make adaptive decisions. Numerical rules in decision making, such as the use of quorum rules, have been widely studied for cohesion and collective movement of social species (Bousquet, Sumpter, & Manser, 2011; Seeley & Visscher, 2004; Ward, Krause, & Sumpter, 2012; Ward, Sumpter, Couzin, Hart, & Krause, 2008). For example, individuals may respond only when a certain number of conspecific informants provide parallel information acquired at least partly independently (Conrad & Roper, 2005; Wolf et al., 2013), or adjust the magnitude of their responses according to the number of conspecific informants (Sloan & Hare, 2008). Despite this work on assessment of reliability within species, there has been little comparable work on assessment of social information from other species.

Like conspecifics, heterospecifics are valuable sources of information about predators, but potentially exacerbate the problem of information unreliability. Animal communities comprise a diversity of species, and individuals often eavesdrop on the alarm calls of heterospecifics with which they share at least some predators (Magrath, Haff, Fallow, & Radford, 2015). Heterospecifics can provide information that complements that provided by conspecifics but with less cost of competition (Seppänen, Forsman, Mönkkönen, & Thomson, 2007), or may be better at detecting predators or providing reliable information than conspecifics (Goodale, Beauchamp, Magrath, Nieh, & Ruxton, 2010; Magrath et al., 2015). Furthermore, heterospecifics usually comprise a larger number of individuals within the community compared with conspecifics, and thus may be richer sources of useful information than conspecifics alone (Goodale et al., 2010; Schmidt, Dall, & van Gils, 2010; Seppänen et al., 2007). However, heterospecifics also increase the number of potential sources of unreliable information, as they may produce erroneous or deceitful alarm calls (Flower, Gribble, & Ridley, 2014; Goodale & Kotagama, 2005; Munn, 1986). Species also vary in the suite of predators to which they are vulnerable, such that not all heterospecific alarm signals are relevant to an eavesdropper (Magrath et al., 2015). For example, yellow-casqued hornbills, *Ceratogymna elata*, are vulnerable to eagles but not leopards and thus respond to 'eagle' but not 'leopard' alarm calls of Diana monkeys, *Cercopithecus diana* (Rainey, Zuberbühler, & Slater, 2004). Thus, evaluating the reliability and relevance of heterospecific alarm calls is fundamentally important to eavesdroppers.

It is unknown whether eavesdroppers pay attention to the number of heterospecific alarm callers when deciding whether and how to respond. Similar to numerical rules used to assess the reliability of conspecific alarm calls and other signals (Blumstein et al., 2004; Sloan & Hare, 2008; Ward et al., 2008; Wolf et al., 2013), eavesdroppers could reduce their vulnerability to false information by responding only when multiple heterospecific callers give alarm calls. It is also likely to be beneficial to respond more strongly, such as for a longer period, to multiple callers because more dangerous predators can prompt a greater number of individuals to call (Blumstein et al., 2004; Sloan & Hare, 2008).

In addition to the number of individuals calling, the number of heterospecific species calling may also indicate the likelihood or type of danger. A simple rule could be to respond in an intermediate

way to multiple species calling compared to the response to each species calling alone: an average over species. Alternatively, the combination of species calling might itself convey information, for several reasons (Magrath et al., 2015). First, as species differ in their vulnerability to different predators, shared or more dangerous predators are likely to elicit alarm calls from multiple species and, indeed, are known to do so (Goodale & Kotagama, 2005). Second, the circumstances that cause errors in predator detection and elicit erroneous alarm calls (such as falling branches or nonpredators) may differ between species owing to their different habitats. Therefore, a second species calling may indicate reliable alarm calls by both species. Third, some general alarm calls are given to a variety of threats and disturbances, rather than only predators (e.g. Fichtel & Kappeler, 2002), so that multiple species calling is more likely to indicate predators than, for example, aggressive interactions among conspecifics. For all these reasons, calling by multiple species could be a more reliable indication of real danger than single-species alarm calls. Thus, eavesdroppers may be more likely to respond, or respond more strongly, to alarm calls from multiple species than to multiple alarm calls by members of a single species. In this case the response would be greater than the average response to the individual calling species, and potentially greater than either species alone.

We used playback experiments to test whether Australian magpies, *Gymnorhina tibicen*, pay attention to the number of callers and the number of species when assessing heterospecific social information about predators. First, we tested whether magpies are more likely to respond, or respond for longer, to alarm calls of two heterospecific callers of the same species versus alarm calls of a single heterospecific caller of that same species. Second, we tested whether magpies are more likely to respond, or respond for longer, when presented with alarm calls of two different species versus two alarm calls of a single species. We predicted that if magpies apply numerical rules to evaluate heterospecific social information, then they will respond more to alarm calls of multiple callers and multiple species than single callers and single species.

## METHODS

### *Study Site and Species*

We studied free-living Australian magpies in and around Weston Park (35°17'S, 149°5'E) and Haig Park (35°16'S, 149°7'E), Canberra, Australia, from April to August 2017. Both locations contained a mixture of open grass, in which birds feed, and trees, required for nesting, roosting and shelter (Higgins, Peter, & Cowling, 2006). Local predators include brown goshawks, *Accipiter fasciatus*, collared sparrowhawks, *Accipiter cirrocephalus*, peregrine falcons, *Falco peregrinus*, and Australian hobbies, *Falco longipennis* (Higgins, 1999; Taylor, 1992), and foxes, *Vulpes vulpes*, cats, *Felis catus*, and dogs, *Canis lupus familiaris* (Cunningham & Magrath, 2017). The magpies in our study areas are habituated to humans, making them amenable subjects for our experiments.

Australian magpies are large, omnivorous passerines (ca. 300 g for local subspecies) that are native and common throughout most of Australia (Higgins et al., 2006). Members of breeding populations live in pairs or family groups, consisting of a dominant pair and offspring, that defend year-round territories. Magpies can be killed by large raptors, including goshawks and peregrine falcons, and mammalian carnivores, and chase and harass both large and small predators (Higgins et al., 2006; Marchant & Higgins, 1993). They have a variety of alarm calls, including general alarm calls and one given specifically to large raptors (Kaplan, Johnson, Koboroff, & Rogers, 2009). Sex and age can be assigned by plumage. Adult male magpies have black and white plumage, adult females have

black and dull white plumage, and juveniles are different shades of grey and dull white. Canberra lies in a zone of hybridization between two subspecies, the black-backed *G. tibicen tibicen* and the white-backed *G. tibicen tyrannica*, producing intraspecific plumage variation (Burton & Martin, 1976). This plumage variation, in combination with sex- and age-related plumage differences and territory location, allowed us to identify individuals (methods in Dawson Pell et al., 2018).

Our experiments examined the responses of magpies to the alarm calls of three other locally common species: noisy miners, *Manorina melanocephala*, Australian magpie-larks, *Grallina cyano-leuca*, and crimson rosellas, *Platyercus elegans*. All three species commonly forage close to magpies, including on the ground. Noisy miners are medium-sized (ca. 75 g) cooperatively breeding honey-eaters (family Meliphagidae) that produce 'aerial' alarm calls in response to raptors in flight and 'mobbing' alarm calls in response to terrestrial or perched avian predators (Cunningham & Magrath, 2017; Farrow, Doohan, & McDonald, 2017). Magpies eavesdrop on noisy miner alarm calls and gain specific information about the nature of the threat (Dawson Pell et al., 2018). Magpie-larks are medium-sized passerines (ca. 85 g) in the family Monarchidae that feed primarily on the ground, and crimson rosellas are medium-sized parrots (ca. 130 g; family Psittacidae) that feed on the ground or in vegetation (Higgins, 1999; Higgins et al., 2006). In contrast to the functionally referential alarm calls of miners, magpie-larks and crimson rosellas each have only a 'general' alarm call given in response to a variety of threats and disturbances including when flushed from the ground, in response to flying predators, when mobbing predators or other threats, and (at least in magpie-larks) in social interactions (Higgins, 1999; Higgins et al., 2006; Ribot, Berg, Buchanan, & Bennett, 2011; B. Igc and C. Ratnayake, personal observations). Their general use means that these alarm calls provide limited information to eavesdropping magpies about the presence or nature of danger; they could range from irrelevant signals of social conflict within those species to signalling immediate danger from raptors. There has been no previous work on magpies' response to either rosella or magpie-lark alarm calls.

