

Cooperatively breeding white-winged choughs use recruitment calls selectively in food-associated contexts

Lola von Kietzell ^{a,*}, Chun-Chieh Liao ^b, Josh J. Arbon ^a, Robert D. Magrath ^b, Andrew N. Radford ^a

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

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

ARTICLE INFO

Article history:

Received 5 February 2026

Initial acceptance 19 May 2026

Final acceptance 2 July 2026

Available online xxx

MS. number: A26-00074

Keywords:

cooperation
food divisibility
food sharing
food-associated call
foraging
group-living
monopolize
playback experiment
recruitment

Many social animals produce vocalizations to attract others to food, with diverse benefits including improved foraging success, reduced predation risk and access to social and reproductive rewards. In some species, the production of such calls varies based on food divisibility, but little is known about the significance of divisibility in food-sharing behaviour. White-winged choughs, *Corcorax melanorhamphos*, are highly social, cooperatively breeding birds with a diverse vocal repertoire. Using a combination of natural observations and field experiments, we investigated whether chough 'peep' calls function in recruitment to food and explored effects of food divisibility on peep calling. We found that peep calls were produced by adults upon discovering high-quality food, and such calls were acoustically distinct from foraging contact calls. Furthermore, choughs gave more peep calls when presented with divisible rather than whole food, and this was associated with a lower tendency to monopolize the food. Both adult and juvenile group members responded to playback of peep calls by looking towards and approaching playback, indicating peep calls function in recruitment to food. Field observations revealed that choughs produced peep calls during group travel and following predator alarms as well as during foraging; we suggest peep calls also function in recruitment in such nonfeeding contexts. Our findings confirm that choughs produce vocalizations to advertise food to groupmates, although they are less likely to call when food is easily defended and challenging to share. Such calls likely allow choughs to gain inclusive fitness and group augmentation benefits by enhancing the foraging success of their groupmates, and represent another aspect of their highly cooperative social system.

© 2026 The Authors. Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

Many social animals produce vocalizations to recruit individuals in a variety of circumstances, such as for joint travel (Gruber & Zuberbühler, 2013), away from danger (Raihani & Ridley, 2007) and to assist in conflict with conspecifics (Gouzoules et al., 1984) and predators (Furrer & Manser, 2009). However, the most well-studied form of recruitment calls is the food-associated call, where animals produce vocalizations to attract individuals to food resources (Clay et al., 2012). Food-associated recruitment calls (hereafter 'food calls') are produced by a variety of social bats (Chaverri & Page, 2024; Wilkinson & Wenrick Boughman, 1998), primates (Hauser et al., 1993; Kitzmann & Caine, 2009; Miglietta et al., 2021) and birds (Evans & Marler, 1994; Hillemann et al., 2019; Radford & Ridley, 2006). Such

calls most commonly recruit conspecifics (C. Brown et al., 1991; Elgar, 1986; but see Goodale & Kotagama, 2006; Hillemann et al., 2019) for joint feeding; in some cases, food calls are produced to attract specific individuals including offspring (Radford & Ridley, 2006; Troisi et al., 2018), close social partners (Slocombe et al., 2010) and potential mates (Evans & Marler, 1994).

Advertising food to others carries obvious costs for callers, including reduced energy intake and diverting effort from other activities (Duque & Stevens, 2016), but there are several possible counteracting benefits. Foraging within a group could directly improve the caller's foraging success, either by joint defence of food against others (Sierro et al., 2020) or improved resource manipulation, such as enabling individuals to track prey movement for longer (C. Brown et al., 1991). Group foraging can also reduce predation risk and costs of vigilance (Elgar, 1986). Where food calls are given to recruit related individuals, sharing food conveys inclusive fitness benefits to callers. For example, adult

* Corresponding author.

E-mail address: lolavonkietzell@gmail.com (L. von Kietzell).

golden lion tamarins, *Leontopithecus rosalia*, produce food-offering calls to attract offspring for both active and passive food sharing (Troisi et al., 2018). Group-living animals might also benefit from attracting groupmates to food via group augmentation effects; living in larger groups can, for example, reduce predation risk and improve outcomes of intergroup conflict (Radford & Ridley, 2006). Alternatively, callers may gain reproductive rewards from sharing food with potential mates: for instance, male chickens, *Gallus gallus*, produce calls to attract females to feeding sites (Evans & Marler, 1994), and females preferentially mate with calling males (Pizzari, 2003). Similarly, food sharing with socially important individuals such as affiliative partners and higher-ranking group members could strengthen social bonds and reduce costs of conflict over food (Bouchard & Zuberbühler, 2022; Miglietta et al., 2021). While there has been considerable work identifying the potential functions of food-associated recruitment calls, most studies are correlative, based on behavioural observations only, with relatively little experimental testing in natural conditions (but see Radford & Ridley, 2006; Troisi et al., 2018).

In many species, the rate of food calling varies depending on food quantity (Chapman & Lefebvre, 1990; Hauser et al., 1993; Pollick et al., 2005), quality (Caine et al., 1995; Clay & Zuberbühler, 2011; Kalan et al., 2015) or divisibility (Elgar, 1986; Hauser et al., 1993; Radford & Ridley, 2006). While the former cases are best explained by the caller's heightened arousal in anticipation of more abundant or preferred food (Clay et al., 2012), the significance of divisibility is less well understood. Several studies have suggested that variation in food sharing is the result of a cost–benefit trade-off, where animals are more likely to share food when associated benefits outweigh potential costs of competitive interactions and reduced energy intake (Elgar, 1986; Hillemann et al., 2019; Silk et al., 2013). For example, tits (Paridae) produce food calls to recruit flockmates in the morning when predation risk is high and flock size is small, but call rate declines throughout the day as more tits join and competition increases (Hillemann et al., 2019). Similar reasoning has been applied to explain why resource divisibility affects food call rate: house sparrows, *Passer domesticus*, presented with breadcrumbs share food with little aggression and call at a high rate to attract flockmates, while whole bread is monopolized and few calls are produced (Elgar, 1986). As such, animals may produce more calls attracting others to divisible food because of the difficulty in monopolizing such foods, as well as the reduced potential for competitive interactions and loss of food intake (Elgar, 1986). However, to our knowledge this hypothesis has not received further research attention to date.

Here, we investigate whether peep calls in white-winged choughs, *Corcorax melanorhamphos*, function in recruitment to food, using a combination of natural observations and field experiments. White-winged choughs (hereafter 'choughs') are cooperatively breeding passerine birds native to southeastern Australia, living in stable social groups of closely related individuals (Beck et al., 2008; Rowley, 1978). Choughs are ground-foraging omnivores feeding mostly on invertebrates; group members forage in close association, sharing feeding sites without apparent conflict, and adults actively provision food to juveniles (Rowley, 1978). Foraging is time intensive and foraging skills are unusually slow to develop: juveniles are provisioned up to 8 months after fledging and take up to 5 years to achieve maximal foraging success (Heinsohn, 1991; Heinsohn et al., 1988). This prolonged development of foraging success has significant survival implications, with low food intake believed to be the primary driver of juvenile mortality (Rowley, 1978). Choughs have a diverse vocal repertoire (Liao et al., 2025) and have been observed to produce loud, high-pitched, short 'peeps' during foraging, usually

on discovery of abundant and high-quality foods such as anthropogenic food items and fruit bushes (L. von Kietzell & C.-C. Liao, personal observations). Field observations suggest peep calls are seldom produced in response to single large items such as caterpillars or snails, indicating call rate may be mediated by food divisibility (L. von Kietzell, personal observation).

In this study, we describe the acoustic structure, context of production and function of chough peep calls. First, we recorded calls produced during foraging to test whether peep calls are acoustically distinct from other vocalizations given while foraging (i.e. contact calls). We conducted field observations of natural behaviour both to characterize the behavioural contexts associated with peep calling and to identify the typical age of callers. We then presented adult choughs with cheese, a high-quality food, to test whether calls are produced when discovering food. We presented choughs with both whole and grated cheese to examine effects of food divisibility on call rate. Furthermore, we scored antagonistic and cooperative behaviours displayed after cheese presentation, to address why peep calling might be mediated by food divisibility. We predicted that choughs would call at a greater rate in response to divisible food based on a greater inclination to share rather than monopolize food. Accordingly, we predicted that choughs would display more cooperative and fewer antagonistic behaviours when finding divisible food. Finally, we used a playback experiment comparing the responses of juvenile and adult choughs to test who would respond to peep calls. Given that group members are closely related and forage cooperatively, we predicted that peep calls function in attracting group members to feeding sites. Moreover, we expected that juveniles, with their low foraging success and experience, would be more likely than adults to respond to peep calls.

