Cooperative bird differentiates between the calls of different individuals, even when vocalizations were from completely unfamiliar individuals

Paul G. McDonald1,2,*

1Behavioural and Physiological Ecology Research Centre, Zoology, University of New England, Armidale 2351, Australia
2School of Biological Sciences, Macquarie University, Sydney 2109, Australia
*paul.mcdonald@une.edu.au

Hypotheses proposed to explain the evolution of cooperative behaviour typically require differentiation between either groups of conspecifics (e.g. kin/non-kin) or, more typically, individuals (e.g. reciprocal altruism). Despite this, the mechanisms that facilitate individual or class recognition have rarely been explored in cooperative species. This study examines the individual differentiation abilities of noisy miners (Manorina melanocephala), a species with one of the most complex avian societies known. Miners permanently occupy colonies numbering into hundreds of individuals. Within these colonies, cooperative coalitions form on a fission–fusion basis across numerous contexts, from social foraging through to mobbing predators. Birds often use individually distinctive calls to recruit others to a caller’s location, facilitating coalition formation. I used the habituation–discrimination paradigm to test the ability of miners to differentiate between the chur calls of two individuals that were both either: (i) familiar, or (ii) unfamiliar to the focal subject. This technique had not, to my knowledge, been used to assess vocalization differentiation in cooperative birds previously, but here demonstrated that miners could correctly use the spectral features of signals to differentiate between the vocalizations of different individuals, regardless of their familiarity. By attending to individual differences in recruitment calls, miners have a communication system that is capable of accommodating even the most complex cooperative hypotheses based upon acoustic information.

Keywords: individual recognition; kin selection; cooperative breeding; altruism

1. INTRODUCTION

Understanding why cooperation is so pervasive, despite natural selection intuitively predicting that individuals should be selfish, remains a great challenge for biology [1,2]. With the notable exception of kin selection [3], there has been little consensus on important hypotheses shaping social interactions across taxa [1]. Research examining the mechanisms underpinning cooperation may help solve this impasse, as most cooperative hypotheses require potential donors to successfully differentiate between subgroups in a population, such as kin [3] or previous donors [4]. Indeed, models predict that the ability to differentiate between individuals in a population greatly enhances the probability of altruism evolving [5]. Understanding the discrimination abilities within populations is thus key; if potential donors cannot differentiate between key subgroups, than hypotheses centred on these subgroups are likely to be biologically irrelevant. For example, individually distinctive calls are treated as homogenous by receivers in at least one social mammal, indicating the irrelevance of individuality in that context [6].

Acoustic-based signals are likely to be particularly salient in identifying population subgroups in avian systems, as inter-individual distance frequently precludes other signalling modalities [7,8]. Despite this, evidence of the individual-level differentiation required for many cooperative hypotheses is currently limited. Differential responses arising from the ‘dear enemy effect’ are commonly cited as evidence of individual recognition, but may simply reflect classification of signals by receivers into categories that coincide with individual identity, such as familiarity [9]. Carefully designed playback studies can demonstrate fine-scale differentiation abilities [10], but not if responses are subtle [11] or influenced by other group members. Here, I adapt the habituation–discrimination paradigm (HDP) to avoid these issues [10,12] and, without training subjects, directly test the acoustic discrimination abilities of a highly social bird, the noisy miner (Manorina melanocephala).

Miners live in large, highly cooperative colonies that may number over 100 individuals [13]. In this complex society, both kin and non-kin regularly cooperate across a range of social contexts, from cooperative breeding to social foraging. More intriguingly, individual miners give ‘chur’ calls when detecting potential threats or disturbances within colonies, such as a ground-based predator or wind-gusts suddenly moving vegetation. Chur calls recruit other colony members to the vicinity [14], but other calls are typically given during any subsequent mobbing [13]. While the spectral properties of chur calls are individually distinctive [14], they nonetheless vary considerably within individuals. Multiple calls from a given individual show a peak overlap in spectral properties of just 28 per cent using spectrographic cross-correlation (see the electronic supplementary material), much less than similar calls from a congener (78%; [8]).

Receivers therefore face a considerable challenge differentiating between the chur calls of different miners. Nonetheless, considerable benefits would exist in indentifying signalers, including reduced energetic costs associated with responding to unreliable callers [15], and the ability to maximize cooperative benefits through preferentially aiding specific individuals [1,2]. By examining how the miner communication system
Miners decode individuality in calls

2. MATERIAL AND METHODS

(a) Acquisition of playback stimuli

Chur calls with high signal-to-noise ratios were recorded from wild noisy miners in temporary captivity (25 bouts each from 17 individuals; electronic supplementary material). Contact calls (n = 54) from two marked, free-living miners were also recorded to provide additional stimuli used in a different social context. Samples were collected over multiple sessions (23 March–18 October 2009) to ensure that individual identity did not correspond to background acoustics [10].