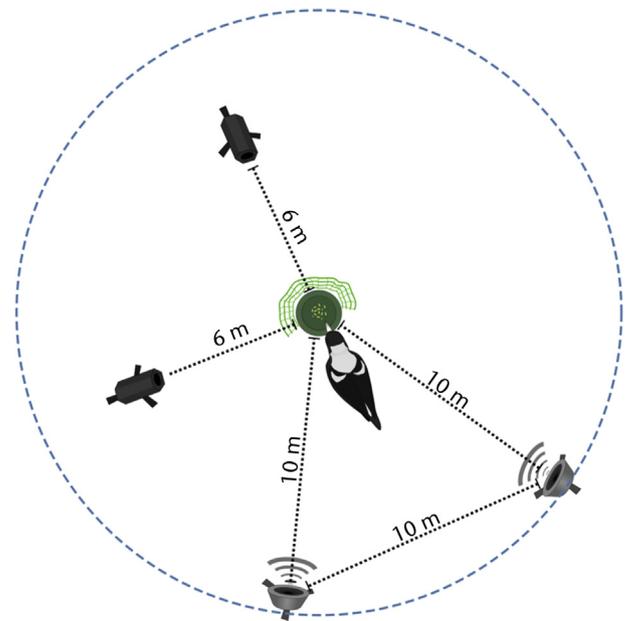
### Experimental Overview and General Methods

#### Experimental overview

We carried out two playback experiments to examine how the number of heterospecific alarm callers and the number of heterospecific calling species affect the magpies' response. In the first experiment, conducted between 27 April and 20 May 2017, we tested whether magpies respond more strongly to two noisy miners producing aerial alarm calls compared to a single miner calling. This functionally referential call provides information specifically about aerial danger. In the second experiment, conducted between 3 and 29 July 2017, we examined the response of magpies to the general alarm calls of crimson rosellas and magpie-larks. We tested whether magpies respond more strongly when there are two different species producing general alarm calls versus two callers of the same species producing general calls. In this case, the alarm calls do not provide specific information about danger, so that the combination of species may provide more reliable information about danger than either species alone. Each experiment was based on a matched design, in which one focal bird on each territory received every playback treatment.

#### Equipment and field methods

We conducted playback experiments on magpies in a virtual circular 'arena' measuring 20 m in diameter, with two speakers and two cameras directed towards a central plate containing grated cheese (Fig. 1). The equipment was set up in an open area free from



**Figure 1.** Arrangement of equipment within a virtual 20 m diameter arena. The focal magpie was lured to feed at a plate of cheese at the centre of the arena. Playbacks were broadcast from two speakers positioned behind the magpie and 10 m from the plate. The response of the magpie was recorded using two video cameras, placed 6 m in front and to the side of the magpie. Green wire mesh was arranged around part of the plate to ensure the magpie was facing away from the speakers at the time of playback.

canopy cover. Two Scan-Speak 4" full-range speakers (Discovery 10F/4424G00, Videbæk, Denmark; frequency response ca. 200–10 000 Hz) were mounted on tripods 0.7 m from the ground, 10 m from the food plate, and placed in the direction of the closest tree. The speakers were 10 m apart, to allow simulation of two calling individuals, and we played sound wave files through an Edirol R-09HR solid-state digital player (Roland, Los Angeles, CA, U.S.A.) connected to a custom-built stereo amplifier. The plate of cheese had a wire-mesh barrier around three sides, so that it was accessible only from the direction of the speakers. We recorded responses of magpies with two Panasonic HC-V770 video cameras (Osaka, Japan) recording at 1920×1080 pixels and 50 frames/s. The cameras were mounted on tripods 0.9 m from the ground and 6 m from the plate. They were 90° apart, as viewed from the plate, giving a clear view of the birds regardless of their orientation.

Once the equipment was set up, we lured the focal magpie with a small amount of food to the plate containing cheese, where its back was towards the speakers. The focal magpie was identified from plumage, using photographs of all group members taken on a previous day (methods in Dawson Pell et al., 2018). We used only adult individuals and used the same number of males and females. While the focal bird was feeding from the plate, playback treatments were broadcast when there were no heterospecifics within 20 m, and after at least 5 min without any predators or alarm calls in the vicinity. The speaker that broadcast the first (or only) call during experiments was alternated equally across magpies within each experiment. Every magpie received each treatment on a separate day, to reduce any order effects, and alarm playbacks were either presented first or preceded by control playbacks, to avoid any carryover effect from alarm call playbacks on the previous day. As magpies are group-living, it was often impossible to conduct playbacks on the focal magpie in isolation from its group members. Instead, we kept the number of nonfocal magpies within 10 m of the plate similar ( $\pm 1$  magpie) across all playback treatments to a focal individual, and subsequently included the number of magpies in statistical models.

### Call recording

We recorded calls from local noisy miners, crimson rosellas and magpie-larks for use in playback experiments (Fig. 2). Alarm calls of all species were recorded by prompting individuals with a sparrowhawk model thrown to glide between 10 and 15 m from a chosen individual, as done in earlier studies (e.g. Cunningham & Magrath, 2017). Songs and contact calls, which were used as experimental controls, were recorded opportunistically from undisturbed birds in the absence of any predators, and not associated in time with any model presentations. All vocalizations were recorded using a Sennheiser ME66 directional microphone (Wedemark, Germany) connected to a Marantz PMD671 digital recorder (Cumberland, RI, U.S.A.) and saved as wave files at 44.1 kHz and 16 bits. Playback audio files were created using Raven Pro 1.5 (Bioacoustics Research Program, 2014). Each magpie received unique recordings or unique combinations of two recordings in both experiments.

### Video analysis and measurement of responses

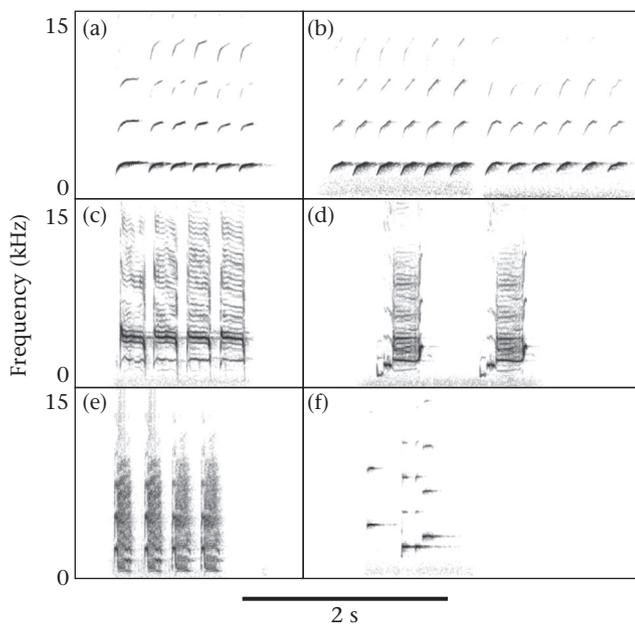
We used video recordings to measure the responses of magpies blindly in relation to playback treatments. Prior to analysis, the timing of playbacks was marked visually on the recording using Adobe Premier Pro, and then each video was given a random number and the playback section of the video was muted before blind scoring. We analysed videos in random order and used two measures to assess the strength of magpie response to playback treatments: (1) type of response at the start of playbacks (flee from the arena, scan or no response/continue feeding); and (2) the delay to resume feeding after the end of a playback, a measure of the duration of response that accounts for differences in the duration of playbacks. The delay to resume feeding was < 0 s for birds that resumed feeding before the end of playback. Time was measured to the nearest frame (20 ms) and analysed in seconds. In six trials,

magpies did not return first to the arena to feed after fleeing in response to a playback. We were still able to score these cases blind because the return to the ground was either visible on the video recording or audible on the audio track of the video by the sound of the bird landing or by our vocal commentary that it had landed. We analysed videos from the two cameras separately, and then calculated mean values for the delay to resume feeding. In all cases, the score for the type of response was the same for both cameras.

