



Original Article

Visual obstruction, but not moderate traffic noise, increases reliance on heterospecific alarm calls

Chaminda P. Ratnayake,^{a,○} You Zhou,^a Francesca S.E. Dawson Pell,^{a,b} Dominique A. Potvin,^{a,○} Andrew N. Radford,^{b,○} and Robert D. Magrath^{a,○}

^aDivision of Ecology and Evolution, Research School of Biology, 46 Sullivan's Creek Road, Australian National University, Canberra 2600, Australia and ^bSchool of Biological Sciences, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

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Animals rely on both personal and social information about danger to minimize risk, yet environmental conditions constrain information. Both visual obstructions and background noise can reduce detectability of predators, which may increase reliance on social information, such as from alarm calls. Furthermore, a combination of visual and auditory constraints might greatly increase reliance on social information, because the loss of information from one source cannot be compensated by the other. Testing these possibilities requires manipulating personal information while broadcasting alarm calls. We therefore experimentally tested the effects of a visual barrier, traffic noise, and their combination on the response of Australian magpies, *Cracticus tibicen*, to heterospecific alarm calls. The barrier blocked only visual cues, while playback of moderate traffic noise could mask subtle acoustic cues of danger, such as of a predator's movement, but not the alarm-call playback. We predicted that response to alarm calls would increase with either visual or acoustic constraint, and that there would be a disproportionate response when both were present. As predicted, individuals responded more strongly to alarm calls when there was a visual barrier. However, moderate traffic noise did not affect responses, and the effect of the visual barrier was not greater during traffic-noise playback. We conclude that a reduction of personal, visual information led to a greater reliance on social information from alarm calls, confirming indirect evidence from other species. The absence of a traffic-noise effect could be because in Australian magpies hearing subtle cues is less important than vision in detecting predators.

Key words: alarm calls, anti-predator vigilance, anthropogenic noise, cross-modal interaction, eavesdropping, information constraint, visual barrier.

INTRODUCTION

Animals acquire information about danger from multiple senses, and from both personal and social sources. Predators can be detected visually, acoustically, chemically, physically, and through substrate vibrations (Stevens 2013). In addition to assessing risk as they engage in any activity, individuals often also show periods of dedicated “vigilance,” when they cease some other activities to enhance their ability to detect danger (Beauchamp 2015). For example, animals often stop feeding and adopt postures or raised positions to increase their ability to scan the environment visually (Caro 2005;

Beauchamp 2015). “Vigilance” can also apply to other senses, such as when mule deer, *Odocoileus hemionus*, stop chewing to enhance hearing and so increase auditory surveillance during periods of greater risk (Lynch et al. 2015). Regardless of the sensory channel, information can be acquired from two sources, personal and social (Danchin et al. 2004; Dall et al. 2005). Personal information derives from direct assessment of danger, such as by seeing or hearing predators, while social information comes indirectly from the behavior of others, such as from alarm calls warning of danger (Caro 2005; Zuberbühler 2009). In general, personal information can be more informative and reliable, but comes at the cost of greater investment in vigilance, while social information may be less informative or reliable, but is likely to be less costly to obtain (Danchin et al. 2004). Overall, therefore, animals face the complex task of integrating information from multiple senses, and from personal and social sources, when making decisions about anti-predator behavior.

Address correspondence to R.D. Magrath. E-mail: robert.magrath@anu.edu.au. F.S.E. Dawson Pell is now at the Department of Animal and Plant Sciences, University of Sheffield, UK. D.A. Potvin is now at the School of Science and Engineering, University of the Sunshine Coast, Australia.

Visual barriers can affect antipredator behavior by reducing the ability to gain personal information and so increasing reliance on social information. While birds and mammals can show reduced vigilance when closer to protective cover, such as vegetation into which they can flee, they show increased vigilance near visual obstructions that do not offer protection but can conceal predators or obscure their approach (Beauchamp 2010). This effect has been shown experimentally, where adding visual barriers can lead to greater vigilance and other changes in behavior that imply an assessment of greater risk (Lazarus and Symonds 1992; Harkin et al. 2000; Devereux et al. 2006; Bednekoff and Blumstein 2009; Embar et al. 2011; McWaters and Pangle 2021). Such differences in personal visual information could affect the flow of information in natural communities, by changing the value of personal versus social information on danger. For example, bird species that sally for flying insects are likely to have a clear view of approaching threats as well, which might explain their low responsiveness to heterospecific alarm calls compared to species that glean food near substrates that block their view (Goodale and Kotagama 2008; Goodale et al. 2010; Martínez and Zenil 2012; Martínez et al. 2016; Jones and Sieving 2019). A within-species contrast also supports this interpretation: New Holland honeyeaters, *Phylidonyris novaehollandiae*, take longer to spot gliding hawk models, and are more likely to flee to playback of alarm calls, when feeding on flowers compared to when perching in the open seeking flying insects (McLachlan et al. 2019). Despite evidence that visual barriers increase the response to alarm calls, we are aware of no direct experimental tests.

Background noise can impose additional informational constraints by compromising the ability to respond to other sounds, and so reduce both personal and social information about danger (Barber et al. 2010). Although predators attempt to be stealthy, locomotion causes at least some sound production (Larsson 2012, 2014), and prey animals can use the sound of movement to detect predators. For example, nestling white-browed scrubwrens, *Sericornis frontalis*, fall silent after playback of the sounds of predator footfalls (Magrath et al. 2007), and female Túngara frogs, *Physalaemus pustulosus*, approach calling males more cautiously if they also hear the flapping sounds of a predatory bat (Bernal et al. 2007). Prey often also attend to calls of predators (review: Hettena et al. 2014). Background noise could reduce detection of these important sounds, by distracting individuals or through acoustic masking, and so could reduce the ability to gain personal information on danger (Barber et al. 2010; Chan et al. 2010; Brumm 2013). In birds and mammals, playback experiments show that background noise can reduce response to alarm calls, indicating that noise can also reduce access to social information about danger. Considering responses to conspecific alarm calls, ambient noise can mask conspecific flee alarm calls in superb fairy-wrens, *Malurus cyaneus* (Zhou et al. 2019), traffic noise can mask great tit, *Parus major*, mobbing alarm calls (Templeton et al. 2016), and white noise can mask parental alarm calls in tree swallows, *Tachycineta bicolor* (McIntyre et al. 2014). Heterospecific alarm calls are also a widespread source of social information about danger (Magrath, Haff, Fallow, et al. 2015), and noise can affect such eavesdropping too. For example, Northern cardinals, *Cardinalis cardinalis*, did not respond to playback of heterospecific alarm calls at noisy locations near roads (Grade and Sieving 2016), and dwarf mongooses, *Helogale parvula*, were less likely to flee to heterospecific alarm calls during playback of traffic noise (Morris-Drake et al. 2017). Overall, both natural and anthropogenic background noise can restrict information on danger, in a similar way to visual barriers but in a different sensory channel.

