

Functionally referential communication about danger in cooperatively breeding white-winged choughs

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Effectively communicating information about danger can enhance the antipredator benefits of group living. Many social mammals use functionally referential alarm calls to convey predator-specific information, such as predator type and threat urgency, enabling appropriate responses. However, relatively few bird species, particularly cooperative breeders, have been subjected to experimental assessment. White-winged choughs, *Corcorax melanorhamphos*, are obligate cooperative breeders living in groups year-round. They have a complex yet barely studied vocal repertoire. We carried out field observations, acoustic analyses and a playback experiment to test whether chough alarm calls are functionally referential. Additionally, we explored the occurrence of a possible visual display when responding to threats. Choughs produced three different alarm calls in response to different threats: terrestrial alarm calls for ground-based predators, aerial whistles for high-flying hawks and flee alarm calls for immediate, high-urgency threats. Blind scoring of video revealed that birds responded appropriately to playbacks of alarm calls alone, typically looking around in response to terrestrial alarms, looking up to aerial whistles and fleeing to flee alarms. Furthermore, birds were much more likely to display 'bulging eyes' in response to aerial whistles compared to terrestrial alarms, suggesting that bulging eyes might be a visual signal associated with aerial threats. Our findings demonstrate that white-winged choughs, a highly social bird species, possess a functionally referential alarm call system that conveys information about the type of threat and urgency. We propose that integrating information from multiple sensory modalities in alarm communication, such as auditory and visual signals/cues, may be common in social animals and warrants further investigation.

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Collective vigilance and coordinated antipredator responses are key benefits of group living, especially when group members can efficiently communicate information about danger (Caro, 2005; Elgar, 1989; Hingee & Magrath, 2009; Liao et al., 2024). Alarm calling, the production of warning vocalizations in response to a threat, is common in many mammal and bird species when a predator is detected (Hollén & Radford, 2009; Klump & Shalter, 1984). Calling is particularly effective as it can quickly alert nearby individuals, even if they are out of sight or not currently vigilant (Devereux et al., 2008; Marler, 1967). This allows receivers

to gain information about danger and respond immediately, enhancing their chances of survival.

Functionally referential alarm calls communicate about the type of threat, enabling receivers to respond appropriately even without detecting the threat directly (Evans et al., 1993). Specifically, functionally referential alarm calls are associated with external objects or events and can convey detailed information, such as predator type (Seyfarth et al., 1980a), size (Templeton et al., 2005), behaviour (Griesser, 2008) and level of urgency (Leavesley & Magrath, 2005). The term 'functional reference' considers the context and consequences of calls, without making assumptions about underlying mechanisms (Evans, 1997; Evans et al., 1993; Macedonia & Evans, 1993). A classic example is vervet monkeys, *Chlorocebus pygerythrus*, which give different alarm calls to snakes, eagles and leopards, *Panthera pardus* (Seyfarth et al., 1980a).

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Similarly, chickens, *Gallus gallus*, produce distinct alarm calls for terrestrial and aerial predators (Evans et al., 1993). In addition to signalling predator type, some alarm calls encode information about urgency. For example, white-browed scrubwrens, *Sericornis frontalis*, communicate about urgency, with a greater number of elements in their aerial alarm call indicating a closer predator and therefore higher urgency (Leavesley & Magrath, 2005). Some species even include both types of information in their alarm calls. Meerkats, *Suricata suricatta*, produce alarm calls that convey both the type of predator and the level of urgency, facilitating coordinated group escape (Furrer & Manser, 2009; Manser, 2001). These examples highlight that group-living animals can produce different calls that convey detailed information about danger (Gill & Bierema, 2013; Townsend & Manser, 2013). Social complexity is thought to drive communicative complexity (Butler et al., 2022; Freeberg et al., 2012; Leighton, 2017) and may favour the evolution of functionally referential alarm communication (Blumstein & Armitage, 1997; Furrer & Manser, 2009; Griesser, 2008; Zuberbühler, 2003). Although such alarm call systems have long attracted interest, few studies have experimentally tested functionally referential alarm communication in birds (Cunningham & Magrath, 2017; Gill & Bierema, 2013; LaPergola et al., 2023; Suzuki, 2016), particularly in cooperative breeders, a complex vertebrate social system.

Predator-specific responses to alarm calls can indirectly reveal the information encoded within them. Gaze direction, for example, is particularly useful for interpreting the meaning of calls because it reflects the receiver's interpretation of the threat (Fichtel, 2004; Seyfarth et al., 1980b). Gaze direction is easy to assess in primates, because of their forward-facing eyes, and has been used to study alarm call meaning in many species (Fichtel, 2004; Fichtel & Kappeler, 2002; Schel et al., 2010; Seyfarth et al., 1980b). For example, vervet monkeys look down in response to snake alarms and look up in response to eagle alarms (Seyfarth et al., 1980a). In birds, despite their lateral vision, gaze direction has also proved to be a valuable indicator (Dawson Pell et al., 2018; Evans et al., 1993; Kaplan & Rogers, 2013; Suzuki, 2012). For instance, chickens increase horizontal scanning in response to both ground and aerial alarm calls but are more likely to look upward, rolling their heads to fixate laterally with one eye, when hearing aerial alarm calls (Evans et al., 1993). Similarly, great tits, *Parus major*, scan the horizon in response to crow-specific alarm calls and gaze towards the ground in response to snake-specific alarm calls (Suzuki, 2012). Australian magpies, *Gymnorhina tibicen*, respond to eagle alarm calls by looking upward and angling their beaks at least 30 degrees above horizontal (Kaplan & Rogers, 2013). These examples demonstrate that gaze direction in birds serves as a reliable indicator for studying functionally referential alarm calls, reflecting how receivers interpret different alarm calls.

In addition to alarm calls, individuals can obtain information about threats from visual cues or signals from others. Responses to detecting a predator, such as the direction of gaze or the direction of fleeing, could often be cues (Lima, 1995; Seyfarth & Cheney, 1980). For example, Australian magpies face flying hawks and point their beaks towards the threat while giving alarm calls, a behaviour that may help conspecifics locate the predator more quickly (Kaplan, 2008). Young vervet monkeys respond more appropriately to alarm calls if they first look at adults (Seyfarth & Cheney, 1980, 1986), implying that they gain additional information from others' responses. Moreover, some responses may be exaggerated or modified to become signals (Caro, 2005; Holley, 1993). For instance, brown hares, *Lepus europaeus*, exhibit visually distinctive antipredator behaviours, standing bipedally, facing approaching red foxes, *Vulpes vulpes*, with erect ears and turning their white ventral surface towards the predator, which is thought

to function as a signal to both predators and conspecifics (Holley, 1993). Taken together, responses to threats can serve as cues or signals that help coordinate antipredator behaviours more effectively and, in some cases, may form part of a multimodal signal. To date, our understanding of how social animals integrate information from multiple sensory modalities, such as auditory and visual signals/cues, remains very limited, despite its likely prevalence in social species (Liao et al., 2024).

White-winged choughs, *Corcorax melanorhamphos*, are obligate cooperative breeders that live in year-round groups with stable membership (Heinsohn, 1992; Rowley, 1978). They forage for invertebrates on the ground, making them vulnerable to both terrestrial and aerial predators such as foxes, feral cats and raptors (Heinsohn, 1987; Rowley, 1978). Additionally, they forage by digging into the substrate, which is likely to reduce their ability to detect predators visually when feeding, thereby increasing the importance of acoustic communication. While their ecology, development and breeding behaviours have been well studied (Beck et al., 2008; Heinsohn, 1987, 1991; Heinsohn & Cockburn, 1994), surprisingly little is known about their vocal communication (Higgins et al., 2006). Choughs are an ideal species for investigating functionally referential alarm communication, given their complex social groups, diverse vocal repertoire and ease of observation, allowing for the quantification of detailed behavioural responses. Furthermore, choughs appear to use visual displays when interacting with other individuals or when facing threats (Heinsohn, 2009; Rowley, 1978). These potential displays include wing-wave–tail-wag motions and 'bulging eyes', when engorging the conjunctiva of their eyes with blood makes them appear more prominent (Rowley, 1978). While the function of these potential visual displays remains unknown, choughs might refine functionally referential communication by using multimodal signals.

We studied alarm calls and communication in choughs through field observations, acoustic analyses and a playback experiment including detailed video analyses of behavioural responses. Demonstrating functionally referential alarm communication in a species requires considering both the production and perception of calls (Evans et al., 1993). We therefore first tested whether choughs produce acoustically different alarm calls to different types of threat. Second, we conducted a playback experiment and used blind-scored video to examine whether different types of alarm calls elicit appropriate antipredator responses. Furthermore, if choughs' alarm calls encode the level of urgency, then we expected that choughs would have a shorter latency to respond and be more likely to flee in response to higher-urgency alarm calls. Finally, we quantified the occurrence of bulging eyes during threatening situations to assess whether they might form part of a multimodal signal.