METHODS

Study Population and Site

White-winged chough groups typically number six to eight, including a single breeding pair and nonbreeding helpers of both sexes, most of which are the offspring from previous years (Beck et al., 2008; Rowley, 1978). Choughs are ground-foraging omnivores and primarily feed on invertebrate prey, which is gathered by sifting through leaf litter and soil (Heinsohn et al., 1988). Age can be determined from iris colour, with juveniles (age 0–1 years) having brown eyes, immature individuals (age 2–4 years) having orange or yellow eyes, and adults (age 5+ years) having red eyes (Rowley, 1978). During the breeding season (August to January), home ranges are limited to an actively defended territory of ca. 20 ha around the nest. However, home ranges expand to up to 1000 ha during the nonbreeding season (February to July) with groups aggregating in flocks of up to 100 individuals for foraging, although group identity is clearly maintained (Rowley, 1978). While individuals forage alone or in subgroups during the breeding season, group members exclusively forage together outside of the breeding period (Heinsohn et al., 1988).

Our study period ran from March to June 2025, within the nonbreeding season. We studied nine groups (group size: mean $\pm$ SD = 9.6 ± 5.3 , range 4–21) in two urban nature reserves, O'Connor Ridge (35°14'42.7"S 149°07'04.2"E) and Lyneham Ridge (35°14'23.7"S 149°07'01.2"E), located adjacent to suburbs in Canberra, Australian Capital Territory, Australia. This population of choughs has been studied for over 40 years (Heinsohn, 1987; Heinsohn et al., 1988) and most individuals are colour-banded or number-ringed for individual identification. Individuals in this population are already well habituated to human presence; we always followed groups on foot for 5 min from 3–5 m away before

starting data collection. As choughs typically moved to suburban areas for foraging during the day, we conducted all fieldwork in the hours after dawn and before dusk when choughs were close to their roosting sites within reserves.

Acoustic Comparison

As well as peep calls, we observed choughs producing contact calls during foraging. These are regularly given soft calls that elicit no obvious behavioural responses in group members; such calls likely play a role in group cohesion and spacing of group members as in other species (Radford & Ridley, 2008; Townsend et al., 2010). To test whether peep calls are acoustically distinct from foraging contact calls, we recorded both call types from 15 adult choughs and statistically compared their acoustic features. As peep calls occurred relatively rarely and recording quality was often inadequate to be used for acoustic analysis, we prompted peep calls by presenting choughs with cheese. We recorded contact calls from the same individuals while foraging without any apparent disturbance (e.g. predator alarms, discovery of unusually high-quality food or agonistic interactions with conspecifics). Calls were recorded as 32-bit WAV files on a Zoom F3 Field recorder, set to a 48 kHz sampling rate, using a Sennheiser ME66 shotgun directional microphone. Only high-quality recordings with minimal background noise were selected for analysis of acoustic characteristics. We generated spectrograms from recordings on Raven Pro Version 1.6.5 set to a Hann window function, 512 sample size, hop size of 0.542 ms with a window overlap of 94.9%, frequency grid spacing of 93.8 Hz, 2.5 s duration and 0–24 kHz frequency bandwidth. Spectrograms were visualized in RavenPro using the Viridis colour map (<https://cran.r-project.org/web/packages/viridis/vignettes/intro-to-viridis.html>), with the brightness and contrast set to 50. As both call types contain multiple harmonics, we measured only the fundamental frequency (i.e. the lowest horizontal frequency band) for consistency. We manually placed selection boxes over the fundamental frequency of each element and calculated the following acoustic parameters: (1) peak frequency (Hz), the frequency with the highest power; (2) bandwidth 90% (Hz), the frequency interval in which 90% of power is found; and (3) duration 90% (s), the time period in which 90% of power is found. We used spectrogram measurements conducted by a single researcher for our analysis; however, to account for possible subjectivity in the placement of selection boxes, a second researcher repeated the measurements of the same calls and interobserver agreement was tested.

Natural Observations

We collected data on natural occurrences of peep calls to describe the typical behavioural context associated with calling and the identity of calling individuals. As these calls occurred relatively infrequently, we conducted sampling ad libitum outside

of experimental trials. Nine social groups were observed from May to June 2025 in both study sites. An observer followed a single group at a time for 10–20 min and dictated all call events, defined as one or more peep calls separated by no more than 60 s, onto audio recordings. For each call event, we noted start time, number of callers, caller age (where possible) and group behaviour (i.e. the behaviour of the majority of group members). Group behaviours were categorized as (1) foraging: head down, searching for, consuming or provisioning food; (2) travelling: head level or raised, moving more than 3 m at a time without stopping to forage; (3) antipredator: scanning surroundings with head level or raised, mobbing, alarm calling and/or fleeing to trees; or (4) any other behaviours (e.g. resting, preening, aggressive behaviour). These are clearly distinct categories, especially when watching large, habituated birds from close range. As we occasionally observed peep calls during regrouping after predator alarms, we also noted the start and end time of all group antipredator behaviour (defined as above), and scored whether this occurred in the 60 s before call onset.

Experiment 1: Food Presentation

To test whether peep calls are prompted by discovery of high-quality food and to investigate effects of food divisibility on the number of calls produced, we conducted a food presentation experiment. All trials ran from April to June 2025 on 16 randomly selected colour-banded or number-ringed adults from eight breeding groups (1–5 focal individuals per group). We focused on adults because preliminary observations suggested it was this age class that mostly produced peep calls. Each focal individual received three separate treatments in a repeated-measures design: 5 g of grated cheese, a 5 g cube of whole cheese or a single grated cheese fragment (<5% of the whole/grated cheese mass) as a control (Fig. 1). We placed each treatment on a wooden block as cheese could otherwise be partially obscured by ground vegetation, possibly leading to perceptual differences between trials. Using a single cheese fragment as a control rather than the block alone was necessary for focal individuals to engage with the treatment.

We separated trials for the same individual by at least 24 h to avoid impacts of satiation on call production, as well as reducing the likelihood of associative conditioning and pre-emptive vocalizations. Daily desensitization presentations of only the wooden block were also performed to reduce further the likelihood of associative conditioning. We separated trials for different individuals within the same group by at least 24 h for the same reason. Each focal individual received all treatments within the same time window, either in the hours after dawn (0600–1000 hours) or before dusk (1400–1800 hours). We counterbalanced treatment order such that no individuals in the same group received treatments in the same order, and each possible order

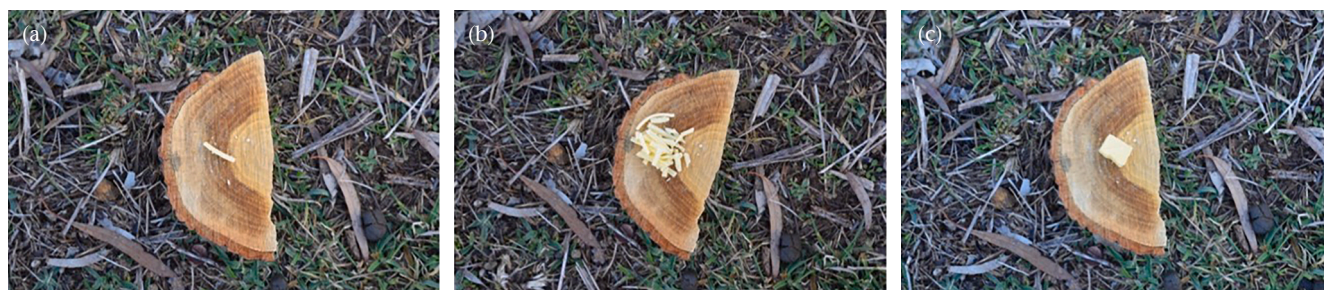


Figure 1. Cheese treatments as presented to focal individuals on a wooden block: (a) control treatment, (b) grated cheese treatment and (c) whole cheese treatment.

occurred two or three times. We abandoned and repeated at least 24 h later any trials interrupted by the following significant disturbances: (1) presence of predators or bouts of antipredator behaviour; (2) presence of competitor species (Australian magpies, *Gymnorhina tibicen*, and pied currawongs, *Strepera graculina*); (3) groups moving foraging site; (4) conspecific peep calls unrelated to the treatment (i.e. >5 m from the cheese block); (5) conspecifics discovering the presentation prior to the focal individual.

During a trial, we placed the wooden block within 3 m of the focal individual in the anticipated direction of travel; the observer then retreated ca. 3 m from the block. To minimize the likelihood of conspecifics discovering the treatment prior to the focal individual, we presented treatments when the latter was separated from its groupmates by at least 2 m. When focal individuals moved away from the block, we followed on foot, taking care to move slowly and maintain 3–5 m distance to minimize any disturbance to natural behaviour. We recorded trials by audio using the same equipment as for call recordings (above). Video recordings were made using a Panasonic HC-VX1 camcorder hand-held by the observer.