In addition to compromising the acquisition of acoustic information, noise can affect the gathering and use of other sensory information. An increase in noise can prompt animals to rely more on visual information, presumably to compensate for reduced ability to conduct acoustic surveillance. For example, playback of traffic noise led to increased vigilance in dwarf mongooses, prairie dogs, *Cynomys ludovicianus*, and white-crowned sparrows, *Zonotrichia leucophrys* (Shannon et al. 2014; Ware et al. 2015; Kern and Radford 2016), and chaffinches, *Fringilla coelebs*, became more vigilant during playback of white noise (Quinn et al. 2006). Similarly, California ground squirrels, *Otospermophilus beecheyi*, were more vigilant in areas with greater wind-turbine noise (Rabin et al. 2006), and after playback of natural background noise from rivers or cicada choruses (Le et al. 2019). Noise can also affect the acquisition of other sensory input, such as playback of boat noise slowing the response of Caribbean hermit crabs, *Coenobita clypeatus*, to a threatening but silent visual stimulus (Chan et al. 2010), and traffic noise reducing dwarf mongoose responses to predator feces (Morris-Drake et al. 2016). In general, there has been little focus on these cross-modal interactions and their ecological consequences, despite the fact that noise and other sensory constraints will often co-occur, especially with increasing anthropogenic noise (Barber et al. 2010; Halfwerk and Slabbekoorn 2015).

We experimentally tested the effect of both visual restrictions and traffic noise on the response of Australian magpies, *Cracticus tibicen*, to heterospecific alarm calls. Magpies feed on the ground and are vulnerable to a variety of predators. They have their own alarm calls (Kaplan et al. 2009; Kaplan and Rogers 2013; Silvestri et al. 2019; Dutour et al. 2020), but also eavesdrop on other species' alarm calls including those of noisy miners, *Manorina melanocephala* (Dawson Pell et al. 2018; Iqic et al. 2019). We predicted that reducing personal information, either through a visual barrier or playback of moderate traffic noise (at a level designed to mask sounds of predators but not nearby alarm calls), would lead to a greater response to audible miner alarm calls. Furthermore, we predicted the greatest response to alarm calls when magpies were subject to both visual and acoustic constraints. This is because the loss of information from one sensory channel could not be compensated by greater reliance on the other channel, so that the two constraints would interact synergistically, rather than being merely additive.

METHODS

Study species and site

Australian magpies are large (ca. 300 g for the local subspecies) passerines in the family Artamidae, that are omnivorous and feed mostly on the ground (Higgins et al. 2006). They are found throughout most of Australia and breed on year-round territories, occupied by pairs or family groups consisting of a dominant pair and their offspring. Magpies are vulnerable to large raptors and terrestrial predators, and are also aggressive to both large and small predators (Higgins and Marchant 1993; Higgins et al. 2006). They give a variety of alarm calls to terrestrial and aerial predators (Kaplan et al. 2009; Dutour et al. 2020). Magpies also eavesdrop on the alarm calls of other species, including noisy miners (Dawson Pell et al. 2018; Iqic et al. 2019). Noisy miners are colonial honeyeaters (family Meliphagidae) that are common in eastern Australia in open woodland and urban areas (Higgins et al. 2001), and forage anywhere from the ground to the tree canopy, eating primarily

invertebrates and nectar (Ashley et al. 2009). Although smaller (ca. 65 g) than magpies, they also aggressively mob many other species, including predators (Dow 1977; Sewell and Catterall 1998; Piper and Catterall 2003). Noisy miners have a variety of alarm calls, including mobbing alarm calls, given primarily to terrestrial predators and perched raptors, and aerial alarm calls, given to airborne raptors (Cunningham and Magrath 2017; Farrow et al. 2017; Holt et al. 2017). Magpies respond appropriately to the different miner alarm calls, including by looking up after playback of aerial alarm calls and looking around after playback of mobbing alarm calls (Dawson Pell et al. 2018).

We studied magpies in Canberra, Australia (35°17'S, 149°08'E), from February to August 2018. The two study sites were the Australian National University and adjacent urban parks, and Weston Park and adjacent parkland. Magpies at both sites are habituated to people (Dawson Pell et al. 2018; Igic et al. 2019), and appeared not to be affected by our presence. We identified individual magpies using a combination of location, sex and plumage patterns, following methods in Dawson Pell et al. (2018). Canberra magpies have variable back patterns, because they lie in a hybrid zone of two subspecies with different patterns, and individuals were photographed and catalogued before being used in experiments. Noisy miners were common throughout both sites, which had areas of lawn, on which magpies feed, and trees, used for refuge and nesting. The study sites had a variety of mammalian and avian predators of magpies and miners, including dogs, *Canis lupus familiaris*, cats, *Felis catus*, foxes, *Vulpes vulpes*, brown goshawks, *Accipiter fasciatus*, collared sparrowhawks, *A. cirrocephalus*, and occasionally other raptors including peregrine falcons, *Falco peregrinus* (Taylor 1992; Higgins et al. 1999; Cunningham and Magrath 2017).

Experimental overview and general methods

Experimental overview

We used two experiments to examine how restrictions on visual and auditory perception affected magpies' responses to noisy miner mobbing alarm calls. In the first experiment, we examined the effect of a visual barrier on the antipredator response to playback of alarm calls. In the second experiment, we investigated the combined effects of a visual barrier and playback of traffic noise on the response to alarm-call playback. Both experiments used a repeated-measures design in which each individual focal bird received all treatments, to control for any individual differences in responsiveness to alarm calls. There was an equal number of each sex in each experiment, and we controlled for group size by experimental design. We give details on designs and predictions below, in the sections on each experiment.

Alarm-call audio recording and playback preparation

Noisy miner mobbing alarm calls were recorded in the Canberra study sites, and prompted by gliding model collared sparrowhawks (model details in Magrath, Haff, McLachlan, et al. 2015). These life-sized models were made of foam and painted to resemble adults or juveniles. The models were thrown by hand, usually travelled for 20–40 m, and were aimed to glide 5–10 m past a miner. Miners produce aerial alarm calls when models are airborne but switch immediately to mobbing alarm calls after models land (Cunningham and Magrath 2017). Calls were recorded from 3 to 28 m, using a Marantz 670 digital recorder, sampling wav files at 44.1 kHz and 16 bits, and a Sennheiser ME66 directional microphone. The experiments used calls recorded at the study sites previously (Magrath

and Bennett 2012; Dawson Pell et al. 2018; Igic et al. 2019), or during this study in 2018.