METHODS

Study Sites and Species

White-winged choughs are large passerine birds (350–380 g) endemic to southeastern Australia. Most breeding groups consist of six to eight individuals, including a monogamous breeding pair and nonbreeding helpers, which are usually the offspring from previous years (Beck et al., 2008; Heinsohn et al., 1988). Groups are highly cohesive, with members travelling, foraging and roosting together, and their group membership can remain stable for over a decade (Rowley, 1978). Choughs do not actively defend foraging territories and have overlapping home ranges of up to 1000 ha (Rowley, 1978). However, during the breeding season (August to January), groups defend their nest, and their home ranges contract

to about 20 ha surrounding the nest site (Beck & Heinsohn, 2006; Heinsohn et al., 1988; Rowley, 1978).

We studied choughs between March and December 2022 in nature reserves and on the edges of suburbs in Canberra, Australian Capital Territory, Australia (35°14'46.0"S, 149°06'49.8"E). This population has been studied since the 1980s, with four distinct study periods (Beck & Heinsohn, 2006; Heinsohn, 1987; Heinsohn et al., 2000; Leon et al., 2022). The birds are well habituated to human presence, allowing close-range observation (<3 m) by observers on foot. In the current study, 176 birds were colour-banded for individual identification using a standard metal leg band and either colour leg bands or a white plastic leg band with a unique number (for methods see Beck & Heinsohn, 2006). We collected data on 16 breeding groups in this population.

Production of Alarm Calls

Natural observations

To examine whether choughs encode specific information about predators in their alarm calls, we opportunistically recorded their vocalizations during natural encounters with predators. During recording, birds were followed at a distance of 3–5 m. Where possible, we noted the number of individuals in the group, the age category (adult, immature and juvenile) of each individual based on its iris colour (Rowley, 1978), the distance between the microphone and the calling bird, the identity of the calling bird and the probable cause of the alarm. All recordings were collected using a Sennheiser ME66 shotgun directional microphone with a K6 power module. Calls were recorded at a sampling rate of 48 kHz as 24-bit WAV files on a Marantz PMD661 recorder.

Based on these natural observations, we identified three call types typically associated with different predator contexts. For ease of reference, we label these call types as follows: 'terrestrial alarm calls', given in response to ground-based threats such as dogs and snakes; 'aerial whistles', given to high-flying hawks (about 50 m high); and 'flee alarm calls', given in response to immediate threats, such as a hawk flying within 15 m. These natural recordings served as preliminary observations to inform our experimental design. They were not used in subsequent acoustic analyses comparing call types, nor were they used to construct playback tracks. We later tested the functional relevance of each call type through a playback experiment using calls prompted in standardized contexts.

Prompted alarm calls

In addition to gathering recordings of alarm calls under natural conditions, we prompted alarm calls by simulating different types of threat, corresponding to the three natural contexts. We presented 16 breeding groups with (1) a ground-based threat, a rubber model resembling an eastern brown snake, *Pseudonaja textilis*, to prompt terrestrial alarm calls, (2) an aerial threat, playback of a chough aerial whistle chorus, to prompt aerial whistles, and (3) an immediate threat, a life-sized gliding model of a brown goshawk, *Accipiter fasciatus*, to prompt flee alarm calls. We used a matched experimental design where each group received each stimulus, using the specific methods described below. Each group received only one stimulus per day, with a minimum of 3 days before receiving the next stimulus. We audiorecorded choughs during all presentations, using the same equipment as for natural recordings, to allow for the measurement of acoustic structure and the construction of exemplars for playback experiments.

We placed the snake model on the ground and covered it with leaves about 15–20 m from the foraging group's movement path. The head of the snake model was tied to a 5 m long piece of thin

fishing line, which an investigator could gently pull to make the model move. A Marantz PMD661 recorder with a Sennheiser ME66 microphone attached to a tripod was positioned 3–5 m away from the model to record the choughs' vocalizations. Having placed the equipment, we used shredded cheese to attract the choughs to the model's location and moved the snake's head as the birds approached.

We were unable to use a physical model to simulate the context of high-flying hawks but, based on our field observations, choughs often gave 'aerial whistles' when they heard similar whistle calls from another group. We therefore constructed a 15 s playback exemplar recorded from a group of choughs during a natural encounter with a high-flying hawk at the Australian National Botanic Gardens (approximately 3.5 km away from our study sites) in 2020. The exemplar was broadcast about 5 m away from a foraging group using WAV files on an iPhone 13 through a JBL Go 3 Bluetooth loudspeaker. The loudspeaker was attached to the investigator's waist, giving it a height of about 1 m. We then used audio equipment to record vocalizations given by the choughs when the exemplar was played. If choughs did not vocalize, or if their calls could not be isolated from the playback or other sounds, we repeated the trial 3 days later ($N = 6$ groups).

The gliding model was thrown by one person standing 10–15 m from a foraging group, while another investigator stood 3–5 m from the group and used audio equipment to record vocalizations when the gliding model was launched. The model typically glided for 10–20 m and passed the group at a distance of 5–10 m. Failed attempts, where the glider veered off course and hit the ground immediately, were repeated as soon as possible. Similar glider presentations to other local group-living species also prompted flee alarm calls, whereas the act of throwing alone (control 'fake throws') never prompted any type of alarm (Cunningham & Magrath, 2017; Magrath et al., 2007). Again, if the vocalizations overlapped and could not be isolated, the trial was repeated 3 days later ($N = 5$ groups).

Acoustic Structure

We measured the acoustic structure from spectrograms of the alarm calls given by choughs during natural encounters with predators and during presentation of experimental stimuli. Spectrograms were generated from the recordings using Raven Pro 1.6, a Hann window function with a 512 sample size, a temporal grid resolution of 0.542 ms with an overlap 94.9%, a frequency grid resolution 93.8 Hz, a 5 s duration and a 0–15 kHz frequency bandwidth. The brightness of the greyscale view was set to 55 and the contrast was set to 70. We selected individual call elements manually by placing selection boxes on the spectrogram. All measurements were then calculated automatically by Raven Pro for each selected element. The measurements were (1) low frequency (Hz), the frequency above which 95% of the energy occurs, (2) high frequency (Hz), the frequency below which 95% of the energy occurs, (3) peak frequency (Hz), the frequency at which amplitude is maximum, (4) bandwidth (Hz), the frequency interval containing 90% of the energy, (5) duration (s), the duration containing 90% of the energy, (6) aggregate entropy (bits), a measure of the disorder in a sound by analysing the energy distribution (pure tone ~0 bits), and (7) peak frequency contour average slope (Hz/ms), the mean of the peak frequency contour slope series of numbers.

To compare differences in the acoustic structure between alarm call types, we restricted our analysis to experimentally prompted calls because (1) the prompted recordings were matched by group, minimizing potential confounding effects of group-level differences, and (2) the exact context was controlled, unlike in natural recordings.

Playback Experiment

Overview of experimental design

Playback experiments are essential to demonstrate functionally referential alarm communication, as they isolate the information conveyed by calls from any contextual information, such as the presence of a predator or the behaviour of conspecifics. We therefore broadcast three types of alarm calls to test whether choughs respond appropriately in the absence of direct cues about the type of threat.

The playback experiment was conducted in November 2022, during the choughs' breeding season, at five locations within our study site: O'Connor Ridge, Lyneham Ridge, Bruce Ridge, the suburb of O'Connor and the area around GIO Stadium Canberra. The experiment included four treatments: (1) terrestrial alarm calls; (2) aerial whistles; (3) flee alarm calls; (4) control (Fig. 1). For the control treatment, we used the 'piping' contact calls of crimson rosellas, *Platycercus elegans*, a parrot species common at the study sites that does not pose a threat to choughs. These control calls were recorded from 16 individuals within the study area. As focal individuals in the experiment, we used one adult chough, which was banded and thus could be individually identified, from each of the 16 breeding groups. Each focal bird received unique playback exemplars of the three types of alarm calls given by its own group members, as well as unique control calls, so there was complete replication. Although we could not reliably identify the caller when recording alarm calls, we ensured that each focal individual received a unique playback track for each treatment, reducing the likelihood that responses of the recipient were driven by calls from a specific class of individual. To control for potential order effects, we randomly

generated treatment orders for each individual using R but rejected those that placed too many specific treatments in the same position, so balancing the order. As a result, each order occurred four times for each treatment across the 16 individuals. To minimize habituation, each bird received only one playback per day, with a minimum of 24 h before the next playback.