### Experiment 1: Number of Callers

We tested whether magpies responded with antipredator behaviour more frequently or for longer to two miners alarm calling than to one miner alarm calling. We used miner aerial alarm calls as previous work showed that magpies react to these calls as if an aerial predator is present (Dawson Pell et al., 2018). We created four playback treatments: (1) one miner giving an aerial alarm call; (2) two miners each giving one aerial alarm call; (3) one crimson rosella producing a 'piping' contact call; and (4) two crimson rosellas each producing one 'piping' contact call (Fig. 2). Crimson rosellas are common at our study sites and pose no threat to magpies or other birds, and we used their contact calls as controls because they are not given in response to danger (Higgins, 1999; Magrath, Pitcher, & Gardner, 2009). Our playbacks were designed to give multiple cues that there were either one or two birds calling. These cues included the number of calls, timing of calls, individual from whom the call was recorded and spatial location of calls. In one-caller treatments, a single call was broadcast through only one of the two speakers. In two-caller treatments, each call was broadcast through a separate speaker, with a 50 ms period of silence between them. This period of silence was too short for a single bird to have moved between speaker locations, and in addition each call was recorded from a different miner. All aerial alarm calls consisted of six elements. We created one-caller or two-caller rosella control playback treatments that roughly matched the duration of noisy miner alarm treatments (mean  $\pm$  SD, range: one-caller:  $1.5 \pm 0.3$  s, 1.2 – 2.1 s; two-caller:  $3.0 \pm 0.5$  s, 2.5 – 4.0 s). All possible treatment order combinations that did not entail sequential alarm calls were presented twice. Calls were broadcast such that the loudest element in the call was 75 dB at 10 m, which is close to the mean amplitude of the loudest element of natural noisy miner aerial alarm calls at 10 m (mean  $\pm$  SD:  $75.3 \pm 3.6$  dB;  $N = 15$ ). All playback audio files were filtered below 300 Hz to remove most of the background noise. In total, we created 16 unique playback audio files for each of the four treatments, so that all 16 focal birds received different playbacks, and individual calls were not reused in the one- and two-caller treatments.

Although our experiment was designed to test the effect on magpie behaviour of the number of callers, a potential complexity is that a greater mean response to playback of two callers might arise if one of the callers has a more evocative alarm call than the single caller. We addressed this possibility first by experimental design, where we controlled for both element number and rate of delivery. We used a constant number of elements in the alarm calls (above), as that is one way in which birds encode information about the degree of danger (Fallow & Magrath, 2010; Leavesley & Magrath, 2005; Templeton, Greene, & Davis, 2005). The rate of delivery of elements within calls can also communicate the degree of danger in some species (Blumstein & Armitage, 1997; Wheatcroft, 2015), so within each set of playbacks to an individual, we matched one-caller and two-caller playbacks by element rate. The mean duration of each alarm call within the two-caller playbacks was always within 0.1 s of the corresponding one-caller alarm, and a similar number of magpies received one-caller alarms with a faster, slower or intermediate element rate



**Figure 2.** Spectrograms showing examples of vocalizations used in experiments. (a) Noisy miner aerial alarm call from a single bird, and (b) noisy miner aerial alarm calls given by two birds in quick succession, played from different speakers, from experiment 1. (c) Magpie-lark general alarm call, (d) magpie-lark song as a control, (e) crimson rosella general alarm call and (f) crimson rosella 'bell' contact call as a control, all from experiment 2. Experiment 1 also used crimson rosella 'bell' contact calls as controls. Each panel shows 0–15 kHz on the y axis. Spectrograms were created using a Blackman window function with a 1024 sample size and 95% overlap in Raven Pro 1.5.

compared with both the corresponding two-caller alarms. Element rate of alarm calls ranged between 3 and 5.6 elements/s.

In addition to controlling for the number and rate of elements within alarm calls in the playback experiment, we also tested experimentally how miner alarm calls might encode information on the degree of danger. To do so, we recorded noisy miner aerial alarm calls given in response to sparrowhawk models gliding past them at about 10 m (greater urgency) or 30 m (lower urgency) at 13 different sites. We assumed that a closer predator implies greater danger. Subsequent acoustic analyses detected only very small and nonsignificant mean differences in six measures of acoustic structure of alarm calls given in response to predator models gliding at the two distances (Table A1). Based on effect sizes, the number of call elements produced per second was the feature most likely to convey information, if any, on the degree of danger. Given that we controlled for this feature in the experimental design, information about the degree of danger was unlikely to have resulted in a greater magpie response to two-caller than one-caller alarm playbacks. See the Appendix for full details on this experiment.

#### Experiment 2: Number of Species Calling

We tested whether magpies responded with antipredator behaviour more frequently or for longer to two different species each giving an alarm call versus two individuals of the same species alarm calling, thus controlling for the number of individuals calling. We used magpie responses to crimson rosella and magpie-lark general alarm calls because both alarms are used by the two species in response to a variety of threats and disturbances, including to flying and terrestrial predators or in social interactions (above; Higgins, 1999; Higgins et al., 2006). Their use across different contexts suggests that either species calling alone is likely to be perceived by magpies as ambiguous or as signalling low risk, yet both species calling would indicate a greater chance that a predator is present. That is because calling by both species suggests that the calls are more likely to be independent and elicited by a predator, as the two species do not form mixed-species groups and alarm calls are unlikely to be both related to within-species conflict.

There were six playback treatments: (1) two magpie-lark alarm calls; (2) two rosella alarm calls; (3) a magpie-lark alarm call and a rosella alarm call; (4) two magpie-lark songs; (5) two rosella contact calls; and (6) a magpie-lark song and a rosella contact call (Fig. 2). We used the song and contact calls as controls. All alarm call playbacks consisted of four-element alarm calls, whereas we matched the control playbacks to the duration of the alarm calls (mean  $\pm$  SD, range: magpie-lark alarms: 1.9  $\pm$  0.1 s, 1.8–2.2 s; rosella alarms: 1.7  $\pm$  0.1 s, 1.7–1.8 s; mixed-species alarms: 1.9  $\pm$  0.1 s, 1.6–2.1 s). As in experiment 1, we created stereo playbacks such that each call was broadcast through a separate speaker. However, in this experiment the second call started in the middle of the first call. Calls were overlapped, rather than played sequentially, as preliminary trials on a different magpie population indicated that magpies were more likely to respond when these calls were overlapped. For the mixed-species treatments, we alternated which species was broadcast first. With 72 possible treatment order combinations, we selected 24 treatment orders randomly to present to 24 focal birds but constrained the choice so that, as much as possible, each of the six treatments was equally broadcast across the sequence of six playbacks. All playback audio files were filtered below 200 Hz, rather than 300 Hz as in the first experiment, because of the low-frequency components of rosella alarm calls. In total, we created 24 unique playbacks for each of the six treatments.

We broadcast vocalizations at natural amplitudes for each species. Magpie-lark vocalizations were broadcast such that the loudest element in the call was 72 dB at 10 m, which is close to the

average amplitude of the loudest element of natural alarm calls at 10 m (mean  $\pm$  SD: 71.9  $\pm$  4.5 dB; range 59.9–77.0 dB;  $N = 11$ ). Rosella vocalizations were broadcast with the loudest element at 63 dB at 10 m, which is again close to the natural mean for the loudest element at 10 m (61.1  $\pm$  4.1 dB; range 51.9–70.5 dB;  $N = 17$ ).

#### Statistical Analysis

We used statistical models to compare within experiments the type of response and delay to resume feeding after the playback finished. To test whether magpies were more likely to respond to alarm treatments than to control treatments, we used bias-reduced binomial response generalized linear models (0 = no response; 1 = response, pooling scan and flee). As magpies often responded to alarm treatments and ignored control treatments, quasi-separation in the data meant we could not use generalized linear mixed models. However, we were able to use generalized linear mixed models, with binomial errors, logit link functions and Laplace approximations, when examining the response just to alarm call playbacks. In experiment 1, magpies always either scanned or fled to the miner alarm playbacks, so we tested whether they were more likely to flee than scan following two noisy miner alarm calls than one noisy miner alarm call. In experiment 2, magpies rarely fled to alarm calls (two cases over all playbacks to all magpies), so we tested whether they were more likely to respond at all (scan or flee) to mixed-species alarm calls than to two same-species alarm calls. We excluded control playbacks for these analyses. To compare the delay to resume feeding across the different treatments, we fitted linear mixed models using REML and used *t* tests with Satterthwaite approximations of degrees of freedom. All models had the following covariates: ID of focal magpie as either a fixed effect (bias-reduced models) or random effect (generalized and linear mixed models); sex of focal magpie; total number of magpies within 10 m of the food plate during the trial; order of presentation; and type of treatment. For experiment 2, we also tested the hypothesis that mixed-species alarm calls produced intermediate responses between the two single-species alarm calls (additive effects, rather than interactive ones) using post hoc contrasts.