Playbacks were prepared using Raven Pro 1.5 software (Charif et al. 2010). Mobbing alarm call tracks comprised five elements, to keep calls comparable among playbacks (Figure 1a). Some were originally five-element calls, while others were trimmed or had one or two later elements duplicated, using original inter-note intervals, to construct the playback tracks. Background noise below 300 Hz was filtered out. The mean (\pm SD) duration of the 40 tracks was 1.4 ± 0.02 s, with a range of 1.2–1.9 s. Alarm calls were broadcast using a Roland R-05 audio player and full-range Scan Speak 10F/4424G00 loudspeaker (frequency response 200–10,000 Hz). Playback tracks were iteratively adjusted so that broadcasts had an amplitude of 68 dB at 10 m (mean amplitude of loudest element, averaged over frequency and time), which was the distance to focal birds during playback and is similar to the mean amplitude of these call elements at that distance (69.3 ± 3.9 dB; Magrath and Bennett 2012). Because each alarm call note is short, their average power was measured in Raven Pro 1.5 using field recordings which also included a tone of known amplitude, as measured by a Brüel & Kjær 2240 sound-level meter (A-weighting, fast).

Experiment arena and field procedure

We conducted experiments in a mobile, virtual arena that included a central 18 cm plate provisioned with grated cheese, and including a visual barrier, audio playback equipment and video cameras recording magpie responses (Figure 2). The barrier was made of a metal frame, 50 cm wide and 54 cm high, covered with acoustically transparent fabric. The fabric was a blue-gray Rycote windshield, designed to cover a parabolic reflector, that was visually opaque but attenuated sounds by <1 dB. The barrier was placed within 1–2 cm of one side of the plate, and could be positioned upright or lying down. Magpie eye height is about 26 cm when standing, so the barrier blocked visibility in the direction of the playbacks when upright, but not when lying down, when the fabric extended <14 cm above the ground. We laid the barrier down, rather than removing it, so that any effect of the presence of the barrier itself was controlled; we could therefore test specifically for the effect of restricted vision. The loudspeaker broadcasting alarm calls was placed 10 m from the food plate, behind the barrier from the perspective of a magpie at the plate. The experimental arena also had two Panasonic HC-V770 video cameras that enabled quantification of magpie behavior. The cameras were placed 6 m from the food plate at a 90° angle, with both cameras unobscured by the barrier, allowing a clear view of birds' responses regardless of their orientation or whether other birds obscured visibility from one camera. The cameras were on tripods and at magpie eye height, and recorded at a resolution of 1920×1080 pixels at 50 frames/s. Both experiments were conducted in the open away from nearby cover (mean \pm SD = 14.3 ± 4.8 m, range = 7.7–29.6 m), and we used the same location and orientation of the arena for each treatment for a focal bird.

We conducted playbacks when the focal magpie was feeding at the plate. After setting up the experimental arena, we first identified the focal individual from photographs, and then started the video cameras and lured the focal bird to the plate containing grated cheese. We waited for at least 1 min of undisturbed feeding before we broadcast the noisy miner alarm call. However, we waited for at least 15 min before conducting playbacks after there were any natural alarm calls or dogs nearby, and at least 5 min after people

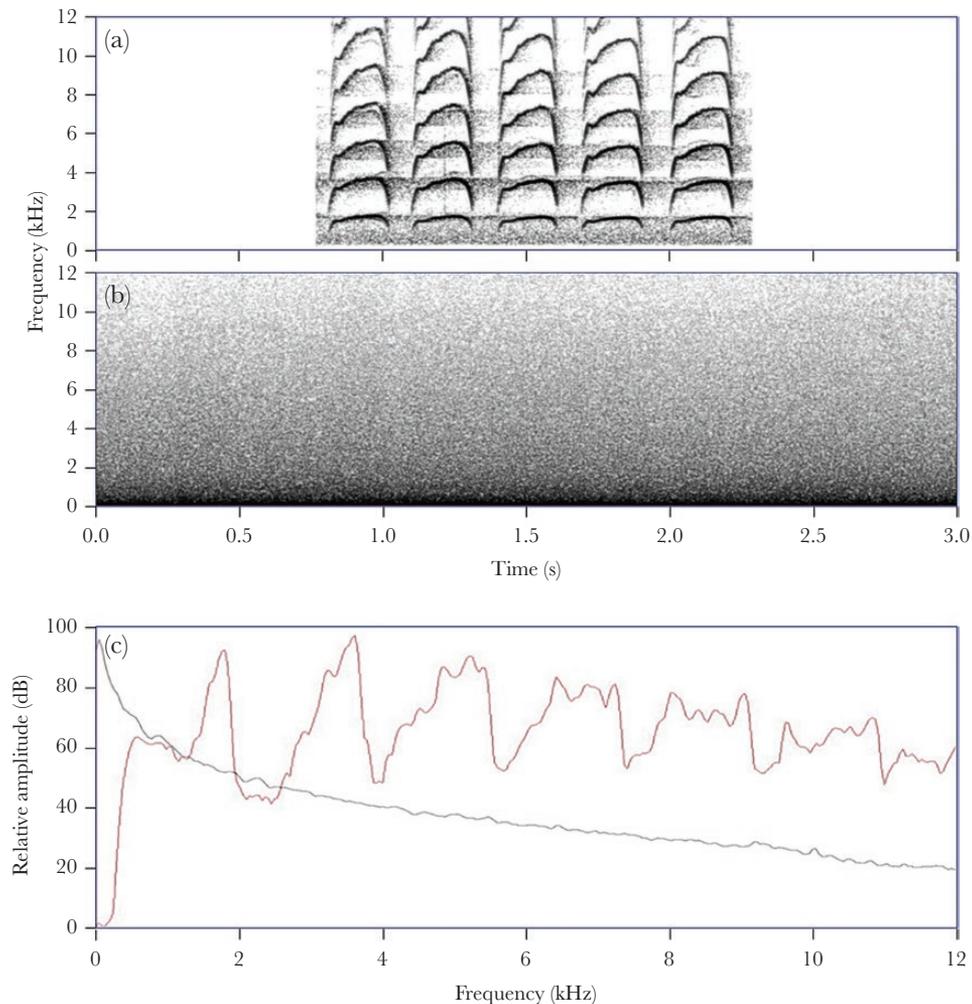


Figure 1

Examples of sounds used in playback experiments. Spectrograms of (a) a noisy miner mobbing alarm call, and (b) a short sample of traffic noise. (c) Spectra of the two sounds, with traffic noise represented by the black, descending line, and the mobbing alarm call by the red line, showing the call harmonics. Sound files were calibrated to be broadcast at 63 dB (traffic noise), and 68 dB (mobbing alarm calls). This 5 dB difference is retained in the figure. Spectrograms and spectra were prepared in Raven 1.5, using a Blackman window function, 1024 sample size and 95% temporal overlap.

passed by. Individuals received successive treatments on separate days, after an interval of 1–3 days, to reduce carry-over effects.