Preparation of playback treatments

For consistency of recording conditions and context, we prepared all alarm playback exemplars from recordings of calls prompted by simulated threats (see [Prompted Alarm Calls](#) above) which were similar in acoustic structure to calls recorded in comparable natural contexts ([Appendix Table A1](#)). We selected high-quality recordings without overlapping calls from other individuals or distinct background noise. Each alarm call treatment contained two duplicate call elements, which was within the natural range of element number for all three alarm call types. We kept the number of call elements constant across treatments to ensure that the number of elements alone could not explain differences in response. The inter-element interval followed each call's mean interval from naturally prompted calls (mean $\pm$ SD: terrestrial alarms: 1.4 ± 0.8 s, $N = 5$; aerial whistles: 1.2 ± 0.9 s, $N = 5$; flee alarms: 0.8 ± 0.2 s, $N = 4$). Similarly, the control treatment included two call elements with a natural inter-element interval of 1.5 ± 0.8 s ($N = 5$). The total duration of the playback was 2.6–4.5 s, with the first 0.5 s of background sound fading in and the last 0.5 s fading out. We filtered all exemplars at 0.5 kHz to remove sounds below the frequency range of all call types.

We broadcast all playbacks at 65 dB at 5 m, which is within the natural range of all types of alarm calls at that distance ([Appendix Table A2](#)). Keeping the same amplitude across treatments

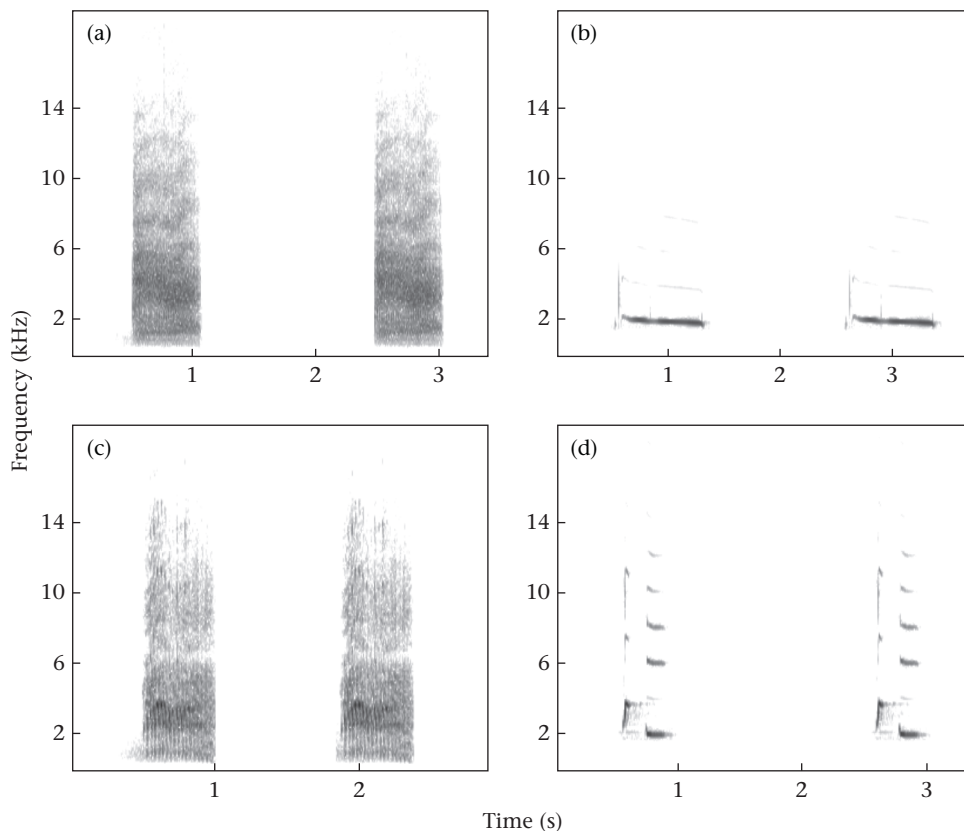


Figure 1. Spectrograms of two-element exemplars used in the playback experiment to white-winged choughs: (a) terrestrial alarm call, (b) aerial whistle, (c) flee alarm call and (d) control contact call of the crimson rosella.

excluded the possibility that differences in response could be due to amplitude alone, rather than to differences in call type. We determined the amplitudes by rerecording playbacks at 5 m, along with a calibration 1 kHz tone measured with a Brüel & Kjær 2240 sound level meter. All playback files were adjusted on a computer to achieve the target amplitude when broadcast.

Field methods

We conducted playback trials in calm, dry weather between 0700 and 1800 hours. On encountering a group, we slowly followed them on foot from a distance of about 5 m for at least 5 min to allow the group to habituate to our presence. During this period, we counted the number of birds and identified banded individuals. We broadcast playbacks to the focal bird from approximately 5 m away, using WAV files on a Roland R-07 via a custom-made amplifier and tweeter loudspeaker (frequency response 2–11 kHz). The loudspeaker was attached to an investigator's waist, giving it a height of about 1 m. We only ran playbacks when (1) the focal bird was the closest to the loudspeaker, (2) the focal bird was foraging at the edge of the group, (3) there were no signs of potential predators around and (4) there was no evidence of anti-predator behaviours by group members. All playback trials were videorecorded at 50 frames/s on a Panasonic HC-VX1 camcorder, hand-held by an investigator.

Response measurement

Videos were prepared and scored using Final Cut Pro V10.6.9. We noted the start and end frames of each playback, and exported videos without sound. The video files and their corresponding identities were renamed by someone not involved in the study, ensuring that each focal bird's response was scored blindly with respect to the playback treatment. Video analysis was conducted by the first author 1 month after the final playback to minimize the likelihood of remembering specific playback events.

We defined the bird's immediate antipredator response to playback as the first behaviour after it stopped feeding and initially raised its head (i.e. became alert). We used a protractor template to assist in scoring the head position of the birds. Responses were classified as follows: (1) look around, the bird raised its head with its bill at an angle of less than 30 degrees above horizontal; (2) look up, the bird raised its head with its bill at an angle of more than 30 degrees above horizontal; (3) startle, the bird raised its head, lowered its body and wings, and jumped; or (4) flee, the bird fled from the ground to cover or to a tree without scanning. If the bird continued feeding without raising its head, it was recorded as no response.

We measured three temporal response variables: the latency to respond, the duration of the response and the duration of scanning. Latency to respond (s) was calculated from the onset of the playback to the time when the bird initiated body movement. The duration of the response (s) was calculated as the period between the start of the response and the moment that the bird resumed feeding, including cases where a chough returned to the ground to feed after fleeing. We measured the total time spent scanning before resuming feeding, as well as subdividing scanning time into 'looking around' and 'looking up' (as defined above). The choughs' head orientations were distinct enough to classify their scanning types reliably (see [Supplementary Video S1–S4](#)). Due to the lateral placement of their eyes, choughs sometimes tilted their heads to one side while looking up, which was also categorized as 'look up' even if the bill angle was estimated at less than 30 degrees. If the focal bird fled, we excluded the scanning data from further analysis as it was difficult to classify the bill angle and the birds were often obstructed by vegetation. All temporal measurements were converted to

seconds for analysis by translating video frames to seconds (at 50 frames/s, each frame represents 0.02 s).

Finally, we scored whether choughs engorged their eyes (0/1) during responses to playbacks.

Statistical Analysis

We performed all statistical analyses and figure plotting in R 4.0.3 ([R Core Team, 2020](#)). We compared both specific acoustic properties and the overall acoustic structure of natural and prompted alarm calls. We used *t* tests to compare specific acoustic features between alarm calls, using the 't.test' function. ANOVA was employed to examine the effect of threat type on the acoustic structure of the alarm calls, using the 'aov' function, with pairwise comparisons using the 'LDuncan' function. Principal components analysis (PCA) was conducted to visualize overall variation in the acoustic structure of the alarm calls elicited by natural predators and experimental stimuli, using 'prcomp' function. The PCA included low frequency, high frequency, peak frequency, bandwidth, duration, aggregate entropy and peak frequency contour average slope (see [Acoustic Structure](#) above for definitions). We assessed differences among the three alarm call types in multivariate acoustic space using a MANOVA on the first two principal components (PC1 and PC2), followed by ANOVAs and Tukey's HSD tests for pairwise comparisons.