All statistical analyses were conducted in R v3.4.0 (R Core Team, 2017). We used the `brglm()` function of the `brglm` package (Kosmidis, 2017) to construct bias-reduced binomial-response generalized linear models. Likelihood ratio tests, used to compare models with and without a variable, were conducted using the `anova()` function, and 95% confidence intervals were calculated using the `confint()` function, both from the base stats R package. We used the `glmer()` and `lmer()` functions of the `lmerTest` package (Kuznetsova, Brockhoff, & Christensen, 2016) to construct generalized and linear mixed models. Contrasts were constructed using the `contrast()` and `lsmeans()` function of the `lsmeans` package (Lenth, 2016).

#### Ethical Note

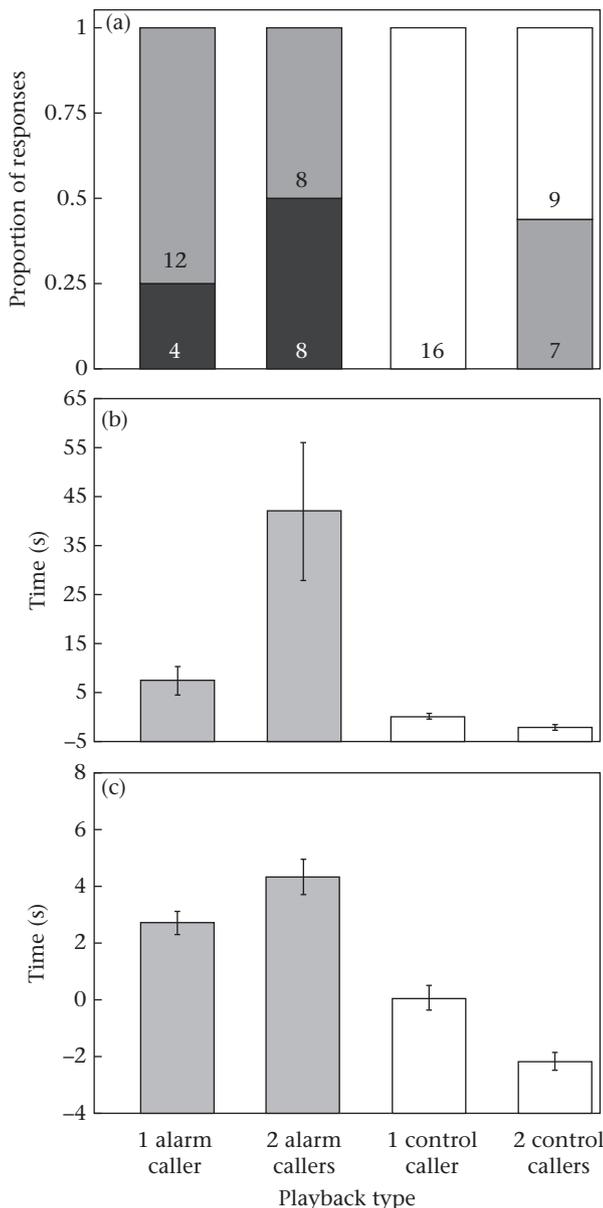
All work was carried out under a licence from the Australian National University Ethics Committee (permit A2015/67). We used matched experimental designs, to control for individual variation and thereby reduce the sample sizes needed. Individual focal birds received only two alarm call playbacks in experiment 1 and three in experiment 2. Most birds scanned after alarm calls, usually for less than 5 s, and so lost very little foraging time. Some birds fled after alarm call playbacks, but usually resumed feeding within 1 min. Control playbacks prompted either no response or a very short period of scanning. We used model predators to prompt sufficient alarm calls to enable fully replicated playback experiments, and to

assess whether information on the degree of danger encoded in alarm calls could have affected our results. We used variation in plumage to identify focal magpies for experiments, and so did not need to capture birds.

## RESULTS

### Experiment 1: Number of Callers

Magpies responded more strongly after playback of two noisy miners giving aerial alarm calls than after a single miner giving an alarm. As expected, magpies were more likely to scan or flee following miner alarm calls than after the control contact calls of crimson rosellas (Fig. 3a; log odds ratio:  $-4.18 \pm 1.12$  SE;  $Z = -3.74$ ,



**Figure 3.** Responses of magpies to playbacks in experiment 1. (a) Immediate responses to playback: black = flee, grey = scan and white = no response; numbers in bars = breakdown of responses. (b, c) Mean  $\pm$  SE delay to resume feeding after playback of noisy miner alarm calls (grey bars) or rosella 'bell' contact calls as controls (white bars); (b) includes all cases whereas (c) excludes the four cases where a bird fled to one alarm caller and eight cases where a bird fled to two alarm callers.  $N = 16$  birds received all treatments. Tables 1–3 show statistical analyses.

$P < 0.001$ ). Focusing just on alarm call playbacks, magpies fled on more occasions when there were two miners calling compared to one miner calling, but the difference was not statistically significant (Fig. 3a, Table 1; 8/16 birds fled after two callers compared to 4/16 after a single caller:  $P = 0.14$ ). None the less, magpies took  $34.5 \pm 13.4$  s longer to resume feeding after the end of playback of two callers compared to playback of one caller (Fig. 3b, Table 2;  $P = 0.02$ ). When treatments where magpies fled were excluded, birds delayed feeding  $1.7 \pm 0.6$  s longer after the end of the two-caller playback (Fig. 3c, Table 3;  $P = 0.01$ ). The sex of the focal magpie, playback order and the number of magpies present during a trial did not significantly affect the response to alarm calls (Tables 1–3).

### Experiment 2: Number of Species Calling

Magpies responded similarly regardless of the number of species giving alarm calls (Fig. 4). Magpies were more likely to respond by either scanning or fleeing after playback of alarm calls than control playbacks (Fig. 4a; contrast of all alarm versus all control playbacks: log odds ratio =  $-2.63 \pm 0.55$ ;  $Z = -4.80$ ,  $P < 0.0001$ ). There was also a longer delay to resume feeding following alarm calls compared to control calls of the same combination of species ( $1.9 \pm 0.4$  s,  $t_{112} = -5.5$ ,  $P < 0.0001$ ; Fig. 4b). Despite this antipredator response, magpies were not more likely to respond to any specific alarm call combination than any other alarm call combination (Fig. 4a, Table 4). Similarly, magpies had a similar delay to resume feeding after a playback had finished, regardless of the alarm call combination (Fig. 4b, Table 5).

In contrast to experiment 1, the sex of the focal bird and the number of nonfocal magpies present both affected the focal bird's responses to alarm calls. Female magpies took  $0.9 \pm 0.4$  s longer to resume feeding than males (Table 5). For every additional magpie present during a trial, there was a  $0.5 \pm 0.2$  s shorter delay to resume feeding (Table 5). Playback presentation order also affected the response, with birds taking approximately 0.6–0.7 s longer to resume feeding after the end of the third alarm call playback than after the end of an alarm call playback on a previous day (Table 5).

**Table 1**

The log odds of magpies fleeing versus scanning in response to one or two noisy miner alarm calls in experiment 1

	Estimate (SE)	Z	P
Intercept	-1.07 (0.84)	-1.27	0.20
Sex (male – female)	0.60 (0.78)	0.76	0.45
Number of other magpies present	-0.10 (0.40)	-0.24	0.81
Presentation order (2nd – 1st)	-0.55 (0.78)	-0.70	0.48
Number of alarm callers (two – one)	1.15 (0.79)	1.47	0.14

Values are from the output of a bias-reduced binomial response generalized linear model.  $N = 16$  birds received both treatments. Bird ID was included as a random effect. Data are shown in Fig. 3a.