The response period ran for 30 s from the moment a focal individual approached within 50 cm of the treatment, which was estimated in the field and dictated onto recordings. This allowed us to capture any calls given before reaching the food. We blind-scored the total number of peep calls produced by the focal individual from audio files only, renamed by a researcher not involved in scoring. We recorded the following behaviours from video files as binary variables: (1) removal of cheese by the focal individual, with at least five steps of directed movement away from the block before eating; (2) provisioning of cheese by the focal individual to a conspecific; (3) proximity of a conspecific within 30 cm of the focal individual; (4) any physical or vocal aggression displayed by the focal individual, which included pecking conspecifics, ruffling feathers and calls associated with agonistic contexts (e.g. mobbing). Swallowing is clearly visible in choughs (Heinsohn et al., 1988), so we could easily determine whether food was removed before eating. Where possible, we also recorded the age of conspecifics to which cheese was provisioned. Behaviours (1) to (4) were scored by a single observer for our analysis; however, to account for possible subjectivity in the judgment of behavioural categories, a second researcher repeated the behavioural scoring of the same videos and interobserver agreement was tested.

Experiment 2: Call Playback

To test how choughs respond to peep calls and determine whether there were any age-related differences in these responses, we carried out a playback experiment. All trials were conducted between April and June 2025 on 28 individuals: 14 pairs of adults and juveniles from the same group; there were one to five unique pairs of colour-banded or number-ringed focal individuals from each of seven groups. We used calls recorded for the acoustic comparison of call types (see above) to generate playback tracks. Each focal individual received playbacks of a peep call and a foraging contact call recorded from the same group member, in a repeated-measures design. Each pair of adult and juvenile individuals received its own unique set of playback treatments (i.e. $N = 14$ playback sets that were recorded from a different individual to other pairs). Focal individuals within a pair received the same sets of calls, in the same order, with the first individual receiving both treatments before moving to its paired individual. We counterbalanced treatment order (i.e. which call type was broadcast first) and focal order (i.e. whether the adult or juvenile individual in a pair was first to receive playbacks) between pairs. Playbacks to the same pair were conducted on the same day where

possible, and always within the same time period, either after dawn (0600–1000 hours) or before dusk (1400–1800 hours). To control for potential carryover effects between treatments, playbacks to the same pair were separated by at least 10 min, and playbacks to different pairs within the same group were separated by at least 24 h. Groups that were presented with cheese (see experiment 1 above) did not receive playbacks for a minimum of 4 h, to avoid carryover effects between experiments.

As peep calls used for playbacks were prompted using cheese, we recorded natural food and contact calls to ensure playback amplitude and temporal pattern was closely based on natural calls. Calls were recorded opportunistically, noting the distance between the observer and caller (Table 1). Call amplitude was calculated by re-recording these calls at 5 m distance and comparing RMS amplitude to a 1 kHz pure tone of known amplitude, adjusting for the distance between caller and observer. All playback exemplars were prepared in Raven Pro Version 1.6.5 (<https://ravensoundsoftware.com/software/raven-pro/>). Each treatment consisted of four identical repeated elements, which is above but within 1 SD of the mean number of elements in natural bouts of peep calling (Table 1), to ensure realism but guarantee focal individuals had adequate opportunity to respond. As the time between elements was not typically consistent within natural bouts of peep calling, this was randomized to the mean $\pm$ SD inter-element interval (2.9 ± 1.8 s; Table 1); again, to ensure that playbacks closely resembled natural call events. We applied the same set and order of inter-element intervals to each set of peep and contact call treatments played to a pair, to control for effects of call rate on response. Recordings were band-pass filtered below 500 Hz to remove excessive background noise while preserving frequencies within the range of food and contact calls. A fade-in and fade-out effect was applied to 0.5 s of background noise before and after each element to avoid playbacks sounding clipped or abrupt. To ensure playback amplitude did not confound variation in response between treatments, we broadcast both peep and contact calls at an amplitude of 50 dB at 5 m; this was within the natural amplitude range of both (Table 1). Natural call amplitude was determined by re-recording calls at 5 m, along with a 1 kHz pure tone for which amplitude was measured using a Brüel & Kjær 2240 sound level meter. We then compared digital amplitude measurements of re-recorded calls and the 1 kHz tone to calculate natural call amplitude, accounting for the original distance between the microphone and vocalizing individual at the time of recording. All playback files were later digitally adjusted to match the target amplitude.

We broadcast all playback treatments from a JBL Go 3 Bluetooth loudspeaker, mounted on a 30 cm tripod to mimic the height of a calling chough and camouflaged using artificial foliage. The loudspeaker was placed 5 m from the focal individual, ensuring that the following four criteria were met before commencing playback: (1) the loudspeaker's main output surface was pointed directly towards the focal individual; (2) the focal individual was the

Table 1
Characteristics of natural peep and foraging contact calls

	Peep calls	Contact calls
Amplitude at 5 m (dB, mean $\pm$ SD)	48.0 $\pm$ 6.9	44.7 $\pm$ 5.0
Amplitude at 5 m (dB, min.–max.)	37.0–62.9	34.5–55.7
No. of elements per bout of calling ¹	2.8 $\pm$ 1.7	–
Inter-element interval ¹ (s, mean $\pm$ SD)	2.9 $\pm$ 1.8	–

Peep calls: $N_{\text{individuals}} = 11$, $N_{\text{elements}} = 47$; contact calls: $N_{\text{individuals}} = 14$, $N_{\text{elements}} = 35$.

¹ Elements more than 5 s apart were taken to represent a new bout of calling. The number of elements and the inter-element interval per call bout were calculated for peep calls only, as contact calls do not occur in distinct bouts.

closest individual to the loudspeaker, actively foraging and at least 30 cm from the nearest conspecific; (3) there was minimal noise from traffic or wind; (4) there were no potential predators present or signs of antipredator behaviour in the group. The observer then retreated 3 m from the loudspeaker and recorded the trial on video using a hand-held Panasonic HC-VX1 camcorder. Responses were dictated by the observer onto the video recording during the trial, noting instances of (1) 'look toward', during which the individual raises its head with the bill horizontal or above and directed within the 180° angle facing the loudspeaker, and (2) 'approach', during which the individual takes at least five steps of directed movement towards the loudspeaker with the bill raised to a horizontal position or above. The response period ran for 20 s from the onset of playback. It was necessary to score responses live in the field, rather than blind scoring from video files later, as it was not feasible to position the camera such that both the focal bird and the loudspeaker were visible in the frame; thus, the focal individual's response relative to the loudspeaker could not be determined from video. However, we chose these response behaviours as both were clearly apparent.

Although every effort was made to conduct playbacks in quiet conditions, study sites were adjacent to roads and observation times sometimes coincided with heavy traffic. As such, background noise amplitude was measured immediately following each trial using a Brüel & Kjær Type 2240 Sound Level Meter (amplitude measured in dB, meter set to LAeq), and variation in background noise was accounted for within statistical analyses. Trials were abandoned and not repeated for at least 24 h in cases when (1) conspecifics gave peep calls during the response period (to avoid such calls affecting focal responses to experimental calls), (2) predators were present or there was a bout of antipredator behaviour or (3) groups moved foraging sites.

Statistical Analysis

All statistical analyses and production of figures were performed in R version 4.5.1 (R Core Team, 2025). We compared acoustic parameters of peep and contact calls using paired *t* tests, performing a square-root transformation to the peak frequency measurement to improve normality. For natural observations of peep call events, we conducted chi-square contingency tests to assess whether the occurrence of predator alarms before the event or multiple callers per event were associated with a particular group behaviour during the event, applying a Monte Carlo simulation in each case to account for values <5.

To account for possible observer bias, interobserver agreement tests were performed for two data sets. For the acoustic comparison of peep and contact calls, we calculated the intraclass correlation coefficient (ICC) using the function 'icc' in the package 'psych' (Revelle, 2015) to determine the consistency in the two raters' measurements of the acoustic parameters. We applied a one-way mixed-effects model and tested absolute agreement for single measurements. For the behavioural responses in the food presentation experiment, we calculated Cohen's κ coefficient using the function 'kappa2' in the package 'irr' (Gamer et al., 2012) to assess the reliability of the two raters' scoring.

For the experimental data, we aimed to use generalized linear mixed effect models (GLMMs). GLMMs were constructed using the 'glmer' function in the 'lme4' package (Bates et al., 2015), and model validation was carried out using the package 'DHARMa'. For all models, we used DHARMa to visualize the spread of residuals and test for over- or underdispersion. For the number of peep calls model in the food presentation experiment, we also tested for zero inflation due to the high number of zeros in the data. No issues with model validity were detected. When required, pairwise

comparisons were conducted using the 'emmeans' function in the 'emmeans' package, applying a Tukey correction. *P* values were derived from likelihood ratio tests (LRTs) between the final model and the model without the term of interest. We report true means and probabilities for all response variables in the main text, while figures show model-predicted estimates.