We analysed immediate categorical responses to playback using a cumulative link mixed model (CLMM), which is appropriate for ordinal data as it orders the strength of response but does not imply quantitatively equal increments between categories. Responses were ranked into four ordered levels: 0 = no response; 1 = scan (including looking around and looking up); 2 = startle; 3 = flee. Playback treatment, group size and playback order were included as fixed effects, with individual identity and location included as random effects. The model was conducted using the 'clmm' function of the 'ordinal' package, with a probit link function and an equidistant threshold. In addition, we used McNemar tests, appropriate for paired dichotomous data, to compare the probability of looking around versus looking up in response to terrestrial alarm calls versus aerial whistles, using the 'mcnemar.test' function.

We examined the effects of playbacks on temporal responses, latency to respond, duration of the response, time spent scanning, time spent looking around and time spent looking up, using separate linear mixed effect models (LMMs). Each model included playback treatment, group size and playback order as fixed effects, and individual identity and location as random effects. In each case, LMMs were constructed with normal distributions and identity link functions, using the 'lmer' function of the 'lme4' package. We carried out pairwise comparisons using 'emmeans' function of the 'emmeans' package. Conditional R^2 values of models were calculated using the 'r.squaredGLMM' function of the 'MuMIn' package. The full model with all factors of interest was fitted before likelihood ratio tests were used to identify significant fixed effects by removing them individually from the model and assessing the change in deviance. One extreme outlier (319 s) was excluded from the analysis of response duration in the aerial whistle treatment (see Results). It was not possible to measure scanning if individuals fled to playbacks, so we excluded the flee alarm call treatment from any analysis of scanning because 11/16 birds fled immediately. In the aerial whistle treatment, three individuals fled after briefly scanning, leaving 13 birds for analyses of scanning.

We analysed the effects of playbacks on eye engorging (dichotomous response) using a bias-reduced generalized linear model (BRGLM). BRGLM can fit uniform responses of some

playback treatments, where the focal individuals all showed the same response, which cannot be achieved using generalized linear mixed effect models. Playback treatment, group size, playback order, individual identity and location were included as factors in the model. The BRGLM was constructed with a binomial distribution and logit link function, using the ‘brglm’ function of the ‘brglm2’ package. We carried out pairwise comparisons using ‘emmeans’ function of the ‘emmeans’ package. As with the scanning analysis, data from the flee alarm call treatment and from three individuals in the aerial whistle treatment were excluded, as these birds fled and eye engorging could not be measured.

Ethical Note

This study was approved by the Australian National University Ethics Committee (protocol A2022/35) and was designed to minimize any adverse effects on the birds. To reduce disturbance, each playback sound lasted less than 5 s and each focal individual was exposed to only one playback per day, with a minimum interval of 24 h. The birds quickly resumed foraging after the playbacks.

RESULTS

Production of Alarm Calls

White-winged choughs produced three different alarm calls in response to different types of threats (Table 1, Fig. 1). Based on our field observations, terrestrial alarm calls were given in response to ground-based threats in low-urgency situations, including mammals (e.g. domestic dogs, *Canis familiaris*, feral cats, *Felis catus*, common brushtail possums, *Trichosurus vulpecula*, and red foxes), reptiles (e.g. bearded dragons, *Pogona barbata*, and eastern brown snakes) and humans. Aerial whistles were produced in response to high-flying hawks. Common triggers for these calls included brown goshawks, wedge-tailed eagles, *Aquila audax* and little eagles, *Hieraaetus morphnoides*. Unlike the other alarm calls, aerial whistles were often given in a chorus, and sometimes prompted other groups to join in. Both terrestrial alarms and aerial whistles were typically followed by birds stopping feeding and becoming vigilant. In high-urgency situations, regardless of whether the threat was terrestrial or aerial, choughs produced flee alarm calls, such as when a hawk flew nearby or a dog ran towards them. These alarm calls were typically followed by birds fleeing immediately to cover.

The three alarm call types associated with different threats differed statistically in their acoustic structure (Fig. 2). Alarm calls elicited by experimental prompts did not differ from those produced in response to comparable natural prompts (Fig. 2, Appendix Table A1). PCA analysis revealed that the first two principal components explained over 80% of the variance (Appendix Table A3), and the three alarm call types differed in multivariate acoustic space (MANOVA: $F_{4,142} = 42.77$, $P < 0.001$; Fig. 2). Alarm call type

also had significant effects on both PC1 and PC2 (ANOVA: PC1: $F_{2,71} = 288.3$, $P < 0.001$; PC2: $F_{2,71} = 9.02$, $P < 0.001$). On PC1, aerial whistles differed from both flee and terrestrial alarms, while the difference between flee and terrestrial alarms was marginal (Appendix Table A4). On PC2, flee alarms differed from both aerial whistles and terrestrial alarms, whereas aerial whistles and terrestrial alarms did not differ (Appendix Table A4). More specifically, aerial whistles had higher PC1 values, which were associated with a greater peak frequency contour average slope (component loading 0.31; Appendix Table A5) and longer duration (0.29). Flee alarm calls tended to have higher PC2 values, primarily driven by a lower frequency (0.86).

Analysis of individual acoustic attributes emphasize that the two broad-frequency vocalizations (terrestrial and flee alarm calls) were acoustically similar but distinct from the pure tone aerial whistles (Fig. 1, Table 1). Despite their similarity, terrestrial and flee alarm calls nonetheless differed in two acoustic features: terrestrial alarm calls had a lower low frequency (mean $\pm$ SD: 1699 ± 344 Hz versus 1998 ± 530 Hz) and a steeper decline in peak frequency contour average slope (-4.2 ± 2.5 Hz/ms versus -2.3 ± 2.8 Hz/ms; Duncan's tests: all $P < 0.05$; Table 1) compared to flee alarm calls. No significant differences were found between terrestrial and flee alarm calls in high frequency, peak frequency, bandwidth, duration or aggregate entropy (Table 1). By contrast, aerial whistles differed significantly from both broad-frequency alarm call types (terrestrial and flee) in most acoustic features, including high frequency, peak frequency, bandwidth, duration, aggregate entropy and the peak frequency contour average slope (Table 1). The only exception was low frequency, which showed no significant difference between aerial whistles and either terrestrial alarm calls or flee alarm calls (Table 1).

Response to Alarm Calls

The choughs' immediate categorical responses to playback were appropriate to the type of alarm call (CLMM, likelihood ratio: $\chi^2_3 = 116.99$, $P < 0.001$; Fig. 3, Appendix Table A6). Among alarm call types, flee alarms prompted 11/16 birds to flee immediately without scanning, indicating a high-urgency threat, while no bird fled immediately in response to terrestrial alarms or aerial whistles (Fig. 3, Appendix Table A6). Both terrestrial alarms (15/16) and aerial whistles (16/16) prompted most birds to scan immediately, but there was a difference in gaze direction (McNemar test: $\chi^2_1 = 9.09$, $P = 0.003$; looking around versus looking up, $N = 15$ with scanning behaviour in both; Fig. 3). Specifically, 15/16 birds looked around after playback of terrestrial alarms, consistent with a ground-based threat, while 12/16 birds looked up after playback of aerial whistles, consistent with an aerial threat. In contrast to alarm calls, only one bird briefly looked around and none fled in response to the control playback (Fig. 3).

Birds took twice as long to react to aerial whistles compared to terrestrial alarms and flee alarms (LMM: $\chi^2 = 24.32$, $P < 0.001$; Fig. 4a, Appendix Table A7), while response times to terrestrial

Table 1
Acoustic differences between chough terrestrial alarm calls (given to a snake model), aerial whistles (given to playback of whistle calls) and flee alarm calls (given to a glider hawk model)

Call type	Low frequency (Hz)*	High frequency (Hz)***	Peak frequency (Hz)***	Bandwidth (Hz)***	Duration (s)***	Aggregate entropy (bits)***	PFC average slope (Hz/ms)***
Terrestrial (N = 16)	1699 $\pm$ 344 ^b	5988 $\pm$ 914 ^a	3223 $\pm$ 503 ^a	4289 $\pm$ 919 ^a	0.3 $\pm$ 0.1 ^a	5.4 $\pm$ 0.3 ^a	-4.2 $\pm$ 2.5 ^a
Aerial (N = 16)	1734 $\pm$ 123 ^{ab}	2139 $\pm$ 120 ^b	1904 $\pm$ 89 ^b	404 $\pm$ 45 ^b	0.5 $\pm$ 0.1 ^b	2.5 $\pm$ 0.1 ^b	-0.3 $\pm$ 0.6 ^b
Flee (N = 16)	1998 $\pm$ 530 ^a	5584 $\pm$ 1183 ^a	3340 $\pm$ 232 ^a	3586 $\pm$ 1426 ^a	0.3 $\pm$ 0.1 ^a	5.2 $\pm$ 0.6 ^a	-2.3 $\pm$ 2.8 ^c

Means $\pm$ SD shown. * $P = 0.055$; *** $P < 0.001$ (ANOVA). Different superscript letters (a, b, c) indicate significant differences among means, as determined by Duncan's post hoc test.