**Table 2**

The duration of magpie responses to noisy miner aerial alarm playbacks in experiment 1, including each bird for each treatment

	Estimate (SE)	t (df)	P
Intercept	11.75 (14.81)	0.79 (23.77)	0.44
Sex (male – female)	-15.40 (14.73)	-1.05 (12.06)	0.32
Number of other magpies present	-4.18 (7.52)	-0.56 (19.79)	0.58
Presentation order (2nd – 1st)	13.41 (13.30)	1.01 (12.60)	0.33
Number of alarm callers (two – one)	<b>34.47 (13.35)</b>	<b>2.58 (12.67)</b>	<b>0.02</b>

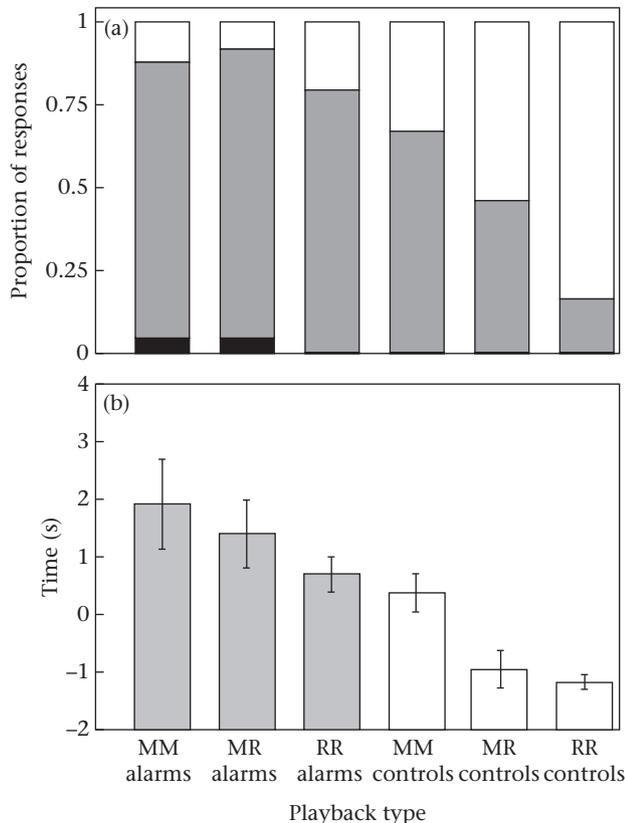
Values are from the output of a linear mixed model. Duration of response is measured as the delay to resume feeding after the end of playback, which controls for playback length.  $N = 16$  birds received both treatments. Bird ID was included as a random effect. Significant term is shown in bold. Means are plotted in Fig. 3b.

**Table 3**

The duration of magpie responses (s) to noisy miner aerial alarm playbacks in experiment 1, excluding cases when a bird fled after playback

	Estimate (SE)	<i>t</i> (df)	<i>P</i>
Intercept	<b>3.89 (0.58)</b>	<b>6.67 (14.72)</b>	<b>&lt;0.001</b>
Sex (male – female)	–0.08 (0.66)	–0.12 (10.13)	0.91
Number of other magpies present	–0.52 (0.34)	–1.55 (9.14)	0.16
Presentation order (2nd – 1st)	–1.24 (0.54)	–2.28 (8.05)	0.05
Number of alarm callers (two – one)	<b>1.74 (0.55)</b>	<b>3.18 (8.01)</b>	<b>0.01</b>

Values are from the output of a linear mixed model. The duration of the response is measured as the delay to resume feeding after the end of playback, which controls for playback length. *N* = 12 birds did not flee to a single alarm caller; *N* = 8 birds did not flee to two alarm callers. Bird ID was included as a random effect. Significant terms are shown in bold. Means are plotted in Fig. 3c.



**Figure 4.** Responses of magpies to playbacks in experiment 2. (a) Immediate responses to playback: black = flee, grey = scan and white = no response. (b) Mean  $\pm$  SE delay to resume feeding after playback of alarm calls (grey bars) or nonalarm control calls (white bars), excluding the two cases where a bird fled (shown in (a)). Controls were magpie-lark song and rosella ‘bell’ contact calls. All playbacks included two individuals calling; MM = two magpie-larks calling, MR = one magpie-lark and one rosella and RR = two rosellas. Half the MR playbacks started with a magpie-lark and half with a rosella. *N* = 24 birds received all treatments. Tables 4 and 5 show statistical analyses.

The response following mixed-species alarm calls was intermediate between those following single-species magpie-lark and crimson rosella alarm calls. The delay until resuming feeding was similar to the mean of the two species (mean of mixed minus species’ mean:  $-0.1 \pm 0.2$  s;  $t_{41.53} = -0.29$ ,  $P = 0.78$ ). This implies that mixed-species alarm calls prompted an additive effect of each individual species’ alarm calls.

## DISCUSSION

When responding to heterospecific alarm calls, magpies were affected by the number of individuals calling but not by the number

**Table 4**

The log odds of magpies responding (scanning or fleeing) versus not responding to two magpie-lark alarms (MM), two crimson rosella alarms (RR) and a mixture of magpie-lark and crimson rosella alarms (MR), in experiment 2

	Estimate (SE)	<i>Z</i>	<i>P</i>
Intercept	6.61 (3.18)	2.08	0.04
Sex (male – female)	–2.76 (1.58)	–1.74	0.08
Number of other magpies present	–1.19 (0.96)	–1.24	0.21
Presentation order (2nd – 1st)	–1.13 (0.96)	–1.17	0.24
Presentation order (3rd – 1st)	1.40 (1.37)	1.02	0.31
Presentation order (3rd – 2nd)	2.53 (1.40)	1.80	0.07
Alarm treatment (MM – MR)	–0.70 (1.21)	–0.57	0.57
Alarm treatment (RR – MR)	–1.25 (1.12)	–1.10	0.27
Alarm treatment (RR – MM)	–0.55 (1.00)	–0.55	0.58

Values are from the output of a generalized linear mixed model. *N* = 24 birds received each treatment. Bird ID was included as a random effect. Data are shown in Fig. 4a.

**Table 5**

The duration of response to playback, in response to two magpie-lark alarms (MM), two crimson rosella alarms (RR) or a mixture of magpie-lark and crimson rosella alarms (MR), in experiment 2

	Estimate (SE)	<i>F</i> (df1, df2)/ <i>t</i> (df) <sup>a</sup>	<i>P</i>
<b>ANOVA</b>			
Sex		<b>4.62 (1, 21.46)</b>	<b>0.04</b>
Number of other magpies present		<b>5.21 (1, 56.33)</b>	<b>0.03</b>
Presentation order		<b>3.83 (2, 41.48)</b>	<b>0.03</b>
Alarm treatment <sup>b</sup>		0.86 (2, 42.16)	0.43
<b>Linear mixed model</b>			
Sex (male – female)	<b>–0.86 (0.40)</b>	<b>–2.15 (21.46)</b>	<b>0.04</b>
Number of other magpies present	<b>–0.45 (0.20)</b>	<b>–2.28 (56.33)</b>	<b>0.03</b>
Presentation order (2nd – 1st)	–0.12 (0.27)	–0.42 (41.38)	0.67
Presentation order (3rd – 1st)	<b>0.60 (0.28)</b>	<b>2.15 (41.64)</b>	<b>0.04</b>
Presentation order (3rd – 2nd)	<b>0.72 (0.28)</b>	<b>2.60 (41.41)</b>	<b>0.01</b>
Alarm treatment (MM – MR)	0.25 (0.28)	0.88 (42.11)	0.38
Alarm treatment (RR – MR)	–0.11 (0.28)	–0.40 (41.58)	0.69
Alarm treatment (RR – MM)	–0.36 (0.28)	–1.28 (42.81)	0.21

Values are from the output of a linear mixed model. The duration of the response is measured as the delay to resume feeding after the end of playback, which controls for playback length. *N* = 24 birds received each treatment, but two cases when a bird fled were excluded (one MM, one MR). Bird ID was included as a random effect. Significant effects are shown in bold. Data are shown in Fig. 4b.

<sup>a</sup> *F* values are given for the ANOVA and *t* values for the linear mixed model.

<sup>b</sup> Effect of alarm treatment was similarly nonsignificant when the two sequence orders of mixed alarm calls were treated as separate ( $F_{3, 45.34} = 0.58$ ,  $P = 0.63$ ).

of species calling. Magpies responded for a longer period to the alarm calls of two noisy miners than the alarm call of a single miner. By contrast, magpies did not respond more strongly after the mixed alarm calls of two individuals of different species, magpie-larks and rosellas, compared with two callers of those same species. The alarm calls of more individuals could therefore indicate a greater probability or degree of danger, as predicted, but we suggest that the value of multiple species calling is likely to depend on the particular species and alarm calls.