For the food presentation experiment, we fitted a Poisson GLMM for the number of peep calls and binomial GLMMs for the probabilities of peep calling, provisioning cheese, removing cheese and moving away before eating, and displaying aggressive behaviour. We added a weak Bayesian prior to the model investigating the probability of removing cheese, using the 'bgfmer' function in the 'blme' package (Chung et al., 2013), to help avoid a singular fit. All models included treatment and treatment order as fixed effects and individual identity as a random effect. Data for the effect of treatment on aggression exhibited near-complete separation, where almost all aggression occurred in response to whole cheese, and the model failed to converge. Consequently, we tested the effect of treatment on the probability of displaying aggression using a Cochran's *Q* test with a Benjamini–Hochberg correction for pairwise comparisons, using the 'cochran.qtest' function. Aggressive behaviour was not confounded by any significant treatment difference in proximity within 30 cm of conspecifics to the focal individual (Cochran's *Q* test: $Q = 1.17$, $P = 0.56$).

For the playback experiment, we examined effects of treatment and focal individual age on the likelihood of looking towards the playback loudspeaker using a binomial GLMM with a weak Bayesian prior added, to help avoid a singular fit. The model also included treatment order, focal order and background noise amplitude as fixed effects, as well as pair identity and focal identity as random effects. Background noise was scaled (mean-centred and divided by one standard deviation) to improve model convergence. We initially included the interaction between treatment and age as a fixed effect; however, a likelihood ratio test showed this interaction was nonsignificant and we removed it from the final model. Background noise was not measured for one trial; we replaced this value with the noise amplitude of the previous trial, conducted 10 min earlier at the same site. No individuals approached the loudspeaker during the contact call playback, hence there was too little variance to model effects of playback treatment on the likelihood of approach using a mixed effect model. So, we instead tested this using an exact McNemar test with the 'mcnemar.exact' function, as is appropriate for paired binomial data.

Ethical Note

This research was conducted under permission from the Animal Welfare and Ethical Review Body, University of Bristol (UIN-24-094), and the Australian National University Ethics Committee (protocol A2022/35). To avoid interfering with natural foraging behaviour and minimize the risk of digestive issues, birds were provided with a maximum of 5 g of cheese per day, and each bird received cheese on no more than five occasions. Disturbance was also minimized by limiting the total length of playback tracks to 15 s or less, and focal individuals were exposed to no more than three playbacks in total. All birds resumed normal foraging behaviour after playbacks ended.

RESULTS

Acoustic Comparison

Peep calls and foraging contact calls (Fig. 2) differed in their acoustic structure. Peep calls had a 33.6% higher peak frequency (paired *t* test: $t_{14} = 10.73$, $P < 0.001$; Fig. 3a) and were 63.2% shorter in duration ($t_{14} = -8.07$, $P < 0.001$; Fig. 3b) than contact calls. Peep

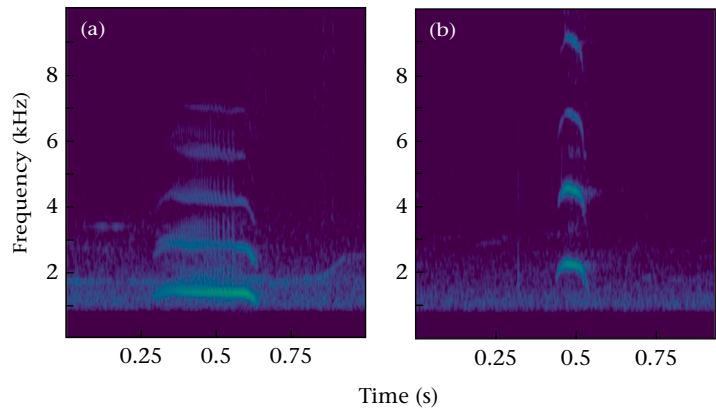


Figure 2. Example spectrograms of a single element of a chough (a) foraging contact call and (b) peep call. Image generated using Raven Pro version 1.6.5.

call bandwidth was also 17.2% narrower than for contact calls, but this was not statistically significant ($t_{14} = -1.92, P = 0.08$; Fig. 3c). Interobserver agreement was excellent for measurements of peak frequency (ICC = 0.97, $P < 0.001$) and duration (ICC = 0.99, $P < 0.001$), and moderate for bandwidth (ICC = 0.57, $P < 0.001$).

Natural Observations

We observed 19 events of peep calling; of these, 12 occurred while groups were foraging and seven while travelling (Fig. 4). Five of 19 events occurred in the 60 s following a predator alarm. Groups were significantly more likely to be travelling (4/5 events) than foraging (1/5 events) during events following a predator alarm (chi-square contingency test: $\chi^2 = 5.43, N = 19, P = 0.04$; Fig. 4). Most events (14/19) involved more than one calling individual; having multiple callers per event was not significantly associated with the type of group behaviour ($\chi^2 = 3.96, N = 19, P = 0.12$). At least one caller could be identified for 15/19 events; of the 30 identified individuals, 23 were adults, six were immature and one was juvenile (mean age structure of focal groups = 54% adults, 24% immatures, 22% juveniles).

Experiment 1: Food Presentation

Choughs gave more peep calls in response to the grated cheese presentation compared to both the whole cheese and the control

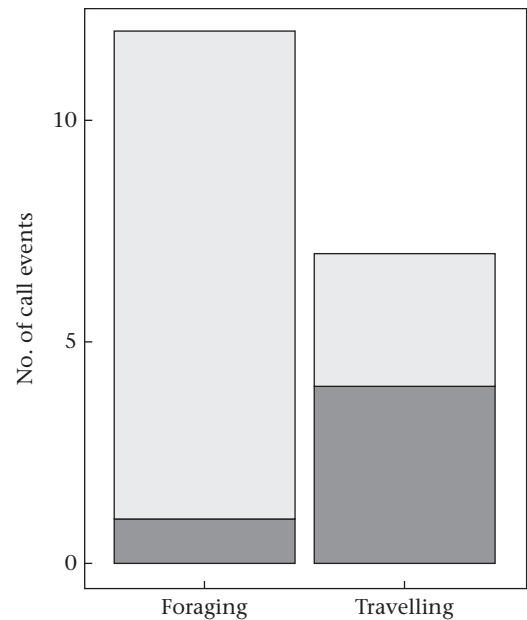


Figure 4. The number of observed events of peep calling depending on the behaviour of the majority of group members at the time of calling. Stacks represent whether predator alarms occurred in the 60 s preceding the event (dark grey = yes; light grey = no). $N = 19$ events in 462 observation minutes.

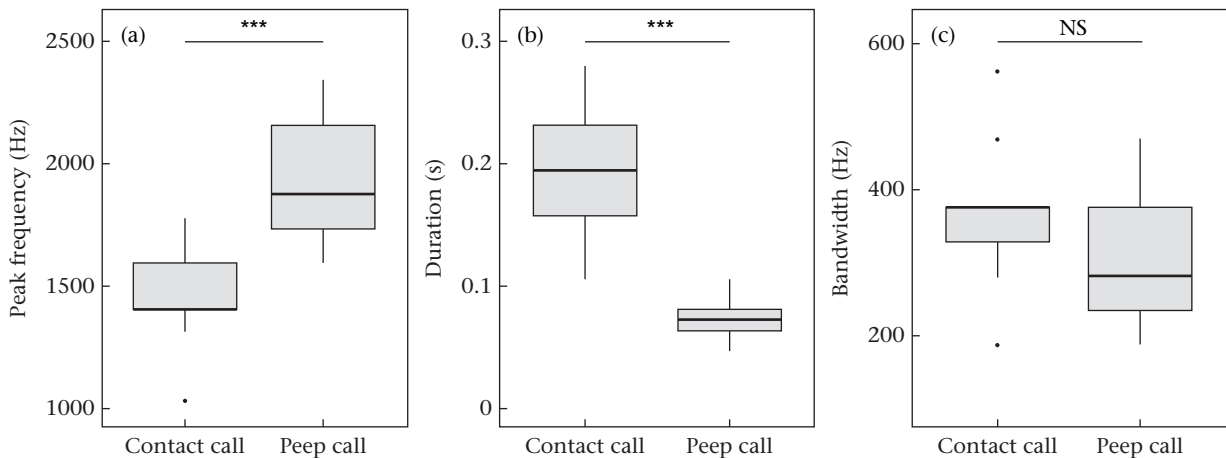


Figure 3. Acoustic comparison of chough foraging contact calls and peep calls: (a) peak frequency, (b) duration and (c) bandwidth. Boxes represent the interquartile range (IQR) with the median shown as the middle line; whiskers extend to 1.5× IQR and outliers are shown as points beyond whiskers. *** $P < 0.001$. $N = 15$ for each call type.

treatments. Most individuals produced peep calls in response to presentation of grated cheese (9/16 individuals), followed by whole cheese (6/16 individuals) and the control (3/16 individuals), but the effect of food treatment on the probability of peep calling was marginally nonsignificant (LRT: $\chi^2_2 = 5.27$, $P = 0.07$; Table 2). After controlling for an effect of treatment order ($\chi^2_1 = 7.07$, $P = 0.008$), the number of calls given by choughs did depend on food treatment ($\chi^2_2 = 26.58$, $P < 0.001$; Table 2, Fig. 5). Individuals gave approximately three times more peep calls in response to grated cheese (mean $\pm$ SD = 3.3 ± 4.7) than to both the control treatment (1.1 ± 3.3 ; Tukey test: $z = 4.28$, $P < 0.001$) and whole cheese (1.2 ± 1.9 ; $z = 3.94$, $P < 0.001$). There was no significant difference in the number of calls given in response to whole cheese compared to the control treatment ($z = 0.42$, $P = 0.91$).