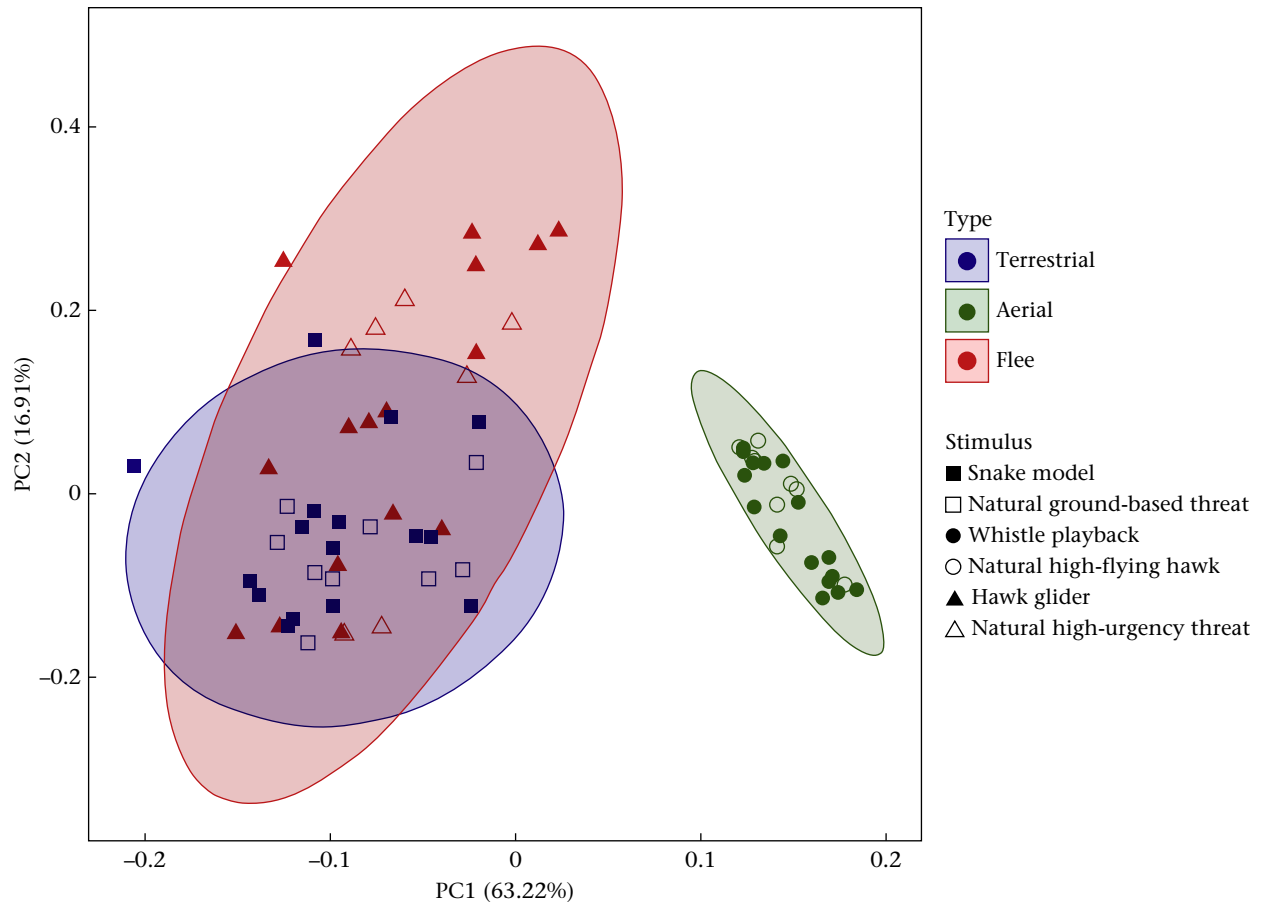


Figure 2. Principal components plot of the acoustic properties of experimentally and naturally prompted white-winged chough terrestrial alarm calls, aerial whistles and flee alarm calls. PCA analysis included low frequency, high frequency, peak frequency, bandwidth, duration, aggregate entropy and peak frequency contour average slope (see Methods, [Acoustic Structure](#), for detailed definitions). Statistical analysis details are given in [Appendix Tables A3 and A5](#).

alarms and flee alarms were similar ([Appendix Table A8](#)). Additionally, the duration of the response was affected by treatment (LMM: $\chi^2 = 14.27$, $P < 0.001$; [Fig. 4b](#), [Appendix Table A7](#)). Birds took more than three times longer to resume feeding after flee alarms compared to terrestrial alarms and aerial whistles, with no

significant difference between terrestrial alarms and aerial whistles ([Fig. 4b](#), [Appendix Table A8](#)).

Scanning over the course of the response differed according to the type of alarm call (LMM: $\chi^2 = 45.97$, $P < 0.001$; [Fig. 5a](#), [Appendix Table A9](#)), with aerial whistles prompting longer

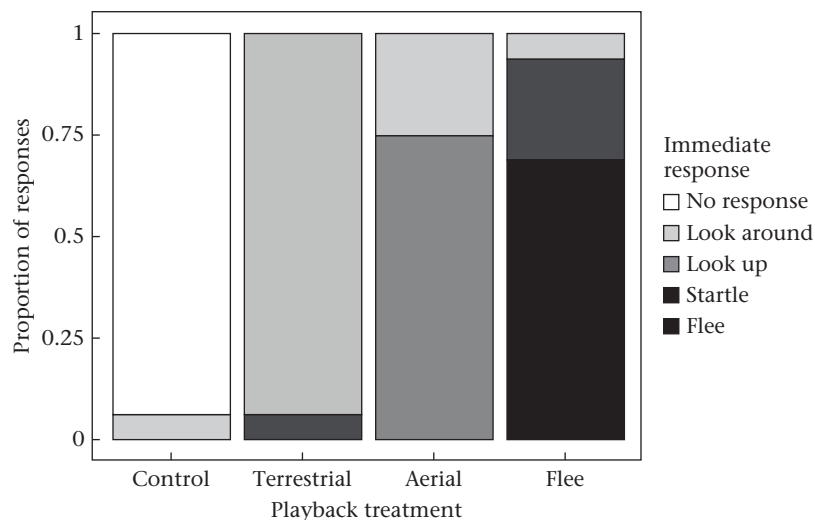


Figure 3. White-winged chough responses to playback of conspecific alarm calls and crimson rosella control calls. The Y axis shows the proportion of immediate categorical responses to playback. $N = 16$ for each playback treatment. Statistical analysis details are given in [Appendix Table A6](#).

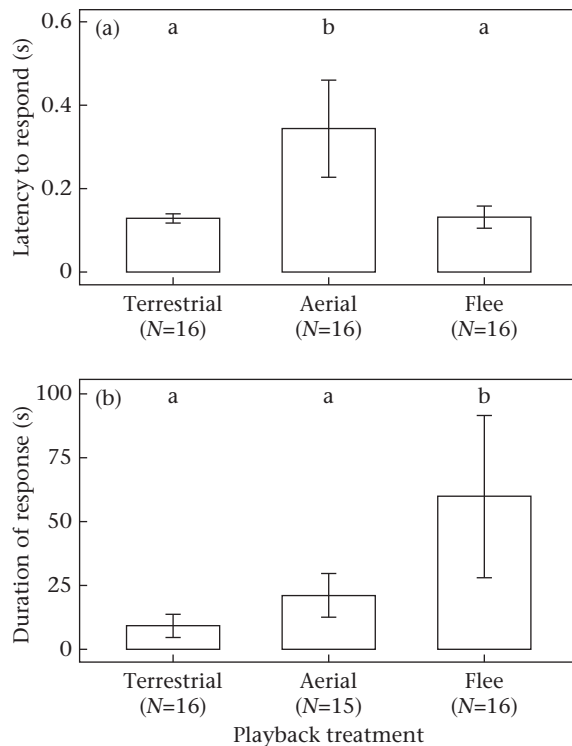


Figure 4. White-winged choughs' (a) latency and (b) duration of response to conspecific alarm call playbacks. Predicted means $\pm$ SEM shown. Different letters indicate significant differences between means as assessed by post hoc Tukey HSD test ($P < 0.05$). Sample sizes are shown for each treatment. Statistical analysis details are given in [Appendix Tables A7–A8](#).

scanning durations and an almost unique looking-up response. We focused on terrestrial alarms and aerial whistles because almost all birds fled immediately to flee alarm calls (see above). Birds spent more than twice as long scanning in response to aerial whistles compared to terrestrial alarms and much longer than in the control (Fig. 5a, [Appendix Table A10](#)). Terrestrial alarms also elicited longer scanning durations than the control (Fig. 5a, [Appendix Table A10](#)). Notably, birds spent the longest time looking up after aerial whistles, with very few or no instances of looking up observed in response to terrestrial alarms or the control (LMM: $\chi^2 = 41.26$, $P < 0.001$; Fig. 5b, [Appendix Tables A9–A10](#)). Birds showed similar looking-around durations in response to both alarm calls, which were longer than in the control (LMM: $\chi^2 = 37.62$, $P < 0.001$; Fig. 5c, [Appendix Tables A9–A10](#)).