Group size can affect response to alarm calls (Iglie *et al.* 2019), so we kept group size constant for any given focal bird to control experimentally for any possible effects. We did so by waiting until the same number of birds was present, and all birds were behind the barrier, before carrying out the alarm-call playback on a focal bird. In the first experiment, five focal birds were tested alone, six had one extra bird, four had two extra birds, and one had four extra birds ($n = 16$ focal birds, two treatments each). In the second experiment, six were tested alone, 10 had one extra bird, and eight had two extra birds, except for two focal birds for which one playback had only one extra bird ($n = 24$ focal birds, four treatments each).

Quantifying behavior

We used video analysis to quantify the focal magpie's immediate response and duration of response. Videos were prepared in Adobe Premiere Pro and Adobe Encoder by one person for scoring by another. A visual marker was placed in the corner of the video frame

to indicate the start and end of the alarm-call playback, and a transparent red square was placed over the focal individual just before playback to ensure the correct bird was scored. The video was then exported without the sound track; playbacks were therefore scored blind in Experiment 2 with respect to whether there was traffic-noise playback, but the barrier was visible in both experiments. We categorized the bird's response to playback as: 1 = no response, the bird continuing to feed without raising its head; 2 = scan, the bird raised its head and looked around while staying in place; 3 = move, the bird raised its head and moved to the side or away from the barrier while looking around; 4 = flee, the bird flew away from the food plate. The score therefore ordered the strength of anti-predator response, from weakest (1) to strongest (4). Birds that responded did so during the playback or within 0.26 s of the end of playback. We also measured response duration as the number of video frames between the start of the response and the resumption of feeding, including when the magpie returned to the ground to feed after it had fled. At 50 frames/s, each frame is 0.02 s.

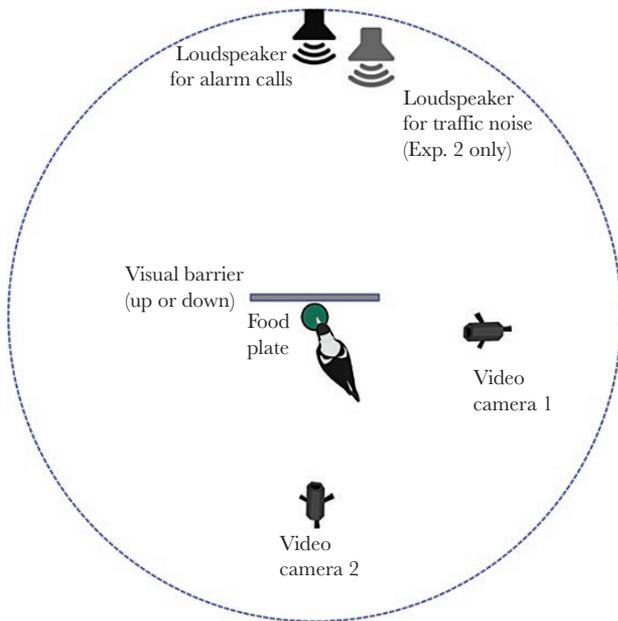


Figure 2

Experimental arena. The mobile, virtual experimental arena was centered on a plate providing food that was placed next to a cloth visual barrier that could be upright, which blocked the view of the focal magpie, or lying down, which did not block the view of the focal magpie. The visual barrier did not block the transmission of sound. Playbacks were carried out when the focal magpie was at the food plate. The loudspeaker playing noisy miner alarm calls was placed 10 m from the food plate, behind the barrier from the perspective of the focal bird. In Experiment 2, there was a second loudspeaker that broadcast traffic noise, placed 8–10 m from the food plate. The two video cameras recorded magpie responses to playback, and were placed 6 m from the food plate at a 90° angle to each other.

Experimental design and predictions

Experiment 1: effect of visual restriction alone

We tested how a restriction on personal visual information, imposed by the visual barrier, affected the response to heterospecific alarm calls. A visual restriction means that individuals are less able to assess danger themselves, through personal information, and so should rely more on acoustic information, including social information from the alarm calls of others. We therefore predicted that magpies would respond more strongly to noisy miner mobbing alarm calls when the visual barrier was up, when they had a restricted ability to assess personally the presence of danger, compared to when the barrier was down, when they had an unrestricted view. Alarm calls were played only when there was no predator nearby, so greater personal information should lead to a reduced response.

We used a matched-pair design to investigate responses toward alarm calls depending on the position of the visual barrier. Each of the 16 focal birds, in different social groups, received playbacks when the barrier was up (visual restriction) or down (no visual restriction). The sample included eight males and eight females, with the playback order balanced within each sex. Each focal individual received a unique alarm-call playback, to avoid pseudoreplication (Kroodsma et al. 2001), but the same playback for the two barrier positions, to control for any differences in evocativeness of exemplars. Ten of the 16 intervals between treatments were of 1 day, four of 2 days, and two of 3 days. This experiment was carried out on the Australian National University campus and adjacent parks.

Experiment 2: combined effects of visual and acoustic restrictions

We tested the combined effect of visual and acoustic restrictions on magpie responses to heterospecific alarm calls. The physical barrier restricted visual information, as in the first experiment, while playback of moderate traffic noise was designed to mask subtle cues of predator presence, but not the mobbing alarm-call playback. Mobbing alarm calls are typically given to predators on the ground, which may betray their presence through vocalizations or sounds of movement including footfalls (Introduction). We therefore predicted that both the visual and acoustic restriction would lead to a greater response to the alarm-call playback. In addition, we predicted that the combination of a visual barrier and moderate traffic noise would lead to the strongest anti-predator responses, because in that situation the loss of information from one sensory mode cannot be fully compensated by the other sensory mode. By contrast, if there was a visual barrier but no noise, birds could compensate for reduced visual information by relying more on acoustic information about the presence of predators, while if there was noise but no visual barrier, birds could compensate for reduced acoustic information by relying more on visual information. We therefore predicted that there would be a statistical interaction between the visual barrier treatment (up vs. down) and the acoustic treatment (playback of moderate traffic noise or not) on the response to alarm-call playback.

We carried out playbacks to 24 individuals, from separate social groups, with each individual receiving all four treatments: 1) traffic noise and barrier up; 2) no traffic noise and barrier up; 3) traffic noise and barrier down; and 4) no traffic noise and barrier down. Each individual received unique traffic-noise and alarm-call playbacks. We used an orthogonal Latin square design with uniform columns and rows to avoid confounding order and carry-over effects on repeated treatment measures (Jones and Kenward 2015). Given four treatments for each individual, there were 96 playbacks, but the video recording failed in two cases, so we could not measure responses; the final analyses therefore included 94 playbacks. The different treatment orders were randomly allocated across individuals. Fifty-five of the 72 intervals between treatments were of 1 day, 10 of 2 days, and seven of 3 days. This experiment was carried out at Weston Park and adjacent areas around Lake Burley Griffin, so includes a different set of birds to Experiment 1.