Choughs were more likely to show monopolizing behaviours when presented with whole cheese compared to other treatments. The likelihood of removing the cheese and moving away before eating was affected by treatment (LRT: $\chi^2_2 = 21.62$, $P < 0.001$; Table 3, Fig. 6a). Almost all individuals (15/16) did so when presented with whole cheese, which was more likely than for grated cheese (5/16 individuals; Tukey test: $z = 3.07$, $P = 0.006$) or the control treatment (4/16 individuals; $z = 3.25$, $P = 0.003$); there was no significant difference between grated cheese and control ($z = 0.44$, $P = 0.90$). Moreover, the display of aggressive behaviour was affected by treatment (Cochran's Q test: $Q = 16.2$, $P < 0.001$; Fig. 6b). Choughs were 10 times more likely to display aggressive behaviour when presented with whole cheese (10/16) than grated cheese (1/16 individuals; $P = 0.006$) or the control treatment (1/16 individuals; $P = 0.006$); there was no significant difference between the grated cheese and control treatments ($P = 1$). Grated cheese was provisioned to a group member more often (5/16 individuals) than whole cheese (1/16 individuals) or the control (1/16 individuals), but this difference was marginally nonsignificant (LRT: $\chi^2_2 = 5.60$, $P = 0.06$; Table 3, Fig. 6c). All provisioned individuals for which age could be identified were juveniles ($N = 6$). Interobserver agreement was excellent for the scoring of behavioural responses to food presentation (Cohen's κ coefficient: removing cheese: $\kappa = 0.88$, $P < 0.001$; aggression: $\kappa = 0.83$, $P < 0.001$; proximity to conspecifics: $\kappa = 0.79$, $P < 0.001$; provisioning cheese: $\kappa = 0.83$, $P < 0.001$).

Experiment 2: Call Playback

Choughs responded to playback of peep calls by looking towards and approaching the loudspeaker. More individuals looked

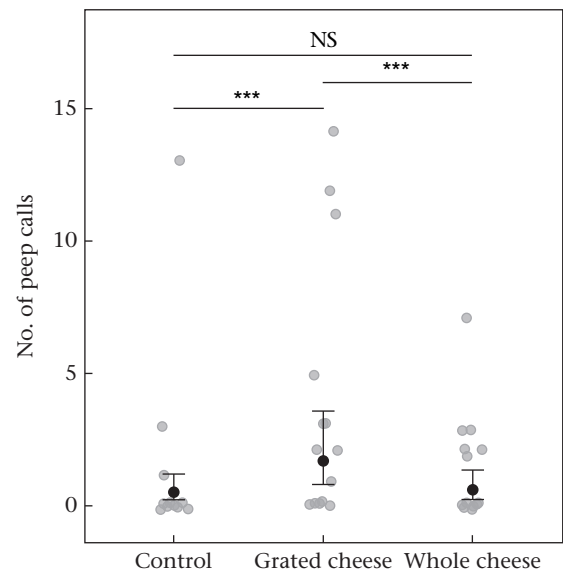


Figure 5. Number of peep calls produced by focal choughs in response to each food treatment. Black points and error bars represent model-predicted means and 95% confidence intervals; grey points are raw data (jittered for ease of viewing). *** $P < 0.001$. $N = 16$ for each treatment.

towards peep calls (21/28) than towards contact calls (12/28; LRT: $\chi^2_1 = 6.20$, $P = 0.01$; Table 4, Fig. 7). This difference in response to the two call types was not affected by age (treatment*age interaction: $\chi^2_1 = 1.63$, $P = 0.20$). Adults (18/28) and juveniles (15/28) also did not differ significantly in their overall likelihood of looking towards the playback ($\chi^2_1 = 0.46$, $P = 0.50$). There was no significant effect of background noise amplitude (mean $\pm$ SD = 52.3 ± 4.6 dB), focal order or treatment order on looking towards the loudspeaker (Table 4). Focal birds never approached a loudspeaker playing contact calls, but 6/28 individuals approached the peep call playback (McNemar exact test: $P = 0.03$). Both age groups were equally likely to approach peep calls (3/14 individuals in each case).

DISCUSSION

White-winged choughs produce peep vocalizations, which are acoustically distinct from foraging contact calls, upon discovery of

Table 2
Food presentation experiment: factors affecting the production of peep calls

Factors	Estimate	95% CI	χ^2	df	P
Probability of peep calling					
Intercept	-0.96	[-26.91, 1.15]			
Treatment			5.27	2	0.07
Treatment (grated cheese)	1.88	[0.51, 35.29]			
Treatment (whole cheese)	1.03	[-0.41, 32.75]			
Treatment order	-0.32	[-1.94, 0.46]	0.63	1	0.43
Individual ID	0.62	[0, 17.13]			
Number of peep calls					
Intercept	0.15	[-1.26, 1.08]			
Treatment			26.58	2	<0.001
Treatment (grated cheese)	1.19	[0.59, 1.84]			
Treatment (whole cheese)	0.14	[-0.63, 0.95]			
Treatment order	-0.41	[-0.79, 0.13]	7.07	1	0.008
Individual ID	1.27	[0.57, 1.86]			

Probability of peep calling was modelled with a GLMM fitted with a binomial error using a logit link function. Number of peep calls was modelled with a GLMM fitted with a Poisson error using a log link function. Random effects are italicized; significant P values are in bold.

Table 3
Food presentation experiment: factors affecting the probabilities of removing cheese and moving away before eating, and provisioning cheese to a conspecific

Factors	Estimate	95% CI	χ^2	df	P
Probability of removing cheese and moving away before eating					
Intercept	-0.38	[-29.01, 15.02]			
Treatment			21.62	2	<0.001
Treatment (grated cheese)	0.38	[-6.02, 44.42]			
Treatment (whole cheese)	4.43	[3.04, 543.72]			
Treatment order	-0.48	[-31.89, 2.33]	0.85	1	0.36
Individual ID	0.96	[0.81, 121.88]			
Probability of provisioning cheese to conspecific					
Intercept	-1.79	[0, 9.59]			
Treatment			5.60	2	0.06
Treatment (grated cheese)	2.23	[0, 185.91]			
Treatment (whole cheese)	-0.12	[0, 79.15]			
Treatment order	-0.74	[0, 0.77]	1.39	1	0.24
Individual ID	1.06	[0, 84.32]			

Both were modelled using GLMMs fitted with a binomial error using a logit link function; the removing cheese model had a Bayesian wrapper fitted. Random effects are italicized; significant P values are in bold.

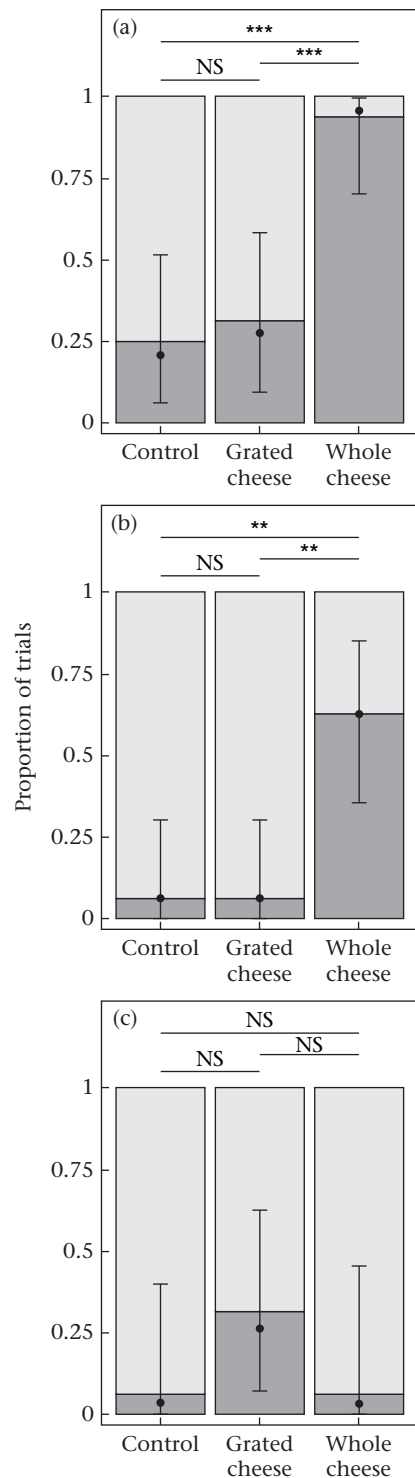


Figure 6. Proportion of trials for each food treatment in which focal choughs (a) removed cheese and moved away before eating, (b) displayed aggressive behaviour and (c) provisioned cheese to a conspecific (dark grey = yes; light grey = no). Points and error bars show model-predicted odds ratios and 95% confidence intervals for (a) and (c), and true proportions and 95% confidence intervals for (b). ** $P < 0.01$; *** $P < 0.001$. $N = 16$ for each treatment.

food as well as during group travel. During natural calling events, peep calls were predominantly produced by adults, while our playback experiment revealed that both adult and juvenile receivers responded by looking towards and approaching such calls.