Birds were more likely to bulge their eyes in response to aerial whistles than in response to terrestrial alarm calls and the control (BRGLM: aerial versus terrestrial: $Z = -2.84$, $P = 0.013$; aerial versus control: $Z = -3.28$, $P = 0.003$; Fig. 6, [Appendix Table A11](#)). When this response occurred, birds bulged their eyes rapidly, with a latency of 2.0 ± 1.4 s (mean $\pm$ SD; range 0.5–5.4 s; $N = 12$ individuals) from playback onset, and the behaviour was typically sustained rather than expressed in short bouts.

DISCUSSION

White-winged choughs exhibit a functionally referential alarm call system that conveys information about threat type and urgency. Choughs produced two low-urgency alarm calls to different types of threats, with terrestrial alarm calls given in response to ground-based threats and aerial whistles given in response to high-flying hawks. By contrast, flee alarm calls were given to nearby, immediate threats regardless of whether they were

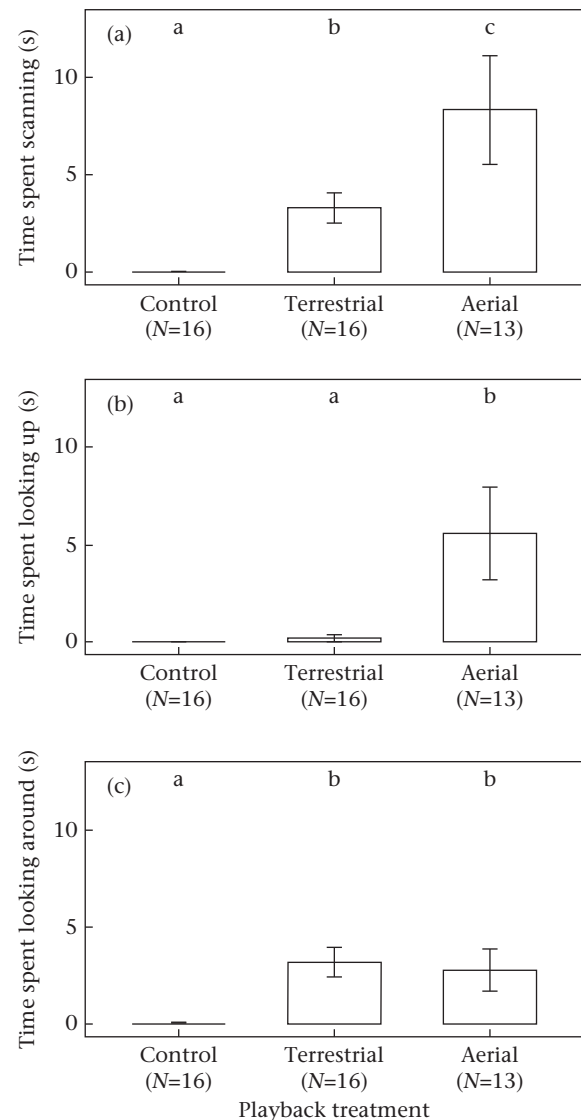


Figure 5. Response of white-winged choughs to conspecific alarm call playbacks, showing the time spent (a) scanning, (b) looking up and (c) looking around. Predicted means $\pm$ SEM shown. Different letters indicate significant differences between means as assessed by post hoc Tukey HSD test ($P < 0.05$). Sample sizes are shown for each treatment. Statistical analysis details are given in [Appendix Tables A9–A10](#).

terrestrial or airborne. The three alarm calls differed acoustically, although with overlap in measured acoustic properties between terrestrial and flee alarm calls. Playback of these alarm calls elicited appropriate responses, even without direct cues from the threat, and regardless of the overlap of measured acoustic features. Birds looked around in response to terrestrial alarms, looked up to aerial whistles while also showing bulging eyes, and immediately fled to cover on hearing flee alarms. This communication system enables individuals to respond in context-appropriate ways to various types of threats.

Choughs produced three different alarm calls in response to specific simulated and natural contexts, fulfilling the production criteria for functional reference ([Macedonia & Evans, 1993](#)). Although we had only single exemplars of models to prompt alarm calls, the alarm calls given in response to the models were similar to those recorded during multiple natural events, with similar variation among individuals, providing replication of contexts when considering both models and natural prompts. Among chough alarm calls, terrestrial and flee alarms were surprisingly

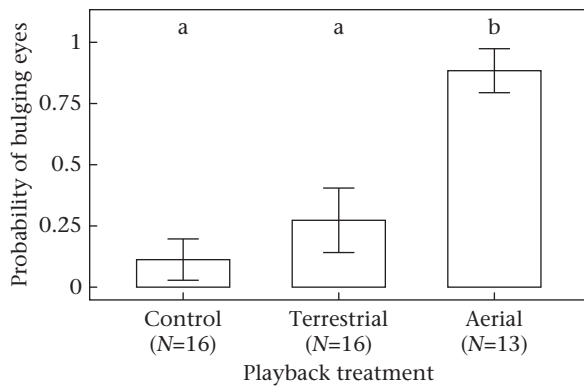


Figure 6. Probability of bulging eyes in white-winged choughs responding to conspecific alarm call playbacks. Predicted means $\pm$ SEM shown. Different letters indicate significant differences between means as assessed by post hoc Tukey HSD test ($P < 0.05$). Sample sizes are shown for each treatment. Statistical analysis details are given in [Appendix Table A11](#).

similar, differing significantly in only two measured acoustic features, although some overlap remained. Similarly, a previous study showed that superb fairy-wrens, *Malurus cyaneus*, produce acoustically similar alarm calls with contrasting functions, demonstrating that these birds use multiple acoustic features to discriminate between these calls (Tegtmann & Magrath, 2020). We suggest that choughs may similarly rely on multiple acoustic features to distinguish between terrestrial and flee alarms. Alternatively, additional acoustic features not measured in this study may also contribute to their differentiation. For instance, flee alarms tend to exhibit more distinct pulses, rapid sequences of short elements separated by brief intervals, than terrestrial alarms. By contrast, aerial whistles showed no acoustic overlap with terrestrial alarms or flee alarms in multivariate space, or across most acoustic features. Aerial whistles also differed from the other alarm calls in often being given in a chorus and sometimes being repeated by other groups, likely facilitating the propagation of information about distant aerial threats across groups. Indeed, narrow-frequency calls, such as whistles, can transmit farther with less spectral degradation compared to broad-frequency calls (Naguib et al., 2008). Aerial whistles could therefore function not only as signals to warn of aerial threats within a group but also as long-distance signals for intergroup communication.

Choughs responded appropriately to the playback of each alarm call type, regardless of the partial overlap of measured acoustic features, which fulfils the perception criterion for functional reference (Macedonia & Evans, 1993). Playback of terrestrial alarm calls prompted the birds to become vigilant and look around, aerial whistles prompted them to look upward, and flee alarm calls triggered immediate flight. These responses were similar to their antipredator behaviour during natural encounters. Among these alarm calls, terrestrial alarms and aerial whistles are associated with low-urgency situations and prompted receivers to seek additional information about threats, while providing clues about where to look. This suggests that chough terrestrial alarms and aerial whistles simultaneously convey information about threat type and urgency. By contrast, flee alarm calls function as 'general' high-urgency signals, conveying nonspecific information about the type of threat, as they are given during close encounters with both terrestrial and aerial predators. For choughs, the main response to an immediate threat is to flee to cover. In such urgent situations, conveying urgency alone seems sufficient, especially since there is no time to gather additional details about the threat. Similar mixed alarm call systems have been observed in mongoose species (e.g. meerkats and dwarf mongooses, *Helogale parvula*),

which produce functionally referential alarm calls that convey both predator type and urgency, as well as nonspecific alarm calls (Collier et al., 2017; Manser, 2001; Manser et al., 2002). Choughs, like mongooses, may have been driven by similar social (e.g. cooperative breeding) and ecological (e.g. ground foraging) factors to develop such a system, enabling effective coordination of antipredator responses to various threats (Furrer & Manser, 2009). Our findings are consistent with the suggestion that social species are likely to develop sophisticated alarm call systems to enhance the antipredator benefits of group living (Blumstein & Armitage, 1997; Furrer & Manser, 2009).