Magpies responded more strongly to heterospecific social information from more individuals, comparable to the use of conspecific information by other species (Conradt & Roper, 2005; Sloan & Hare, 2008; Wolf et al., 2013). When playbacks mimicked two noisy miners giving alarm calls, rather than a single caller, magpies responded for a longer period, during which they became vigilant and often fled. The longer duration of response did not simply reflect the duration of alarm calling, because we measured the time to resume feeding after the end of each playback. Furthermore, even for those magpies that did not flee, birds scanned for longer in response to two miners. These results are consistent with empirical and theoretical work showing that individuals can reduce uncertainty of social information by collating

information from multiple individuals (Sumpter, Krause, James, Couzin, & Ward, 2008; Wolf et al., 2013). Calling by multiple individuals could more reliably indicate danger either because there is a reduced probability of multiple false alarms (Sumpter et al., 2008; Wolf et al., 2013), or because urgent threats and dangerous predators prompt more individuals to call (Blumstein et al., 2004; Sloan & Hare, 2008). In either case, individuals should benefit from responding more strongly when more individuals call, regardless of whether the recipient of the calls is the intended receiver or an eavesdropper.

Magpies did respond to the general alarm calls of magpie-larks and rosellas but appeared to respond much less to either species' alarm calls than to noisy miner aerial alarm calls. Birds were more likely to respond, either by scanning or fleeing, to the alarm calls of these species than to the corresponding control, nonalarm, vocalization of the species. However, they also responded less to the alarm calls of either species than to the aerial alarm calls given by two noisy miners (the relevant comparison because it controls for the number of callers). In the first experiment, eight of the 16 individuals fled when two miners were giving aerial alarms, and all other individuals scanned. By contrast, in the second experiment only one of 24 individuals fled to magpie-lark alarms, while none of the 24 birds fled to the rosella alarms. Similarly, magpies responded for longer after two miners' alarm calling than after the alarm calls of either two magpie-larks or two rosellas (Figs 3 and 4). These results support our assumption that magpies perceive magpie-lark and rosella alarm calls as ambiguous or indicating lower danger than miner aerial alarms, given the broad contexts in which these two species' alarms are given. By contrast, miner aerial alarm calls are given specifically to airborne threats, including raptors, signalling more immediate danger (Cunningham & Magrath, 2017; Farrow et al., 2017).

Contrary to our prediction, magpies did not respond more strongly when there were two species calling (magpie-larks and rosellas) compared to two individuals of the same species. They were no more likely to respond with flight or scanning to the mixed-species alarm playback, and responded for similar periods. We suggest that the lack of difference might be because each of the calling species provides similar information on danger, so that their combination did not provide additional information. By contrast, if two calling species did provide different information, then their combination could provide new information to a listening species. For example, suppose the listening individual of one prey species was vulnerable to medium-sized predators and that it can be alerted to predators by two other prey species, one of which is mostly vulnerable to small predators and the other to large predators. If either of the two species calls alone, then the predator will usually be too small or large to pose a threat, whereas if they both call, this would indicate a medium-sized predator (Magrath et al., 2015). In our experiment, magpie-larks and rosellas are both substantially smaller than magpies, and so may be vulnerable to a similar suite of predators, including those that pose little threat to magpies, so that their combined calls do not indicate greater danger. A related issue could occur with general alarm calls that may or may not indicate the presence of any predator. If individuals within a species often give alarm calls during within-species social conflict, as well as when a predator is present, then a listening species would judge either calling alone as unreliable. However, both species calling at the same time would imply the presence of a predator; within-species conflict is unlikely to synchronize calls between species, whereas the presence of a predator could do so. By contrast, if the calling species merely vary in the proportion of true and false alarms, and give relatively few alarms in a social

context, then there may be little additional information derived from the combination of species calling. It would clearly be useful to quantify the contexts of magpie-lark and rosella alarms; perhaps one or both rarely give alarm calls in a social context.

Our results suggest that magpie responses to a mixture of rosella and magpie-lark alarm calls could be of intermediate intensity between multiple calls for each of these individual species. Although there was no significant difference in any measures of response across alarm playback treatments, the duration of response to mixed-species playbacks was very similar to the mean of the individual species playbacks (Fig. 4). An average response might occur if listeners assess different sources of risk independently to get an overall probability of danger, rather than assessing risk associated with specific combinations of calls or responding just to the species indicating the greater danger. We are aware of no previous experiment directly comparing avian responses to mixed-species alarms with those to the constituent species alone. However, indirect evidence from birds suggests that there could be variable outcomes. For example, pied currawongs, *Strepera graculina*, respond more strongly to mimicry by brown thornbills, *Acanthiza pusilla*, of a two-species alarm chorus than to the alarm calls of thornbills alone (Igc, McLachlan, Lehtinen, & Magrath, 2015). Furthermore, a follow-up experiment in that study suggested this was because of the number of species mimicked, so that the response to a mixed-species chorus would be greater than to either species alone. By contrast, playbacks of natural alarm choruses given by members of mixed-species bird flocks in Sri Lanka did not prompt greater responses than to alarms by two of the species that contributed to the natural choruses (Goodale & Kotagama, 2008). Overall, we suggest that responses to mixed-species alarm choruses will vary according to the reliability, relevance and meaning of constituent calls, but we clearly need further direct tests in a range of species.

Female magpies responded for a longer period to the general alarm calls of magpie-larks and crimson rosellas than did males, and the presence of other magpies reduced the duration of responses to those calls. Differences in foraging may make female birds more vulnerable to predators and allow less time for vigilance (Post & Götmark, 2006a; 2006b). If this was true of magpies, then females may place greater value on social information about predators. We did not measure time budgets, but female magpies may spend more time foraging than males, particularly leading up to the breeding season, which is when our experiments were conducted. In addition to the sex difference, focal birds responded for shorter periods when there were more magpies nearby, potentially because individuals face a lower risk of predation in larger groups (Brown, Bongiorno, DiCapua, Ivan, & Roh, 2006; Lazarus, 1979; but see ; Hollén & Manser, 2006). Another possibility is that greater competition for food in larger groups led to a quicker resumption of feeding. In contrast to their responses to general alarm calls in experiment 2, we did not detect sex or group size differences in response to miner aerial alarm calls, perhaps because the risks of a partial response are too great in that context. Sex-specific and group size differences might occur only for situations of lower danger.

In conclusion, our study reveals how an eavesdropping species takes the number of callers and the species calling into account when responding to heterospecific alarm calls. Assessing the reliability of social information is challenging, even if it originates from conspecifics (Beauchamp, 2010; Blumstein et al., 2004; Giraldeau et al., 2002; Wolf et al., 2013), and it is more complex when assessing heterospecifics (Magrath et al., 2015; Schmidt et al., 2010; Seppänen et al., 2007). Using information from other species

presents additional challenges because it increases the number of sources of information, which are also likely to vary in both reliability and relevance. Future work will need to address how individuals use information from multiple species. They might assess each calling species independently, and subsequently use an averaged response, or they might respond solely to the most reliable and relevant species. Alternatively, individuals might respond to specific combinations of calls, which could be more, or less, informative than those from either species alone. Our results are consistent with independent assessment of calling species, but stronger tests are likely to require different species or call types.