Traffic noise for use in playbacks was recorded from eight locations, near roads bounding the study sites. We again used a Marantz 670 recorder, sampling wav files at 44.1 kHz and 16 bits, but with a Sennheiser ME62 omnidirectional microphone. We recorded during busy periods when there was a stream of traffic, so that we had a fairly uniform level of noise. We then prepared 24 unique 20-min playback tracks, edited to avoid quiet periods and prominent loud sounds, and including a fade in of 10 s that avoided startling any birds during the onset of traffic noise (Figure 1b,c). The sounds were not filtered. Noise was broadcast from a JBL Charge 3 amplified loudspeaker with two 10-W drivers, with a frequency response of 65–20,000 Hz. This loudspeaker was used for traffic playback as it had a greater power output and broader frequency range than the loudspeaker used for alarm-call broadcast (above), which was appropriate for those calls and was used for all treatments. Noise playback tracks were iteratively adjusted on computer to produce an output of 61–63 dBA at 10 m, so that the loudspeaker could be placed between 8 and 10 m from the food plate to make the traffic noise 63 dBA at the focal individual's location, as

measured using a Brüel & Kjør 2240 sound-level meter. This amplitude corresponded to a distance of about 30 m from the local roads (mean estimate at 30 m: 63.1 dBA \pm 3.3 SD, range = 58.9–66.2; estimates based on measurement at four sites using the sound-level meter). The traffic-noise loudspeaker was placed about 1 m to one side of the loudspeaker broadcasting alarm calls, as viewed from the food plate, so was also behind the barrier for the focal bird.

In the field, we started the noise playback once the arena was set up and started the video cameras when magpies entered the experimental arena. We then waited to play the alarm call until the focal individual was at the food plate, together with the appropriate number of other group members for that location (above). There was a variable period from when the noise loudspeaker was turned on and when the alarm call was broadcast, depending on when the conditions for playback were met (above). The experimental design was to carry out the alarm-call playback before the 20 min traffic-noise playback had stopped. We noted the time the loudspeaker was turned on in a subset of playbacks with noise, and the median period until alarm-call playback was 2.1 min, IQR 1.5–4.3, with a range of 1.0–19.0 ($n = 34$ of 48 playbacks with noise). We avoided places with prominent background noise, such as that of construction, so that background noise was of much lower amplitude than the 63 dBA traffic-noise playback, and would have little effect on the overall noise perceived by the focal bird. The mean \pm SD background noise before playbacks was of 44.2 \pm 3.5 dBA, range = 36–54, and after playback 43.9 \pm 3.5 dBA, range = 36–54.

The moderate traffic-noise playback was designed to impair a magpie's ability to detect subtle acoustic information about danger, and so disrupt auditory surveillance, but not to mask the mobbing alarm-call playback. This subtle information could include the low-amplitude sound of movement, from a nearby predator (Barber et al. 2010) or distant alarm calls (Grade and Sieving 2016; Templeton et al. 2016; Zhou et al. 2019). Although the traffic-noise playback was likely to mask acoustic cues of danger, it was unlikely to mask the alarm-call playbacks because of differences in both amplitude and frequency (Figure 1; Brumm and Slabbekoorn 2005; Dooling and Blumenrath 2013). Mobbing alarm calls were broadcast at 68 dB, compared to traffic noise at 63 dB. In addition, as is generally true of urban noise (Slabbekoorn and den Boer-Visser 2006; Francis and Barber 2013), our traffic recordings were dominated by low frequencies, whereas miner alarm calls had much higher amplitudes than traffic noise at their higher peak frequencies.

Statistical analyses

We used cumulative link mixed models (CLMM) to analyze the immediate categorical response to alarm-call playback. The response was measured as an ordered categorical variable with four levels: 1 = no response, 2 = scan in place, 3 = move while scanning, and 4 = flee. CLMM analysis is appropriate for our ordinal measure of response, that orders the strength of response but does not imply quantitatively equal increments between categories (Agresti 2013). In both experiments, barrier position (up or down) and order of treatment were included as fixed effects, and focal individual was included as a random term to account for individual differences. Experiment 2 additionally included traffic-noise playback (presence or absence) and its interaction with barrier position as fixed effects. We used the `clmm` and `clmm2` functions of the `ordinal` package, and model fitting was assessed using Hessian number (Christensen 2019). We used a probit link function and an equidistant threshold in all CLMM models. Maximum likelihood estimates of parameters

were obtained using Gauss-Hermite quadrature method with 20 quadrature nodes.

We used generalized linear mixed models (GLMMs) to analyze the duration of response to alarm-call playbacks. Duration was measured as the number of video frames (50 per second) and, in both experiments, barrier position (up or down) and order of treatment were fixed effects, and individual identity was the random term. In Experiment 2, traffic-noise playback (presence or absence) and its interaction with barrier position were additionally included as fixed effects. We fitted cumulative distribution functions to identify the best fit for the response variable and, subsequently checked for zero-inflation using simulations with `Sim()` function comparing observed and predicted zeros (Zuur and Ieno 2016). Experiment 1 responses were fitted with negative binomial error structure and log link function with quadratic parameterization (Hardin and Hilbe 2018). In Experiment 2, we found excessive zeros, due to individuals not always responding to playbacks (true zeros), so fitted a hurdle model with a negative binomial distribution with quadratic parameterization (`truncated_nbinom2`) and log link function using the `glmmTMB` package (Brooks et al. 2017). Model appropriateness was assessed using `simulateResidual()` function of the `DHARMA` package (Hartig 2020). We used the `emmeans()` function in the `emmeans` package (Lenth 2020) to get model predictions. Likelihood Ratio Tests (LRTs) were performed using the `anova()` function to assess the significance of single-terms, with the significance of individual estimates in Experiment 2 assessed using Wald Z statistics. All models were fitted using R version 4.0.3 (R Core Team 2020).

Ethical note

The study was approved by the Australian National University Ethics Committee (protocol A2015/67). We aimed to use the smallest sample size sufficient to answer our questions, by using a repeated-measures design in which individuals acted as their own controls. Individuals were subjected to only two short alarm-call playbacks in Experiment 1, only four in Experiment 2, and to no more than one call in a single day. Birds almost always returned to feed within 30 s of the alarm-call playback (123/128 cases over the two experiments). Traffic noise was a common sound for these urban birds so that playback appeared to cause minimal disturbance.