Counterintuitively, choughs initiated their response to low-urgency terrestrial alarms as quickly as they did to high-urgency flee alarms, 0.13 s in both cases, although the response was quite different. Choughs never fled in response to terrestrial alarms, whereas most birds fled immediately upon hearing flee alarms and took six times longer to resume feeding. One possible explanation for the comparable response times is that the similar call structure enhances detectability, while subtle acoustic differences then allow discrimination (Tegtmann & Magrath, 2020). This similarity may therefore trigger an equally rapid detection and initial motor response before the birds fully process and recognize the specific call type. A similar example has been observed in New Holland honeyeaters, *Phylidonyris novaehollandiae*, which respond extremely quickly to alarm calls (about 0.1 s) (McLachlan & Magrath, 2020). Honeyeaters assess the urgency level based on the acoustic structure of the first element of the alarm calls, which varies with threat level, and adjust their escape strategy depending on the number of subsequent elements (McLachlan & Magrath, 2020). In choughs, terrestrial alarms are highly efficient signals, prompting both a fast initial response but also a rapid resumption of feeding, which balances predator vigilance with foraging efficiency.

When a threat is not immediate, receivers may seek additional information, such as by observing the caller's behaviour, to enhance the effectiveness of their antipredator responses. Functionally referential alarm calls can convey limited information about a threat's location, such as on the ground or in the sky, but there is currently no evidence that such calls provide specific directional details about an approaching threat, such as from the left or right (Liao et al., 2024). Therefore, complementary input from other senses, such as vision, can help receivers refine this information. In choughs, aerial whistles are specifically given in response to high-flying aerial threats, prompting most birds to look upward immediately. However, about 30% of their total scanning time was spent looking around. While this 'looking around' might appear redundant, it could help receivers gather additional information about the exact direction of an approaching hawk by observing the caller's behaviour, such as their gaze direction. Although no studies have directly tested this possibility, similar behaviour has been observed in other species (Evans et al., 1993; Schel et al., 2010; Seyfarth & Cheney, 1980). For example, chickens were more likely to look up following playback of aerial alarm calls, but the frequency of horizontal scanning did not differ between aerial and terrestrial alarm calls (Evans et al., 1993). As each sensory modality has its own strengths and limitations, this seemingly 'redundant' response may enhance the accuracy of their antipredator behaviour, particularly in low-urgency situations. Therefore, we suggest that it would be valuable, in future studies of functionally referential communication, to integrate information from multiple sensory modalities, such as auditory and visual signals/cues.

Choughs were more likely to display bulging eyes in response to aerial whistles compared to other alarm call types, suggesting that this might be a visual signal associated with aerial threats.

Bulging eyes might have various functions that explain association with aerial whistles. First, they might signal to predators that they have been detected (Caro, 2005; Holley, 1993). However, this seems unlikely because high-flying hawks are typically distant (over 50 m high) and, if bulging eyes functioned as an advertisement signal, then it might also be expected in response to terrestrial predators. Second, bulging eyes might not have a signalling function, but perhaps enhance visual acuity when searching for distant predators. This explanation seems improbable, as bulging eyes also occur during close social interactions (Rowley, 1978). Third, we propose bulging eyes are most likely a visual signal to conspecifics (Sherman, 1977; J. Smith, 1965; C. Smith & Evans, 2008) either (1) as a redundant component of a multimodal signal, reinforcing the message that the threat is airborne and distant, or (2) as a nonredundant component, conveying directional information about the threat or caller by emphasizing eye orientation. Based on our field observations, choughs often bulge their eyes while producing aerial whistles and looking towards high-flying hawks, which could signal hawk location. However, playback of aerial whistles alone was sufficient to elicit this behaviour, so the eye bulging can occur when the individual has not itself seen the predator. In this situation, a bird's direction of gaze may signal the location of the alarm caller, from whom others could gain information. Further research is needed to test the possible signalling function of eye bulging, such as whether it affects the gaze direction of listeners.

Individuals in social groups rely heavily on communication to coordinate diverse activities, particularly antipredator behaviours (Freeberg, 2006; Freeberg et al., 2012; Liao et al., 2024). White-winged choughs, as obligate cooperative breeders, encode information about threat type and urgency in their alarm calls, similar to social mongoose species (Collier et al., 2017; Manser, 2001). Their distinctive eye bulging occurred specifically in response to aerial whistles, and so may represent a visual signal associated with high-flying threats and potentially serve to enhance the alarm signal. We therefore propose that the integration of multiple sensory modalities to convey complementary information may be common in alarm communication and warrants further investigation.

Author Contributions

Chun-Chieh Liao: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Andrew N. Radford:** Writing – review & editing, Validation, Supervision, Methodology, Conceptualization. **Robert Heinsohn:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Conceptualization. **Robert D. Magrath:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Data Availability

Data for this study are available in the Mendeley Data repository (<https://doi.org/10.17632/j6vbb7jvx7.1>; Liao et al., 2025).

Declaration of Interest

We declare that we have no conflicts of interest related to this study.

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Supplementary Material

Supplementary Material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2025.123330>.

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Appendix

Table A1
Acoustic differences in chough alarm calls produced in response to experimental stimuli and in natural contexts

Call type	Low frequency (Hz)	High frequency (Hz)	Peak frequency (Hz)	Bandwidth (Hz)	Duration (s)	Aggregate entropy (bits)	PFC average slope (Hz/ms)
Terrestrial alarm call							
Snake model (<i>N</i> = 16)	1699±344	5988±914	3223±503	4289±919	0.3±0.1	5.4±0.3	-4.2±2.5
Natural predator (<i>N</i> = 9)	1510±190	5427±1057	3146±452	3917±1070	0.3±0.1	5.4±0.4	-3.4±1.5
<i>t</i> value	1.77	1.34	0.39	0.88	1.40	0.42	-0.96
<i>P</i> value	0.09	0.20	0.70	0.39	0.18	0.68	0.35
Aerial whistle							
Whistle playback (<i>N</i> = 16)	1734±123	2139±120	1904±89	404±45	0.4±0.1	2.5±0.1	-0.3±0.6
Natural predator (<i>N</i> = 10)	1811±111	2201±108	1969±109	391±42	0.4±0.1	2.5±0.1	-0.3±0.6
<i>t</i> value	-1.63	-1.38	-1.59	0.78	0.44	-0.60	-0.06
<i>P</i> value	0.12	0.18	0.13	0.44	0.67	0.56	0.95
Flee alarm call							
Hawk glider (<i>N</i> = 16)	1998±530	5584±1183	3340±232	3586±1426	0.3±0.1	5.2±0.6	-2.3±2.8
Natural predator (<i>N</i> = 7)	1862±470	5290±703	3429±222	3429±716	0.3±0.1	5.1±0.3	-0.6±2.6
<i>t</i> value	0.62	0.74	-0.87	0.35	1.35	0.53	-1.45
<i>P</i> value	0.55	0.47	0.40	0.73	0.21	0.60	0.17

Means ± SD shown. *P* value from independent *t* test.

Table A2
The amplitude (dB at 5 m) of white-winged chough naturally prompted alarm calls

Call type	<i>N</i>	No. of elements	Amplitude (dB; mean ± SD)	Range (dB; min.–max.)
Terrestrial alarm call	5	46	63.8±4.2	53.6–70.6
Aerial whistle	5	26	59.0±3.0	53.6–65.0
Flee alarm call	5	11	62.4±2.9	57.5–68.0

N refers to the number of different individuals recorded.

Table A3
Eigenvalues and proportion of variance explained from the principal component analysis (PCA) of acoustic properties of alarm calls

PC axis	Eigenvalue	Proportion of variance explained	Cumulative proportion of variance explained
1	2.10	0.63	0.63
2	1.09	0.17	0.80
3	0.80	0.09	0.89
4	0.73	0.08	0.97
5	0.41	0.02	0.99
6	0.20	0.01	1.00

Table A4
Pairwise comparisons of alarm call types along the first two principal components (PC1 and PC2), showing the mean difference between group centroids and *P* values from Tukey's HSD tests

PC axis	Alarm call types	Mean difference between groups	<i>P</i>
PC1	Aerial vs flee	-3.86	<0.001
	Aerial vs terrestrial	4.34	<0.001
	Flee vs terrestrial	0.48	0.057
PC2	Aerial vs flee	0.90	0.006
	Aerial vs terrestrial	0.25	0.64
	Flee vs terrestrial	1.15	<0.001

Table A5
Loadings of the seven measured acoustic variables on each principal component axis

Variable	PC1	PC2	PC3	PC4	PC5	PC6
Low frequency (Hz)	0.04	0.86	-0.19	-0.41	-0.19	-0.06
High frequency (Hz)	-0.46	0.05	-0.25	0.09	-0.38	0.30
Peak frequency (Hz)	-0.43	0.19	-0.15	0.01	0.84	0.23
Bandwidth (Hz)	-0.46	-0.11	-0.21	0.17	-0.33	0.31
Duration (s)	0.29	-0.31	-0.86	-0.26	0.08	-0.05
Aggregate entropy (bits)	-0.46	-0.02	-0.13	0.12	-0.02	-0.87
PFC average slope (Hz/ms)	0.31	0.33	-0.27	0.85	0.03	-0.02

Rows represent acoustic properties, and columns correspond to the principal components derived from the PCA.