Table 4
Playback experiment: factors affecting the probability of looking towards playback

Factors	Estimate	95% CI	χ^2	df	P
Intercept	-0.75	[-34.97, 22.77]			
Treatment			6.20	1	0.01
Treatment (peep call)	1.90	[0.92, 44.05]			
Focal age (juvenile)	-0.63	[-28.14, 9.61]	0.46	1	0.50
Background noise amplitude ¹	0.27	[-6.70, 17.32]	0.90	1	0.34
Focal order	0.24	[-12.90, 23.23]	0.06	1	0.81
Treatment order	0.20	[-11.39, 14.34]	-0.01	1	1.00
<i>Individual ID</i>	0.95	[0.84, 84.76]			
<i>Pair ID</i>	0.90	[0.79, 74.00]			

GLMM fitted with a Bayesian wrapper and binomial error using a logit link function. The interaction between treatment and focal age was nonsignificant ($\chi^2 = 1.63$, $P = 0.20$) and was removed from the final model. Random effects are italicized; significant P values are in bold.

¹ Mean-centred and divided by one SD.

Furthermore, our food presentation experiment showed that choughs produced peep calls at a higher rate and were less likely to act antagonistically on finding divisible compared to whole food. As such, the peep vocalization appears to act as a recruitment call but individuals appear to use it selectively to advertise food only in certain circumstances.

Peep call rate was strongly predicted by food divisibility: choughs produced three times as many peep calls upon finding grated cheese than upon finding whole cheese or the control. This is in line with previous findings in pied babblers, *Turdoides bicolor* (Radford & Ridley, 2006), chimpanzees, *Pan troglodytes* (Hauser et al., 1993), and house sparrows (Elgar, 1986) (but see Roush & Snowden, 2000). It has been suggested that as divided food occupies a greater volume, it is perceived as greater in quantity than whole food, and variation in food call rate is driven by the perceived differences in abundance (Hauser et al., 1993). However, this seems unlikely to be the explanation for our results as choughs

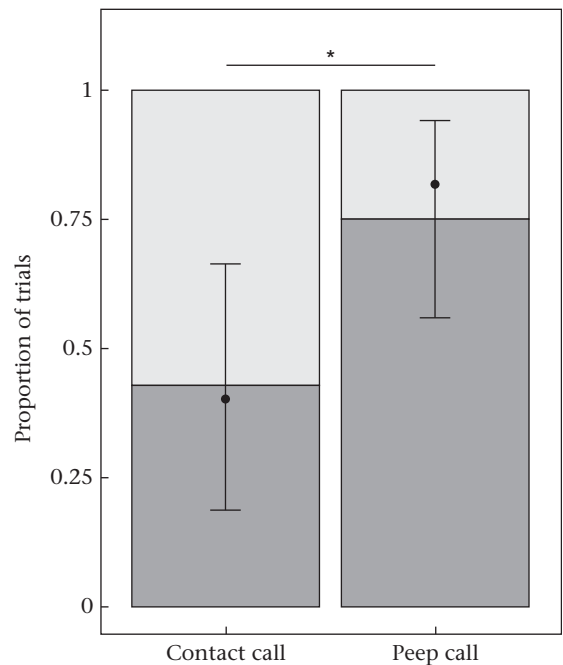


Figure 7. Proportion of trials for each playback treatment in which focal choughs looked towards the loudspeaker (dark grey = yes; light grey = no). Points and error bars show model-predicted odds ratios and 95% confidence intervals. * $P < 0.05$. $N = 28$ for each treatment.

called at the same rate for whole cheese and the control treatment, which clearly differed in quantity. Instead, we propose that choughs produced fewer calls for whole food (presumably reducing the likelihood of attracting groupmates) because it was easily monopolized by taking it away and could similarly be easily lost to others.

Resource defence theory predicts that individuals should tend towards monopolizing rather than sharing food when competition is high and the resource is easily defensible (J. Brown, 1964). Findings from our food presentation experiment support this prediction. Choughs were three times more likely to remove cheese and move away before eating and 10 times more likely to display aggression for whole food compared to divisible food, indicating a much greater tendency to monopolize a single, large food item. To the best of our knowledge, only one previous study has empirically addressed effects of food divisibility on monopolization: in ruddy turnstones, *Arenaria interpres*, dominants consistently attempted to defend food from subordinates regardless of the food's divisibility, but these attempts were less successful when the food was divided (Vahl & Kingma, 2007). Our findings differ in that choughs were less likely to attempt monopolization of divisible food, although we cannot provide any insight into the success of such monopolization attempts. As such, there are two axes by which food divisibility could affect the allocation of resources: first, by affecting the probability of exhibiting monopolizing behaviours and, second, by impacting the effectiveness of such monopolization attempts. We further predicted that choughs would be more likely to provision grated cheese than whole cheese to group members. While there was a slightly higher likelihood of provisioning grated cheese, this difference was not statistically significant. However, as the experiment was conducted in a wild setting, we could not standardize the distance between focal choughs and group members across trials, which may have confounded motivation to provision others.

The probability of peep calling followed a similar pattern to call rate, where choughs tended to be more likely to give peep calls for grated cheese than for whole cheese or the control, but this difference was statistically nonsignificant. Peep calls given in response to the control treatment could be explained by learned associations between the block and large quantities of cheese. However, this appears unlikely as we found no effect of treatment order on the probability of peep calling, which would be expected if choughs were primed to produce calls by prior experience. We used a single cheese fragment as the control to ensure focal choughs reliably engaged with the treatment, but even this minimal quantity of cheese was sometimes sufficient to elicit a peep call. As such, individuals may produce a single call when any cheese is first encountered, while the production of further calls is more deliberate and depends on the nature of the food. Future work should consider whether peep call rate has meaningful implications for receiver responses as in other taxa; for example, calling at a higher rate can decrease the time taken for callers to be joined and increase the number of joining individuals (Chapman & Lefebvre, 1990; Elgar, 1986; but see Kitmann & Caine, 2009).

Surprisingly, there were several grated cheese trials where no peep calls were produced. In other species, variation in food calling has been proposed to constitute a form of deception, as withholding calls should benefit signallers by lowering the chance of attracting foraging competitors, while receivers lose out on the feeding opportunity (Chapman & Lefebvre, 1990; Di Bitetti, 2005). Choughs exhibit deception when provisioning nestlings (helpers occasionally 'false-feed' nestlings, placing food into their bill but consuming it themselves; Boland et al., 1997), so they might plausibly do so when finding divisible food too. Future work should establish whether individuals are punished for not

calling in response to food (Caine et al., 1995; Hauser & Marler, 1993; Ischer et al., 2020) and are less likely to call in the absence of groupmates, when there is a lower probability of being discovered to withhold calls (Caine et al., 1995; Di Bitetti, 2005). Variation in the likelihood of calling may also result from differences in the relatedness and/or social connectivity of the potential signaller to its groupmates, but testing these ideas would require additional data.

As predicted, choughs responded to playback of peep calls by looking towards and approaching the loudspeaker, demonstrating that these calls function in social recruitment. Choughs may gain several benefits from recruiting others to feeding sites. First, foraging within groups can offer greater protection from predators, diluting each individual's risk and reducing the time needed for vigilance (Elgar, 1986). However, because choughs already forage in relatively close association during the nonbreeding season, often within 1–2 m of groupmates (Rowley, 1978), any additional protection gained from attracting others to a specific food patch is likely minimal. More importantly, callers likely gain long-term inclusive fitness benefits by improving the foraging success of their groupmates, who are often close relatives (Beck et al., 2008). Furthermore, improving groupmate survival maintains and boosts group size, which in turn provides individuals with reproductive and energetic benefits: more than seven group members are required for choughs to raise young successfully (Heinsohn, 1992), and individuals in larger groups invest less time into vigilance, with more time available for foraging (Heinsohn, 1987).