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## References

- Bartoń, K. (2017). *MuMIn: Multi-Model Inference. R package version 1.40.0*. <https://cran.r-project.org/web/packages/MuMIn/index.html>.
- Beauchamp, G. (2010). Determinants of false alarms in staging flocks of semi-palmated sandpipers. *Behavioral Ecology*, *21*, 584–587.
- Beauchamp, G., & Ruxton, G. D. (2007). False alarms and the evolution of antipredator vigilance. *Animal Behaviour*, *74*, 1199–1206.
- van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society B*, *271*, 957.
- Bioacoustics Research Program. (2014). *Raven Pro: Interactive sound analysis software (Version 1.5)*. Ithaca, NY: The Cornell Lab of Ornithology.
- Blumstein, D. T., & Armitage, K. B. (1997). Alarm calling in yellow-bellied marmots: I. The meaning of situationally variable alarm calls. *Animal Behaviour*, *53*, 143–171.
- Blumstein, D. T., Verneyre, L., & Daniel, J. C. (2004). Reliability and the adaptive utility of discrimination among alarm callers. *Proceedings of the Royal Society of London B*, *271*, 1851–1857.
- Bousquet, C. A., Sumpster, D. J., & Manser, M. B. (2011). Moving calls: A vocal mechanism underlying quorum decisions in cohesive groups. *Proceedings of the Royal Society of London B Biological Sciences*, *278*, 1482–1488.
- Bro-Jørgensen, J., & Pangle, W. M. (2010). Male topi antelopes alarm snort deceptively to retain females for mating. *American Naturalist*, *176*, E33–E39.
- Brown, G. E., Bongiorno, T., DiCapua, D. M., Ivan, L. I., & Roh, E. (2006). Effects of group size on the threat-sensitive response to varying concentrations of chemical alarm cues by juvenile convict cichlids. *Canadian Journal of Zoology*, *84*, 1–8.
- Burton, T., & Martin, A. A. (1976). Analysis of hybridization between black-backed and white-backed magpies in south-eastern Australia. *Emu*, *76*, 30–36.
- Caro, T. (2005). *Antipredator defenses in birds and mammals*. Chicago, IL: University of Chicago Press.
- Champely, S. (2017). *pwr: Basic Functions for Power Analysis. R package version 1.2-1*. <https://cran.r-project.org/web/packages/pwr/index.html>.
- Conradt, L., & Roper, T. J. (2005). Consensus decision making in animals. *Trends in Ecology & Evolution*, *20*, 449–456.
- 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., 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.
- Dawson Pell, F. S. E., Potvin, D. A., Ratnayake, C. P., Fernández-Juricic, E., Magrath, R. D., & Radford, A. N. (2018). Birds orient their heads appropriately in response to functionally referential alarm calls of heterospecifics. *Animal Behaviour*, *140*, 109–118.
- Dittus, W. (1984). Toque macaque food calls: Semantic communication concerning food distribution in the environment. *Animal Behaviour*, *32*, 470–477.
- Evans, C., & Evans, L. (1999). Chicken food calls are functionally referential. *Animal Behaviour*, *58*, 307–319.
- 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.
- Fichtel, C., & Kappeler, P. M. (2002). Anti-predator behavior of group-living Malagasy primates: Mixed evidence for a referential alarm call system. *Behavioural Ecology and Sociobiology*, *51*, 262–275.
- Flower, T. P., Gribble, M., & Ridley, A. R. (2014). Deception by flexible alarm mimicry in an African bird. *Science*, *344*, 513–516.
- Giraldeau, L. A., Valone, T. J., & Templeton, J. J. (2002). Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London - B*, *357*, 1559–1566.
- 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.
- Goodale, E., & Kotagama, S. W. (2005). Alarm calling in Sri Lankan mixed-species bird flocks. *Auk*, *122*, 108–120.
- Goodale, E., & Kotagama, S. W. (2008). Response to conspecific and heterospecific alarm calls in mixed-species bird flocks of a Sri Lankan rainforest. *Behavioral Ecology*, *19*, 887–894.
- Hare, J. F., & Atkins, B. A. (2001). The squirrel that cried wolf: Reliability detection by juvenile Richardson's ground squirrels (*Spermophilus richardsonii*). *Behavioral Ecology and Sociobiology*, *51*, 108–112.
- Higgins, P. J. (1999). *Handbook of Australian, New Zealand and Antarctic birds. In Parrots to Dollarbird (Vol. 4)*Melbourne, Australia: Oxford University Press.
- Higgins, P. J., Peter, J. M., & Cowling, S. J. (2006). *Handbook of Australian, New Zealand and Antarctic birds. In Boatbill to Starlings (Vol. 7)*Melbourne, Australia: Oxford University Press.
- Hollén, L. I., Bell, M. B., & Radford, A. N. (2008). Cooperative sentinel calling? Foragers gain increased biomass intake. *Current Biology*, *18*, 576–579.
- Hollén, L. I., & Manser, M. B. (2006). Ontogeny of alarm call responses in meerkats, *Suricata suricatta*: The roles of age, sex and nearby conspecifics. *Animal Behaviour*, *72*, 1345–1353.
- Igc, B., McLachlan, J., Lehtinen, I., & Magrath, R. D. (2015). Crying wolf to a predator: Deceptive vocal mimicry by a bird protecting young. *Proceeding of the Royal Society B*, *282*, 20150798.
- Kaplan, G., Johnson, G., Koberoff, 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.
- Kern, J. M., Sumner, S., & Radford, A. N. (2016). Sentinel dominance status influences forager use of social information. *Behavioral Ecology*, *27*, 1053–1060.
- Koops, M. A. (2004). Reliability and the value of information. *Animal Behaviour*, *67*, 103–111.
- Kosmidis, I. (2017). *brglm: Bias Reduction in Binary-Response Generalized Linear Models. R package version 0.6.1*. <https://cran.r-project.org/web/packages/brglm/index.html>.
- Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2016). *lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-33*. <https://cran.r-project.org/web/packages/lmerTest/index.html>.
- Lazarus, J. (1979). The early warning function of flocking in birds: An experimental study with captive quails. *Animal Behaviour*, *27*, 855–865.
- Leavesley, A. J., & Magrath, R. D. (2005). Communicating about danger: Urgency alarm calling in a bird. *Animal Behaviour*, *70*, 365–373.
- Lenth, R. V. (2016). Least-squares means: the R package lsmeans. *Journal of Statistical Software*, *69*, 1–33.
- 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., Pitcher, B. J., & Gardner, J. L. (2009). An avian eavesdropping network: Alarm signal reliability and heterospecific response. *Behavioral Ecology*, *20*, 745–752.
- Handbook of Australian, New Zealand and Antarctic birds. In Marchant, S., & Higgins, P. J. (Eds.), *Raptors to Lapwings (Vol. 2)*, (1993). Melbourne, Australia: Oxford University Press.
- Møller, A. P. (1988). False alarm calls as a means of resource usurpation in the great tit *Parus major*. *Ethology*, *79*, 25–30.
- Møller, A. P. (1989). Deceptive use of alarm calls by male swallows, *Hirundo rustica*: A new paternity guard. *Behavioral Ecology*, *1*, 1–6.
- Munn, C. A. (1986). Birds that 'cry wolf'. *Nature*, *319*, 143–145.
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*, 133–142.
- Post, P., & Götmark, F. (2006a). Foraging behavior and predation risk in male and female Eurasian Blackbirds (*Turdus merula*) during the breeding season. *Auk*, *123*, 162–170.
- Post, P., & Götmark, F. (2006b). Predation by sparrowhawks *Accipiter nisus* on male and female pied flycatchers *Ficedula hypoleuca* in relation to their breeding behaviour and foraging. *Journal of Avian Biology*, *37*, 158–168.
- R Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