RESULTS

Experiment 1: effect of visual restriction alone

As predicted, magpies responded more strongly to noisy miner mobbing alarm calls when their visual information was restricted (CLMM, probit link: barrier position: $\chi^2 = 19.51$, $df = 1$, $P < 0.0001$; parameter estimate [up–down] \pm SE = 2.22 \pm 0.58; Figure 3a). When the visual barrier was lying down, allowing magpies a clear view of their surroundings, most individuals only scanned in place after playback of alarm calls and the remainder showed no response. By contrast, when the visual barrier was upright, obscuring the magpies' view, they always responded and usually moved while scanning or fled in response to alarm-call playback. We detected no significant effect on response of treatment presentation order ($\chi^2 = 0.17$ $df = 1$, $P = 0.68$; parameter estimate [2nd–1st] \pm SE = 0.18 \pm 0.43).

Consistent with their immediate response, magpies responded to alarm-call playback for longer when the barrier was upright compared to lying down (GLMM, negative binomial with log

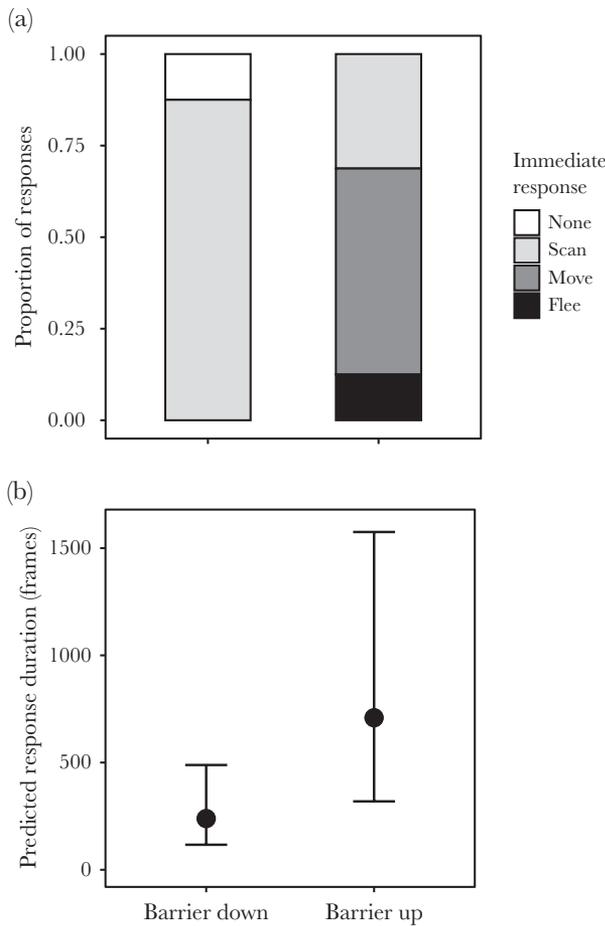


Figure 3
 Experiment 1: response of magpies to playbacks of noisy miner mobbing alarm calls according to the presence of a visual barrier. (a) Immediate categorical response to playback, and (b) predicted duration of response from the model including bird ID as the random term, and back-transformed to the original response scale (number of frames). When the barrier was down, the birds had an unobstructed view, while when the barrier was up the bird’s view was blocked in the direction of the loudspeaker. The results of statistical analyses are presented in the text; $n = 32$ playbacks on 16 focal birds.

link: $\chi^2 = 5.06$, $df = 1$, $P = 0.02$; parameter estimate [up–down] \pm SE = 1.09 ± 0.48 ; **Figure 3b**). There was no significant effect of treatment order on the duration of response ($\chi^2 = 0.07$, $df = 1$, $P = 0.79$; parameter estimate [2nd–1st] \pm SE = 0.13 ± 0.47).

Experiment 2: combined effects of visual and acoustic restrictions

The immediate response to alarm-call playback was affected by visual restriction but not traffic noise, and contrary to prediction there was no interaction between visual and acoustic restrictions. Consistent with Experiment 1, magpies responded more strongly to alarm calls when the visual barrier was upright compared to lying down (CLMM: $\chi^2 = 24.36$, $df = 1$, $P < 0.0001$; **Figure 4a**, **Table 1** for model estimates). By contrast, we found no significant effect of traffic-noise playback ($\chi^2 = 0.71$, $df = 1$, $P = 0.40$) nor the interaction between traffic-noise playback and visual-barrier presence

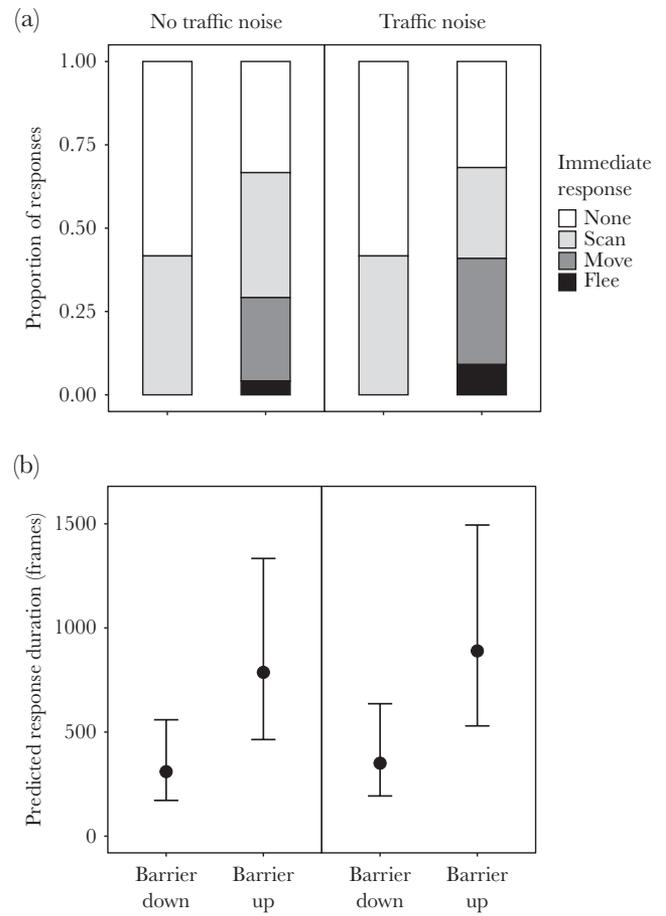


Figure 4
 Experiment 2: response of magpies to playbacks of noisy miner mobbing alarm calls according to the presence of a visual barrier and the presence of simultaneous traffic-noise playback. (a) Immediate categorical response to playback, and (b) predicted duration of response from the model including bird ID as the random term, and back-transformed to the original scale (number of frames). When the barrier was down, the birds had an unobstructed view; when the barrier was up, the bird’s view was blocked in the direction of the loudspeaker. The results of statistical analyses are presented in **Table 1**, for the immediate response, and in **Table 2**, for duration of response; $n = 94$ playbacks on 24 focal birds (data unavailable for two playbacks because the video failed).