Contrary to expectations, juvenile choughs did not show stronger responses to peep calls than adults. This is surprising given juveniles have a markedly inferior foraging success compared to adults (Heinsohn, 1991), and should therefore have a greater motivation to approach to such calls. In pied babblers and golden lion tamarins, for example, food calls are more likely to attract juveniles than adults, and juveniles gain direct foraging benefits from approaching callers (Radford & Ridley, 2006; Rapaport, 2011). Previous work has shown that juvenile choughs are slow to develop appropriate responses to alarm calls (Liao et al., 2026). Thus, it may be that there are cognitive constraints which limit the ability of juvenile choughs to recognize and respond to peep calls, although this is perhaps less likely with such a simple vocalization. We often observed adults actively running to provision juveniles (L. von Kietzell, personal observation); such direct provisioning by adults may diminish the incentive for juveniles to respond to peep calls. Direct provisioning in the food presentation experiment occurred exclusively from adults to juveniles; as adults lose out on obtaining food through provisioning, they should have a greater incentive to respond to peep calls than juveniles. There is also no obvious disincentive for adults to respond to peep calls, in contrast to pied babblers where adults approaching food calls receive aggression from callers (Radford & Ridley, 2006). While we did not record aggressive interactions during natural peep call events, there was little aggression in response to grated cheese in the food presentation experiment, where calls were produced at a high rate. As such, peep calls may serve more generally to support the foraging success of groupmates, rather than to enhance juvenile food intake specifically. Responses to peep calling may also vary depending on the caller's identity and their likelihood of sharing food with the receiver, but further testing would be required to investigate this possibility.

While choughs predominantly produced peep calls during foraging, about a third of natural call events occurred while groups were travelling, although our observational sample size was small. Producing food calls during travel is reasonably common in other

species; for example, adult pied babblers give such calls to facilitate the movement of offspring (Raihani & Ridley, 2007) and male chimpanzees call while travelling to join other males (Fedurek et al., 2014). We suggest that, as during foraging, travel-related peep calls in choughs might function in social recruitment, alerting individuals to the group's imminent departure and maintaining group cohesion while travelling, although this hypothesis needs testing. Some peep calls were heard following predator alarms, and groups were typically travelling on such occasions. In pied babblers, adults use food calls in nonfeeding contexts to coordinate offspring movement away from predators (Raihani & Ridley, 2007). A similar function could apply to choughs; although our playback experiment showed that adults and juveniles responded equally to peep calls, peep calls could also more generally serve to recruit group members away from predators and restore cohesion when individuals scatter. From a proximate perspective, at least some peep calling (e.g. on finding food or after predator alarms) could be triggered by heightened arousal; in other species, food calls are often seen in situations of elevated arousal such as changes in weather (Dittus, 1984) and intergroup encounters (Halloy & Kleiman, 1994). While the focus of our study was on peep calls in a food-associated context during the nonbreeding season, further work should elaborate on peep calls in other contexts, for example addressing whether there are any differences in call acoustic structure or function across behavioural contexts and seasons.

Group-living animals gain many potential benefits from producing vocal signals to share information about food. White-winged choughs produce such calls to recruit group members to shareable food sources, which represents another aspect of their highly cooperative social system (Rowley, 1978). Choughs move over vast areas to find food, and advertising food to group members likely plays an important role in improving group foraging efficiency. However, peep calling is a plastic trait and food divisibility appears to be a key factor in the decision to advertise food. As food availability and distribution fluctuate over seasons, areas and levels of anthropogenic influence, patterns of food-sharing behaviour could also shift with implications for starvation risk, group dynamics and sociality.

Author Contributions

Lola von Kietzell: Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Chun-Chieh Liao:** Writing – review & editing, Resources, Methodology, Investigation, Conceptualization. **Josh J. Arbon:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Robert D. Magrath:** Writing – review & editing, Supervision, Resources, Methodology, Conceptualization. **Andrew N. Radford:** Writing – review & editing, Visualization, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization.

Data Availability

Data for this study are available within the Supplementary Material.

Declaration of Interest

We confirm that there are no conflicts of interest related to this study.

Acknowledgments

This study was supported by funding from the School of Biological Sciences, University of Bristol and the UK Acoustics Network (UKAN+). Many thanks to Brendah Nyaguthii for her contributions in the field and to Abby Bryce for her assistance with validating results. We are also grateful to the anonymous reviewers for providing feedback on the manuscript.

Supplementary Material

Supplementary material associated with this article is available at <https://doi.org/10.1016/j.anbehav.2026.123722>.

The Supplementary Material has not been copy-edited and the content, formatting and file functionality are the sole responsibility of the author(s).

References

- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Beck, N. R., Peakall, R., & Heinsohn, R. (2008). Social constraint and an absence of sex-biased dispersal drive fine-scale genetic structure in white-winged choughs. *Molecular Ecology*, 17(19), 4346–4358. <https://doi.org/10.1111/j.1365-294X.2008.03906.x>
- Boland, C. R. J., Heinsohn, R., & Cockburn, A. (1997). Deception by helpers in cooperatively breeding white-winged choughs and its experimental manipulation. *Behavioral Ecology and Sociobiology*, 41(4), 251–256. <https://doi.org/10.1007/s002650050386>
- Bouchard, A., & Zuberbühler, K. (2022). Male chimpanzees communicate to mediate competition and cooperation during feeding. *Animal Behaviour*, 186, 41–55. <https://doi.org/10.1016/j.anbehav.2022.01.00>
- Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bulletin*, 76(2), 160–169.
- Brown, C. R., Brown, M. B., & Shaffer, M. L. (1991). Food-sharing signals among socially foraging cliff swallows. *Animal Behaviour*, 42(4), 551–564.
- Caine, N. G., Addington, R. L., & Windfelder, T. L. (1995). Factors affecting the rates of food calls given by red-bellied tamarins. *Animal Behaviour*, 50(1), 53–60. <https://doi.org/10.1006/anbe.1995.0220>
- Chapman, C. A., & Lefebvre, L. (1990). Manipulating foraging group size: Spider monkey food calls at fruiting trees. *Animal Behaviour*, 39(5), 891–896. [https://doi.org/10.1016/S0003-3472\(05\)80953-4](https://doi.org/10.1016/S0003-3472(05)80953-4)
- Chaverri, G., & Page, R. A. (2024). Food-associated calls in disc-winged bats. *Behavioral Ecology and Sociobiology*, 78(12), Article 119. <https://doi.org/10.1007/s00265-024-03534-8>
- Chung, Y., Rabe-Hesketh, S., Dorie, V., Gelman, A., & Liu, J. (2013). A nondegenerate penalized likelihood estimator for variance parameters in multilevel models. *Psychometrika*, 78(4), 685–709. <https://doi.org/10.1007/s11336-013-9328-2>
- Clay, Z., Smith, C. L., & Blumstein, D. T. (2012). Food-associated vocalizations in mammals and birds: What do these calls really mean? *Animal Behaviour*, 83(2), 323–330. <https://doi.org/10.1016/j.anbehav.2011.12.008>
- Clay, Z., & Zuberbühler, K. (2011). Bonobos extract meaning from call sequences. *PLoS One*, 6(4), Article e18786. <https://doi.org/10.1371/journal.pone.0018786>
- Di Bitetti, M. S. (2005). Food-associated calls and audience effects in tufted capuchin monkeys, *Cebus apella nigratus*. *Animal Behaviour*, 69(4), 911–919. <https://doi.org/10.1016/j.anbehav.2004.05.021>
- Dittus, W. P. J. (1984). Toque macaque food calls: Semantic communication concerning food distribution in the environment. *Animal Behaviour*, 32(2), 470–477. [https://doi.org/10.1016/S0003-3472\(84\)80283-3](https://doi.org/10.1016/S0003-3472(84)80283-3)
- Duque, J. F., & Stevens, J. R. (2016). Voluntary food sharing in pinyon jays: The role of reciprocity and dominance. *Animal Behaviour*, 122, 135–144. <https://doi.org/10.1016/j.anbehav.2016.09.020>
- Elgar, M. A. (1986). House sparrows establish foraging flocks by giving chirrup calls if the resources are divisible. *Animal Behaviour*, 34, 169–174. [https://doi.org/10.1016/0003-3472\(86\)90020-5](https://doi.org/10.1016/0003-3472(86)90020-5)
- Evans, C. S., & Marler, P. (1994). Food calling and audience effects in male chickens, *Gallus gallus*: Their relationships to food availability, courtship and social facilitation. *Animal Behaviour*, 47(5), 1159–1170. <https://doi.org/10.1006/anbe.1994.1154>
- Fedurek, P., Donnellan, E., & Slocumbe, K. E. (2014). Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. *Behavioral Ecology and Sociobiology*, 68(8), 1345–1355. <https://doi.org/10.1007/s00265-014-1745-4>
- Furrer, R. D., & Manser, M. B. (2009). Banded mongoose recruitment calls convey information about risk and not stimulus type. *Animal Behaviour*, 78(1), 195–201. <https://doi.org/10.1016/j.anbehav.2009.05.002>
- Gamer, M., Lemon, J., Fellows, I., & Singh, P. (2012). Package 'irr' (Vol. 22, pp. 1–32). Comprehensive R Archive Network. <https://doi.org/10.32614/cran.package.irr>