Table A6

CLMM output testing the effect of playback treatment on the immediate response of white-winged choughs (also see Fig. 3)

Fixed effects	Estimate $\pm$ SE	Likelihood ratio	df	Z	P
Treatment		116.99	3		<0.001
Treatment (control vs terrestrial)	-0.33 $\pm$ 0.03			-12.20	<0.001
Treatment (control vs aerial)	-0.32 $\pm$ 0.03			-11.24	<0.001
Treatment (control vs flee)	-0.86 $\pm$ 0.05			-17.08	<0.001
Treatment (terrestrial vs aerial)	0.01 $\pm$ 0.03			0.45	0.97
Treatment (terrestrial vs flee)	-0.52 $\pm$ 0.05			-10.11	<0.001
Treatment (aerial vs flee)	-0.54 $\pm$ 0.05			-10.74	<0.001
Group size	-0.04 $\pm$ 0.07	0.33	1	-0.57	0.57
Playback order	-0.18 $\pm$ 0.20	0.88	1	-0.91	0.35

Responses are categorized as follows: 0 = no response; 1 = scan (including looking around and looking up); 2 = startle; 3 = flee. Significant outcomes are shown in bold ($P < 0.05$).

Table A7

Results of linear mixed effects models (LMMs) examining how different playback treatments affect white-winged chough: latency to respond (s) and duration of response (s) (also see Fig. 4)

Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests			R^2 ^b
		Factor levels	Effect $\pm$ SE	df	χ^2	P ^a	
Latency to respond	(Intercept)		0.08 $\pm$ 0.06				0.41
	Treatment (terrestrial)	Aerial	0.22 $\pm$ 0.05	2	24.32	<0.001	
		Flee	0.00 $\pm$ 0.05				
	Group size		0.00 $\pm$ 0.00	1	0.00	0.99	
	Playback order		0.02 $\pm$ 0.02	1	1.29	0.26	
	Location ID		0.00				
Random factor	Individual ID		0.00				
Duration of response	(Intercept)		-8.77 $\pm$ 17.70				0.29
	Treatment (terrestrial)	Aerial	10.90 $\pm$ 13.06	2	14.27	<0.001	
		Flee	47.93 $\pm$ 12.99				
	Group size		2.21 $\pm$ 1.63	1	2.04	0.15	
	Playback order		1.80 $\pm$ 4.78	1	0.16	0.69	
	Location ID		0.00				
Random factor	Individual ID		0.00				
	Location ID		0.00				

Significant outcomes ($P < 0.05$) are shown in bold.

^a P value for each factor is derived from a likelihood ratio test for changes in deviance when models with and without that factor are compared.

^b Conditional R^2 values.

Table A8

Results of post hoc Tukey HSD tests comparing playback treatments for latency to respond and duration of response (also see Fig. 4)

Variable	Treatment	Mean $\pm$ SE (s)	t value	P
Latency to respond (s)	Terrestrial vs aerial	0.13 $\pm$ 0.02 vs 0.35 $\pm$ 0.22	4.73	<0.001
	Terrestrial vs flee	0.13 $\pm$ 0.02 vs 0.13 $\pm$ 0.05	-0.01	1
	Aerial vs flee	0.35 $\pm$ 0.22 vs 0.13 $\pm$ 0.05	4.66	<0.001
Duration of response (s)	Terrestrial vs aerial	9.2 $\pm$ 8.3 vs 21.2 $\pm$ 15.5	-0.83	0.69
	Terrestrial vs flee	9.2 $\pm$ 8.3 vs 59.9 $\pm$ 59.8	3.66	0.003
	Aerial vs flee	21.2 $\pm$ 15.5 vs 59.9 $\pm$ 59.8	2.80	0.02

Table A9

Results of linear mixed effects models (LMMs) examining how different playback treatments affect white-winged chough time (s) spent scanning, looking up and looking around (also see Fig. 5)

Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests			R^2 ^b
		Factor levels	Effect $\pm$ SE	df	χ^2	P ^a	
Time spent scanning	(Intercept)		-0.35 $\pm$ 1.43				0.64
	Treatment (control)	Terrestrial	3.32 $\pm$ 0.93	2	45.97	<0.001	
		Aerial	8.35 $\pm$ 0.97				
	Group size		-0.02 $\pm$ 0.13	1	0.03	0.87	
	Playback order		0.21 $\pm$ 0.36	1	0.38	0.54	
	Location ID		0.00				
Random factor	Individual ID		0.48				
Time spent looking up	(Intercept)		-0.36 $\pm$ 1.14				0.59

(continued on next page)

Table A9 (continued)

Response variable	Fixed effects	Parameter estimates		Likelihood ratio tests			R^2 ^b
		Factor levels	Effect $\pm$ SE	df	χ^2	P ^a	
Random factor	Treatment (control)	Terrestrial	0.14 $\pm$ 0.76	2	41.26	<0.001	0.57
		Aerial	5.58 $\pm$ 0.80				
	Group size		-0.03 $\pm$ 0.10	1	0.09	0.76	
	Playback order		0.24 $\pm$ 0.29	1	0.73	0.39	
	Individual ID		0.14				
Time spent looking around	Location ID		0.00				0.57
	(Intercept)		-0.06 $\pm$ 0.71				
	Treatment (control)	Terrestrial	3.18 $\pm$ 0.46	2	37.62	<0.001	
		Aerial	2.77 $\pm$ 0.49				
	Group size		0.02 $\pm$ 0.06	1	0.07	0.79	
Random factor	Playback order		-0.02 $\pm$ 0.18	1	0.03	0.87	
	Individual ID		0.00				
	Location ID		0.11				

Significant outcomes ($P < 0.05$) are shown in bold.

^a P value for each factor is derived from a likelihood ratio test for changes in deviance when models with and without that factor are compared.

^b Conditional R^2 values.

Table A10

Results of post hoc Tukey HSD tests comparing playback treatments on the time white-winged choughs spent scanning, looking up and looking around (also see Fig. 5)

Variable	Treatment	Mean $\pm$ SE (s)	t value	P
Time spent scanning (s)	Control vs terrestrial	0.02 $\pm$ 0.08 vs 3.4 $\pm$ 1.5	3.57	0.004
	Control vs aerial	0.02 $\pm$ 0.08 vs 8.4 $\pm$ 4.6	8.55	<0.001
	Terrestrial vs aerial	3.4 $\pm$ 1.5 vs 8.4 $\pm$ 4.6	5.13	<0.001
Time spent looking up (s)	Control vs terrestrial	0 vs 0.2 $\pm$ 0.3	0.19	0.98
	Control vs aerial	0 vs 5.6 $\pm$ 4.0	6.94	<0.001
	Terrestrial vs aerial	0.2 $\pm$ 0.3 vs 5.6 $\pm$ 4.0	6.74	<0.001
Time spent looking around (s)	Control vs terrestrial	0.02 $\pm$ 0.08 vs 3.2 $\pm$ 1.5	6.83	<0.001
	Control vs aerial	0.02 $\pm$ 0.08 vs 2.8 $\pm$ 1.8	5.67	<0.001
	Terrestrial vs aerial	3.2 $\pm$ 1.5 vs 2.8 $\pm$ 1.8	0.83	0.69

Table A11

Results of bias-reduced generalized linear models (BRGLMs) with pairwise comparisons examining how different playback treatments affect the probability that white-winged choughs exhibit bulging eyes (also see Fig. 6)

Fixed effects	Effect $\pm$ SE	Z	P
Treatment (control vs terrestrial)	-1.09 $\pm$ 1.06	-1.02	0.56
Treatment (control vs aerial)	-4.09 $\pm$ 1.25	-3.28	<0.01
Treatment (terrestrial vs aerial)	-3.00 $\pm$ 1.06	-2.84	<0.05
Group size	0.10 $\pm$ 0.22	0.43	0.67
Playback order	-0.27 $\pm$ 0.47	-0.58	0.56

Significant outcomes ($P < 0.05$) are shown in bold.