Table 1
Experiment 2: the effect of the visual barrier and traffic noise on the immediate response of magpies to noisy miner alarm-call playbacks

Fixed effects	Estimate \pm SE	χ^2	df	P
Barrier (up–down)	1.41 \pm 0.31	24.36	1	<0.0001
Noise (present–absent)	0.22 \pm 0.26	0.71	1	0.40
Treatment order		17.33	3	<0.001
Treatment order (2nd–1st)	-0.22 \pm 0.34			
Treatment order (3rd–1st)	-0.85 \pm 0.36			
Treatment order (4th–1st)	-1.53 \pm 0.43			

Responses were on an ordered, categorical scale (1, no response; 2, scan in place; 3, move while scanning; 4, flee), and are shown in **Figure 4a** ($n = 94$ responses by 24 birds). Analysis used a CLMM model (see text); significant terms are shown in bold.

($\chi^2 = 0.07$, $df = 1$, $P = 0.79$) on the response to alarm calls. In contrast to Experiment 1, responses diminished with playback order ($\chi^2 = 17.33$, $df = 3$, $P < 0.001$; Table 1).

Consistent with their immediate responses, the magpies' duration of response to alarm calls was affected by the visual barrier but not traffic-noise playback, and we again detected no interaction between visual and acoustic restrictions (Figure 4b, Table 2). The hurdle model showed overall that magpies responded for longer when the visual barrier was upright compared to lying down ($\chi^2 = 20.98$, $df = 1$, $P < 0.001$), but there was no significant effect of traffic-noise playback ($\chi^2 = 0.23$, $df = 1$, $P = 0.89$) or the interaction between visual-barrier presence and noise treatment ($\chi^2 = 1.22$, $df = 2$, $P = 0.54$). The conditional model, considering the duration of response on those 51 occasions when birds responded, revealed longer responses when the visual barrier was upright compared to lying down ($Z = 3.41$, $p = 0.0007$), but there was no significant effect of traffic noise or treatment order (Table 2 (a)), or any interaction between visual-barrier presence and traffic noise playback ($\chi^2 = 1.22$, $df = 1$, $P = 0.27$). The zero-inflation model, considering the likelihood of not responding at all, also found a greater response when the visual barrier was upright ($Z = -2.67$, $P = 0.008$), and a declining response with treatment order (Table 2 (b)), again with no significant interaction between visual-barrier presence and traffic noise playback ($\chi^2 = 0.002$, $df = 1$, $P = 0.97$).

DISCUSSION

We tested how constraints on personal information affect the response to social information from alarm calls. As predicted, birds responded more strongly to heterospecific alarm calls when a visual barrier restricted their view of surroundings, but their response to alarm calls was unaffected by playback of traffic noise designed to

reduce the ability to hear subtle cues of danger. Overall, our experimental results confirm previous indirect evidence that a reduction in personal visual information leads to a greater response to indirect, social information about danger. The lack of an effect of moderate traffic noise suggests that it did not obscure valuable information or that magpies rely primarily on vision for personal assessment of danger.

Our results extend previous work by showing experimentally that individuals respond more to social information from alarm calls when their personal visual information is reduced. In the first experiment, magpies usually only scanned in place to playback of alarm calls when their view was unobstructed, and sometimes did not respond at all, whereas they usually scanned while moving away from the visual barrier, and sometimes fled, when their view was obstructed by the barrier. They also responded for longer if there was a visual barrier. Magpies showed the same patterns in the second experiment. Previous experimental work has shown that visual barriers can lead to greater vigilance and other changes in behavior that imply an assessment of greater danger (Introduction; e.g. Lazarus and Symonds 1992; Embar et al. 2011). Furthermore, foraging near obstructive cover appears to constrain personal information and leads to a greater reliance on alarm calls from conspecifics or members of other species (Introduction; Goodale and Kotagama 2008; Goodale et al. 2010; Martínez and Zenil 2012; Martínez et al. 2016; Jones and Sieving 2019; McLachlan et al. 2019). We extend these studies by examining the response to heterospecific alarm calls while also experimentally manipulating an individual's view of their surroundings. All individuals were feeding on the same resource type in a similar context, so the experimental controls for any effect that the current situation has on the decision to respond to alarm calls, such as a reduced response if the rewards of feeding are greater or the bird is feeding in a safer location. The pairwise design, and constant location of playbacks to a focal bird, also meant that each individual was tested for visual-barrier effects while in the same-sized group and at the same distance from protective cover. Furthermore, because our experiment was carried out on a single species, it eliminates potential confounding species differences that may affect responsiveness to alarm calls. For example, reduced response of aerial insectivores might relate to sensory or acrobatic abilities, or morphology, rather than reduced visual obstruction from the habitat (Martínez and Zenil 2012; Jones and Sieving 2019). Our results therefore show directly that visual restriction on personal information does affect the response to alarm calls, while eliminating any confounding differences between species or in resource value, group size, or distance to cover.

Contrary to prediction, we found no effect of moderate traffic noise on magpie responses to alarm calls. We predicted that birds would respond more strongly to playback of mobbing alarm calls when also broadcasting traffic noise that could obscure subtle cues of danger of lower amplitude than the alarm-call playbacks. We consider the most plausible explanation of our results is that magpies forage in open habitats and live in pairs or larger groups, so may generally rely on a combination of personal, visual information and the nearby alarm calls of conspecifics and heterospecifics (Igic et al. 2019; Dutour et al. 2020). Given these other conspicuous and reliable sources of information about danger, it may be difficult to learn to associate subtle cues with danger, because of the process of overshadowing in which learning highly salient cues can diminish learning of secondary cues (Mackintosh 1976; Shettleworth 2010; Kazemi et al. 2014). Another possibility is that there may be little benefit of learning

Table 2

Experiment 2: the effect of a visual barrier and traffic noise on the duration of response to playback of noisy miner mobbing alarm calls

Fixed effects	Estimate \pm SE	Z	P
(a) Duration of response (conditional model)			
Intercept	4.96 \pm 0.34		
Barrier (up–down)	0.93 \pm 0.27	3.41	0.0007
Noise (present–absent)	0.12 \pm 0.26	0.47	0.64
Treatment order (2nd–1st)	–0.37 \pm 0.32	–1.17	0.24
Treatment order (3rd–1st)	–0.30 \pm 0.36	–0.83	0.41
Treatment order (4th–1st)	–0.61 \pm 0.43	–1.43	0.15
(b) Probability of no response (zero-inflation model) ^a			
Intercept	–0.67 \pm 0.81		
Barrier (up–down)	–2.01 \pm 0.75	–2.67	0.008
Noise (present–absent)	0.03 \pm 0.59	0.04	0.97
Treatment order (2nd–1st)	0.10 \pm 0.84	0.12	0.90
Treatment order (3rd–1st)	1.97 \pm 0.91	2.15	0.03
Treatment order (4th–1st)	3.29 \pm 1.12	2.94	0.003

Analysis of the duration of response used a hurdle model with two parts: (a) duration of response (video frames), using the conditional model for the 51 cases where individuals responded, with a negative binomial distribution and log link (Figure 4b); and (b) probability that there was no response, using the zero-inflated part of the Hurdle model, with a binomial error distribution and a logit link. There was no significant interaction between visual barrier position and noise in any analysis (text). $N = 94$ responses by 24 birds; significant terms are shown in bold.