- Goodale, E., & Kotagama, S. W. (2006). Vocal mimicry by a passerine bird attracts other species involved in mixed-species flocks. *Animal Behaviour*, 72(2), 471–477. <https://doi.org/10.1016/j.anbehav.2006.02.004>
- Gouzoules, S., Gouzoules, H., & Marler, P. (1984). Rhesus monkey (*Macaca mulatta*) screams: Representational signalling in the recruitment of agonistic aid. *Animal Behaviour*, 32(1), 182–193. [https://doi.org/10.1016/S0003-3472\(84\)80336-X](https://doi.org/10.1016/S0003-3472(84)80336-X)
- Gruber, T., & Zuberbühler, K. (2013). Vocal recruitment for joint travel in wild chimpanzees. *PLoS One*, 8(9), Article e76073. <https://doi.org/10.1371/journal.pone.0076073>
- Halloy, M., & Kleiman, D. G. (1994). Acoustic structure of long calls in free-ranging groups of golden lion tamarins, *Leontopithecus rosalia*. *American Journal of Primatology*, 32(4), 303–310. <https://doi.org/10.1159/000064791>
- Hauser, M. D., & Marler, P. (1993). Food-associated calls in rhesus macaques (*Macaca mulatta*): II. Costs and benefits of call production and suppression. *Behavioral Ecology*, 4(3), 817–819. <https://doi.org/10.1093/beheco/4.3.206>
- Hauser, M. D., Teixidor, P., Field, L., & Flaherty, R. (1993). Food-elicited calls in chimpanzees: Effects of food quantity and divisibility. *Animal Behaviour*, 45(4), 206–212. <https://doi.org/10.1006/anbe.1993.1096>
- Heinsohn, R. G. (1987). Age-dependent vigilance in winter aggregations of cooperatively breeding white-winged choughs (*Corcorax melanorhamphos*). *Behavioral Ecology and Sociobiology*, 20(4), 303–306. <https://doi.org/10.1007/BF00292183>
- Heinsohn, R. G. (1991). Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *American Naturalist*, 137(6), 864–881. <https://doi.org/10.1086/285198>
- Heinsohn, R. G. (1992). Cooperative enhancement of reproductive success in white-winged choughs. *Evolutionary Ecology*, 6(2), 97–114. <https://doi.org/10.1007/BF02270705>
- Heinsohn, R. G., Cockburn, A., & Cunningham, R. B. (1988). Foraging, delayed maturation, and advantages of cooperative breeding in white-winged choughs, *Corcorax melanorhamphos*. *Ethology*, 77(3), 177–186. <https://doi.org/10.1111/j.1439-0310.1988.tb00202.x>
- Hillemann, F., Cole, E. F., Keen, S. C., Sheldon, B. C., & Farine, D. R. (2019). Diurnal variation in the production of vocal information about food supports a model of social adjustment in wild songbirds. *Proceedings of the Royal Society B: Biological Sciences*, 286(1897), Article 20182740. <https://doi.org/10.1098/rspb.2018.2740>
- Ischer, G., Zuberbühler, K., & Fedurek, P. (2020). The relationship between food calling and agonistic behaviour in wild chimpanzees. *Behavioural Processes*, 178, Article 104182. <https://doi.org/10.1016/j.beproc.2020.104182>
- Kalan, A. K., Mundry, R., & Boesch, C. (2015). Wild chimpanzees modify food call structure with respect to tree size for a particular fruit species. *Animal Behaviour*, 101, 1–9. <https://doi.org/10.1016/j.anbehav.2014.12.011>
- Kitzmann, C. D., & Caine, N. G. (2009). Marmoset (*Callithrix geoffroyi*) food-associated calls are functionally referential. *Ethology*, 115(5), 439–448. <https://doi.org/10.1111/j.1439-0310.2009.01622.x>
- Liao, C. C., Radford, A. N., Heinsohn, R., & Magrath, R. D. (2025). Functionally referential communication about danger in cooperatively breeding white-winged choughs. *Animal Behaviour*, 229, Article 123330. <https://doi.org/10.1016/j.anbehav.2025.123330>
- Liao, C.-C., Zhou, Y., Heinsohn, R., Radford, A. N., & Magrath, R. D. (2026). *Slow development of alarm-call responses in a highly social bird species* (Manuscript in preparation).
- Miglietta, S., Bardino, G., Sotto-Mayor, A., Galli, A. S., Meulman, E., Breuer, T., Fuh, T., & Masi, S. (2021). Absence of specific individuals and high food abundance elicit food calls in wild western gorillas. *Behavioral Ecology and Sociobiology*, 75(6), Article 98. <https://doi.org/10.1007/s00265-021-03027-y>
- Pizzari, T. (2003). Food, vigilance, and sperm: The role of male direct benefits in the evolution of female preference in a polygamous bird. *Behavioral Ecology*, 14(5), 593–601. <https://doi.org/10.1093/beheco/arg048>
- Pollick, A. S., Gouzoules, H., & De Waal, F. B. M. (2005). Audience effects on food calls in captive brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, 70(6), 1273–1281. <https://doi.org/10.1016/j.anbehav.2005.03.007>
- Radford, A. N., & Ridley, A. R. (2006). Recruitment calling: A novel form of extended parental care in an altricial species. *Current Biology*, 16(17), 1700–1704. <https://doi.org/10.1016/j.cub.2006.06.053>
- Radford, A. N., & Ridley, A. R. (2008). Close calling regulates spacing between foraging competitors in the group-living pied babbler. *Animal Behaviour*, 75(2), 519–527. <https://doi.org/10.1016/j.anbehav.2007.05.016>
- Raihani, N. J., & Ridley, A. R. (2007). Adult vocalizations during provisioning: Offspring response and postfledging benefits in wild pied babblers. *Animal Behaviour*, 74(5), 1303–1309. <https://doi.org/10.1016/j.anbehav.2007.02.025>
- Rapaport, L. G. (2011). Progressive parenting behavior in wild golden lion tamarins. *Behavioral Ecology*, 22(4), 745–754. <https://doi.org/10.1093/beheco/arr055>
- Revelle, W. (2015). Package 'psych'. *Comprehensive R Archive Network*, 337(338), 161–165. <https://doi.org/10.32614/cran.package.psych>
- Roush, R. S., & Snowdon, C. T. (2000). Quality, quantity, distribution and audience effects on food calling in cotton-top tamarins. *Ethology*, 106(8), 673–690. <https://doi.org/10.1046/j.1439-0310.2000.00581.x>
- Rowley, I. (1978). Communal activities among white-winged choughs *Corcorax melanorhamphos*. *Ibis*, 120(2), 178–197. <https://doi.org/10.1111/j.1474-919X.1978.tb06774.x>
- Sierro, J., Loretto, M. C., Szpl, G., Massen, J. J., & Bugnyar, T. (2020). Food calling in wild ravens (*Corvus corax*) revisited: Who is addressed? *Ethology*, 126(2), 257–266. <https://doi.org/10.1111/eth.12991>
- Silk, J. B., Brosnan, S. F., Henrich, J., Lambeth, S. P., & Shapiro, S. (2013). Chimpanzees share food for many reasons: The role of kinship, reciprocity, social bonds and harassment on food transfers. *Animal Behaviour*, 85(5), 941–947. <https://doi.org/10.1016/j.anbehav.2013.02.014>
- Slocombe, K. E., Kaller, T., Turman, L., Townsend, S. W., Papworth, S., Squibbs, P., & Zuberbühler, K. (2010). Production of food-associated calls in wild male chimpanzees is dependent on the composition of the audience. *Behavioral Ecology and Sociobiology*, 64(12), 1959–1966. <https://doi.org/10.1007/s00265-010-1006-0>
- Townsend, S. W., Hollén, L. I., & Manser, M. B. (2010). Meerkat close calls encode group-specific signatures, but receivers fail to discriminate. *Animal Behaviour*, 80(1), 133–138. <https://doi.org/10.1016/j.anbehav.2010.04.010>
- Troisi, C. A., Hoppitt, W. J., Ruiz-Miranda, C. R., & Laland, K. N. (2018). Food-offering calls in wild golden lion tamarins (*Leontopithecus rosalia*): Evidence for teaching behavior? *International Journal of Primatology*, 39(6), 1105–1123. <https://doi.org/10.1007/s10764-018-0069-z>
- Vahl, W. K., & Kingma, S. A. (2007). Food divisibility and interference competition among captive ruddy turnstones, *Arenaria interpres*. *Animal Behaviour*, 74(5), 1391–1401. <https://doi.org/10.1016/j.anbehav.2007.01.006>
- Wilkinson, G. S., & Wenrick Boughman, J. (1998). Social calls coordinate foraging in greater spear-nosed bats. *Animal Behaviour*, 55(2), 337–350. <https://doi.org/10.1006/anbe.1997.0557>