- Rainey, H. J., Zuberbühler, K., & Slater, P. J. (2004). Hornbills can distinguish between primate alarm calls. *Proceedings of the Royal Society B*, 271, 755.
- Ramakrishnan, U., & Coss, R. G. (2000). Age differences in the responses to adult and juvenile alarm calls by bonnet macaques (*Macaca radiata*). *Ethology*, 106, 131–144.
- Ribot, R. F. H., Berg, M. L., Buchanan, K. L., & Bennett, A. T. D. (2011). Fruitful use of bioacoustic alarm stimuli as a deterrent for crimson rosellas (*Platycercus elegans*). *Emu*, 111, 360–367.
- Ridley, A. R., & Raihani, N. J. (2007). Facultative response to a kleptoparasite by the cooperatively breeding pied babbler. *Behavioral Ecology*, 18, 324–330.
- 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.
- Searcy, W. A., & Nowicki, S. (2005). *The evolution of animal communication: reliability and deception in signaling systems*. Princeton, NJ: Princeton University Press.
- Seeley, T. D., & Visscher, P. K. (2004). Quorum sensing during nest-site selection by honeybee swarms. *Behavioral Ecology and Sociobiology*, 56, 594–601.
- Selya, A. S., Rose, J. S., Dierker, L. C., Hedeker, D., & Mermelstein, R. J. (2012). A practical guide to calculating Cohen's  $f^2$ , a measure of local effect size, from PROC MIXED. *Frontiers in Psychology*, 3, 111. <https://doi.org/10.3389/fpsyg.2012.00111>.
- Seiple, S., & McComb, K. (1996). Behavioural deception. *Trends in Ecology & Evolution*, 11, 434–437.
- 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.
- Sirof, E. (2006). Social information, antipredatory vigilance and flight in bird flocks. *Animal Behaviour*, 72, 373–382.
- Sloan, J. L., & Hare, J. F. (2008). The more the scarier: Adult Richardson's ground squirrels (*Spermophilus richardsonii*) assess response urgency via the number of alarm signalers. *Ethology*, 114, 436–443.
- Sumpter, D. J., Krause, J., James, R., Couzin, I. D., & Ward, A. J. (2008). Consensus decision making by fish. *Current Biology*, 18, 1773–1777.
- Taylor, M. (1992). *Birds of the Australian Capital Territory: An Atlas*. Canberra, Australia: Canberra Ornithologists Group.
- Templeton, J., & Giraldeau, L. (1995). Patch assessment in foraging flocks of European starlings: Evidence for the use of public information. *Behavioral Ecology*, 6, 65–72.
- Templeton, J., & Giraldeau, L. (1996). Vicarious sampling: The use of personal and public information by starlings foraging in a simple patchy environment. *Behavioral Ecology and Sociobiology*, 38, 105–114.
- Templeton, C. N., Greene, E., & Davis, K. (2005). Allometry of alarm calls: Black-capped chickadees encode information about predator size. *Science*, 308, 1934–1937.
- Ward, A. J., Krause, J., & Sumpter, D. J. (2012). Quorum decision-making in foraging fish shoals. *PLoS One*, 7, e32411.
- Ward, A. J., Sumpter, D. J., Couzin, I. D., Hart, P. J., & Krause, J. (2008). Quorum decision-making facilitates information transfer in fish shoals. *Proceedings of the National Academy of Sciences*, 105, 6948–6953.
- Ward, P., & Zahavi, A. (1973). The importance of certain assemblages of birds as "information centres" for food-finding. *Ibis*, 115, 517–534.
- Wheatcroft, D. (2015). Repetition rate of calls used in multiple contexts communicates presence of predators to nestlings and adult birds. *Animal Behaviour*, 103, 35–44.
- Wolf, M., Kurvers, R. H., Ward, A. J., Krause, S., & Krause, J. (2013). Accurate decisions in an uncertain world: Collective cognition increases true positives while decreasing false positives. *Proceedings of the Royal Society of London B*, 280, 20122777.

## APPENDIX. ACOUSTIC COMPARISON OF ALARM CALLS

To examine the possibility that urgency-based information from noisy miner aerial alarm calls could influence differences between one-caller and two-caller treatments in experiment 1, we compared the acoustic structure of noisy miner alarm calls given towards near and far gliding predator models. The acoustical structure of alarm calls that conveys urgency-based information can be examined by presenting individuals with predators at different distances, with predators at closer proximity constituting a greater degree of danger (Fallow & Magrath, 2010; Leavesley & Magrath, 2005). Here, we presented noisy miners with a hawk model thrown to glide by at either 10 m or 30 m from the caller. We

chose these distances as they were at the two extremes at which we presented gliding hawks to collect noisy miner aerial alarm calls for experiment 1.

Upon arriving at a site, we located a focal noisy miner that we subsequently followed for at least 5 min. If during a 5 min period there were no aerial alarm calls or predators present in the area, we presented the focal noisy miner with a hawk model gliding at one of the two distances while another observer recorded its vocal responses using a Sennheiser ME66 directional microphone connected to a Marantz PMD671 digital recorder, and saved in a wave file of 44.1 kHz and 16 bits. Following the first presentation, we waited at least 15 min and presented another individual within the same location with the hawk model gliding at the other distance. As noisy miners are highly mobile, it was impossible to target the same individual with gliders thrown at both distances. We repeated this at 13 different sites across Canberra to ensure we tested different populations.

We used Raven Pro 1.4 to measure frequency and time characteristics of the alarm calls. For each element in a call we measured the: (1) lowest frequency and (2) highest frequency (Hz), defined as the frequencies where the amplitude was 20 dB lower than at the peak frequency; (3) peak frequency (Hz), the frequency with the maximum amplitude; (4) duration (s); and (5) average entropy, which measures the tonality of the sound, with more tonal sounds having lower entropy. In addition, for the full call we measured (6) element rate, defined as the number of elements in the call per second. Spectrograms used for measurements were created using a Blackman window function with a 372 sample size, a temporal grid resolution of 0.75 ms with 90.3% overlap and a frequency grid resolution of 11.7 Hz.

We used linear mixed models and linear models to compare the acoustic structure of the alarm calls given towards close and distant gliding hawk models. For acoustic measurements taken on individual elements, we created mixed models with the measurement of interest as the response, site ID (1–13), the sequential order of the element in the call and the distance of the glider (10 m or 30 m) as fixed effects, and call ID as a random intercept (as we measured multiple elements per call). For element rate, we created a linear model with element rate set as the response, and site ID and distance of glider set as covariates. To improve model fit, as well as homogeneity and normality of residuals, we rank transformed element rate in the analysis. To calculate effect sizes for hawk models at the two distances, we calculated Cohen's  $f^2$  following Selya, Rose, Dierker, Hedeker, and Mermelstein (2012), and using either conditional  $R^2$  values for mixed models calculated following Nakagawa and Schielzeth (2013) or multiple  $R^2$  for the element rate model. We then conducted a power analysis to calculate the sample size required for us to detect a significant effect at least 80% of the time given that there is a difference between alarm calls given to hawk models gliding at the two distances. Linear mixed models and linear models were respectively fitted using the lmer() and lm() functions. Conditional  $R^2$  values for mixed models were calculated using the r.squaredGLMM() of the MuMIn package (Bartoń, 2017), and power analyses were conducted using the pwr.f2.test() function of the pwr package (Champely, 2007).

**Table A1**Attributes of noisy miner aerial alarm calls given to hawk models gliding at 10 m ( $N = 13$ ) or 30 m ( $N = 13$ ) from the caller

Effect	Estimate (SE)	<i>F</i>	<i>df</i> 1, <i>df</i> 2	<i>P</i>	Cohen's $f^2$ *	<i>N</i> required†
<b>Lowest frequency (Hz)</b>						
Site ID	NA	2.43	12, 12.9	0.06		
Element order	−0.19 (3.60)	0.003	1, 164.4	0.96		
Distance (10 m–30 m)	−29.05(50.68)	0.33	1, 13.2	0.58	0.008	941
<b>Highest frequency (Hz)</b>						
Site ID	NA	0.15	12, 13.9	0.99		
Element order	27.34 (4.22)	41.90	1, 161.2	<0.001		
Distance (10 m–30 m)	−71.37 (76.70)	0.87	1, 14.0	0.37	0.023	343
<b>Peak frequency (Hz)</b>						
Site ID	NA	1.26	12, 13.2	0.34		
Element order	23.62 (4.21)	31.50	1, 166.3	<0.001		
Distance (10 m–30 m)	−22.36 (53.91)	0.17	1, 13.5	0.68	0.018	425
<b>Element duration (s)</b>						
Site ID	NA	4.03	12, 11.0	0.01		
Element order	−0.001 (0.0004)	8.04	1, 164.9	0.005		
Distance (10 m–30 m)	0.0004 (0.004)	0.01	1, 12.4	0.92	0.011	694
<b>Element entropy (u)</b>						
Site ID	NA	1.83	12, 13.7	0.14		
Element order	0.01 (0.006)	5.52	1, 166.0	0.02		
Distance (10 m–30 m)	−0.06 (0.07)	0.61	1, 14.1	0.45	0.024	333
<b>Element rate (number/s)</b>						
Site ID	NA	2.17	12, 13	0.09		
Distance (10 m–30 m)	−0.32 (0.34)	1.41	1, 13	0.26	0.108	73

Values are from the output from linear mixed models (all measures except element rate, with call ID as a random effect) or a linear model (element rate). NA: not applicable.

\* Effect sizes (small:  $f^2 = 0.02$ ; medium:  $f^2 = 0.25$ ).

† Sample sizes required to detect a significant effect when there is a difference between calls given to the hawk model gliding at close and far distances. Calculations are based on a power analysis with  $\alpha = 0.05$ ,  $\beta = 0.20$ , and Cohen's  $f^2$  was calculated from our data.