^aNote that the estimates from the model give the probability of no response, so a negative sign means a greater probability of response.

about and responding to subtle cues, particularly as response to such cues could increase the risk of false alarms (Wiley 2006, 2015). The value of subtle acoustic cues of danger might be especially low in environments with chronic anthropogenic noise, in which case the effect of noise could be long-term rather than immediate.

Three additional possible explanations for why magpie responses to alarm calls were not affected by noise we consider less plausible. First, the traffic-noise playback may have been too low an amplitude to mask any potential cues of danger. However, miner mobbing alarm calls are often given to predators moving on the ground, which can make low-amplitude noise that is vulnerable to masking even by moderate traffic noise. For example, the sound of predator locomotion, such as footfall, is likely to be of low amplitude, particularly on substrates such as lawn (Goerlitz et al. 2008; Larsson 2012, 2014). Furthermore, distant alarm signals will also be of low amplitude, but could indicate an approaching or nearby predator, given that birds can call at a distance from the predator itself. Noisy miner mobbing alarm calls, with a mean amplitude of 69 dB at 10 m (Magrath and Bennett 2012), will be about 63 dB at only 20 m, the same amplitude as the traffic-noise playback at the feeding plate, and so will become vulnerable to masking when miners are at greater distances. Similarly, the alarm “wing whistle” of crested pigeons, *Ocyphaps lophotes*, to which the pigeons flee and magpies become vigilant, is about 42 dB at 20 m (Hingee and Magrath 2009; Murray 2015; Murray et al. 2017). Work on other species has found a reduced response to avian alarm calls, at least partly due to masking, that are 3–16 dB lower than background sound, despite spectral differences between the alarm call and background (Grade and Sieving 2016; Templeton et al. 2016; Zhou et al. 2019). Second, magpies may become more vigilant when subject to traffic-noise playback, and so rely more on personal vigilance than social information from alarm calls. In some species, enhanced vigilance does appear to explain a reduced response to alarm-call playback (Morris-Drake et al. 2017). This cannot be a full explanation in our study because playbacks were carried out when focal birds were behind the barrier, and so we experimentally restricted their view of surroundings; greater vigilance could not provide complete information. Nonetheless, it would be useful to design an experiment to test the effect of noise on vigilance in magpies, as it might influence response to social cues, including alarm calls. Third, since traffic noise is a fairly uniform and ongoing sound, birds may habituate to it, leading to lack of response. Future work could test experimentally if the duration of exposure to noise affects response to alarm calls. However, although distraction may decline with time, habituation is unlikely to solve the problem of acoustic masking of unpredictable and subtle sounds of predator presence (Brumm and Slabbekoorn 2005; Francis and Barber 2013).

In addition to predicting a greater response to alarm calls during traffic-noise playback, we also predicted an interaction between the presence of a visual barrier and traffic noise, given that personal information lost from one sensory channel could not be easily compensated by the other. Other research has found that noise can affect how animals respond in other sensory domains: noise often provokes vigilance, implying assessment of greater risk, and more reliance on visual information (Introduction; Quinn et al. 2006; Rabin et al. 2006; Kern and Radford 2016). The lack of cross-model effects in magpies could mean that magpies do not use subtle acoustic cues to detect danger, so such sounds never compensate for loss of visual information. This is consistent with

a strong and uniform effect of the visual barrier on responses, and with the lack of an effect of noise. Further assessment of noise-induced informational constraints requires additional playbacks of different types and amplitudes of noise.

Although not a focus of our study, our results suggest that traffic noise did not distract magpies. Distraction is a separate mechanism from masking by which noise can affect behavior (Chan et al. 2010). Sensory input from one source can use some of an animal's finite ability to process information, so that noise can reduce attention to other sensory input (Dukas 2004). For example, playback of boat noise slowed the response of Caribbean hermit crabs to a threatening but silent visual stimulus (Chan et al. 2010), blocked appropriate responses of fathead minnows, *Pimephales promelas*, to conspecific alarm cues (Hasan et al. 2018), and reduced responses of Ambon damselfish, *Pomacentrus amboinensis*, to simulated predator attacks (Simpson et al. 2016). Among terrestrial vertebrates, playback of traffic noise reduced appropriate responses to predator feces (Morris-Drake et al. 2016), and playback of pink noise increased the latency of great tits to find cryptic prey (Halfwerk and van Oers 2020). Distraction by noise might therefore be expected to reduce the response to alarm calls, independently of any effect of direct masking of those calls. We are aware of only one study explicitly testing whether distraction could reduce response to alarm calls: playback of moderate-amplitude ambient noise masked superb fairy-wren alarm calls, but there was no evidence of distraction (Zhou et al. 2019). In that study and the current one, noise playbacks were of common background sounds, at natural amplitudes, and were broadcast with a gradual onset and then little fluctuation. These acoustic attributes are likely to reduce non-masking effects on subsequent alarm calls, perhaps explaining why we detected no effect of distraction.

Overall, we confirm experimentally that a restriction of personal visual information can increase the response to social information from alarm calls, but we found no effect of moderate traffic noise. Previous work on the effect of visual restriction on response to alarm calls has relied on indirect evidence, rather than directly manipulating the availability of visual information (Goodale and Kotagama 2008; Martínez and Zenil 2012; Martínez et al. 2016; Jones and Sieving 2019; McLachlan et al. 2019). Our results therefore support the idea that access to personal visual information, dependent in part on the foraging niche, could affect response to alarm calls and information flow within natural communities (Goodale et al. 2010; Martínez and Zenil 2012; Jones and Sieving 2019). Given the pervasive effects that noise can have on animal behavior and physiology (Shannon et al. 2016; Duarte et al. 2021), it is reassuring to find no effect of moderate traffic noise on magpie responses to alarm calls. This suggests that moderate traffic noise has little effect on their perception of risk. Future work could assess directly what subtle acoustic cues and signals are used to assess risk, and so make specific predictions about the types of anthropogenic or natural noise that may compromise antipredator behavior in magpies and other species.

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Data availability: Analyses reported in this article can be reproduced using the data and information provided by Ratnayake et al. (2021).

AUTHOR CONTRIBUTIONS

R.D.M. and A.N.R. conceived the project; F.S.E.D.P. and D.P. developed methods during a pilot experiment; C.P.R. and Y.Z. conducted and helped design the experiments; C.P.R. performed statistical analyses; R.D.M. and C.P.R. drafted the manuscript; and all authors contributed to writing and editing.

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