(b) Source of test subjects

Two groups of 17 birds (n = 34) were tested. The first were from the same colony as birds from which stimuli were recorded. These were assumed to be ‘familiar’ with the stimuli used during HDP, and indeed were frequently observed foraging with recorded individuals. The second group were captured from a different colony 13.5 km away, more than 100 times further than the average miner home range [13]. These birds were assumed to be ‘unfamiliar’ with playback stimuli and effectively unrelated to recorded individuals.

(c) Playback protocol

Playbacks were carried out in a sound booth and filmed for later analysis (see the electronic supplementary material). Each bird heard the same number of stimuli, with calls presented 30 s apart. The first stage, the habituation phase, consisted of playback of 23 different exemplars from individual A. The 24th stimulus (test call) was a chur call recorded from a different individual (i.e. B), enabling a test of the focal bird’s ability to differentiate between the different stimulus classes. The 25th call was an additional, as yet unheard, chur call exemplar from individual A. This ‘rebound’ call assessed any ‘false-positive’ responses to test stimuli. The 26th and final call (new context) was from both a different bird (C) and context (contact call). One subject that failed to respond to this final stimulus was assumed to be no longer attending to any stimuli and removed from analyses. The number of ‘elements’ in each bout presented was standardized for each subject across relevant calls (1st, 23rd, 24th, 25th and 26th; see the electronic supplementary material). Recorded individuals were used once only to provide test or habituation stimuli, providing 17 unique comparisons of the calls of two different individuals that were subsequently assessed by both the familiar and unfamiliar groups.

In addition to the above experiment (hereafter experiment A, n = 34), seven individuals from the familiar group underwent an additional experiment (experiment B). Experiment order was rotated across subjects with at least an hour between trials. In experiment B, subjects heard the same stimuli in the same order as experiment A, but stimuli were first converted into white noise correlates of the original signal. These correlates were identical across the time and frequency domain, but differed in their spectral structure with energy distributed evenly across their entire bandwidth (see the electronic supplementary material). This effectively removes spectral features and allows an assessment of the importance of temporal variation on call differentiation [16]. Experiment B ceased after seven trials when it became clear that subjects were unable to differentiate between the different stimulus classes.

(d) Response scoring

The following responses were scored using FINAL CUT EXPRESS (Apple, CA, USA) after removing audio and renaming sequences to ensure that I was blind to both familiarity and stimulus type:

- duration to first movement (frames),
- degree of initial head turn,
- maximum head turn during 20 s post-playback (SCREEN PROTRACTOR v. 3.2; ICONICO).

(e) Statistical analyses

Responses were log-transformed to generate normal distributions before reduction with principal components analysis (PCA; see the electronic supplementary material). General linear models assessed familiarity (familiar versus unfamiliar, experiment A only) and stimulus type (five levels: first and last in habituation series, test, rebound, new context). Subject identity was included as a random effect for all analyses. Significant stimulus-type differences were assessed post-hoc using least significant difference (LSD) tests. Interactions were not significant and are not presented for brevity. Analyses used IBM STATISTICS (v. 19, SPSS), applying two-tailed tests and a p-value of 0.05 or, for LSD tests, 0.01 to account for multiple testing.

3. RESULTS

Increasing values of the sole PCA component extracted (see the electronic supplementary material) indicated faster and larger head turns by birds upon hearing stimuli. In experiment A, call familiarity did not significantly influence component scores (F1,32 = 1.119, p = 0.298; figure 1), indicating similar responses regardless of whether or not birds were hearing stimuli...
from familiar or unfamiliar individuals. By contrast, the effect of stimulus type was significant ($F_{4,132} = 11.346, p < 0.005$; figure 1). Subjects showed a significantly decreased response to the last habituation and rebound stimuli relative to test calls (figure 1). Responses elicited from the first habituation, test and new context stimuli were not significantly different. Together, these results fit a priori predictions for differentiation of chur calls from different individuals: responses declined during the habituation phase, before dishabituation was observed when a call from another individual (test) was played. Significantly, low responses to rebound stimuli preclude differentiation of chur calls from different individuals: responses declined during the habituation phase, before dishabituation was observed when a call from another individual (test) was played. Significantly, low responses to rebound stimuli preclude spontaneous dishabituation driving these results. When signals were presented with information on temporal variation only (experiment B), subjects were no longer able to differentiate between the calls of different individuals (stimulus-type effect: $F_{4,30} = 2.141, p = 0.100$).

4. DISCUSSION

This study shows that a cooperative bird can differentiate between the calls of different individuals using spectral features or ‘voice’ characteristics alone. Further, miners were equally adept at differentiating between the calls of two unfamiliar individuals as they were birds with whom they regularly interacted, despite considerable variation in call structure within individuals. Differentiating between individuals may well be the basis by which cooperation in the extremely complex societies of miners is maintained [5].

Chur vocalizations attract other individuals to the caller’s location, enabling cooperative coalitions to form [14]. Propensity to engage in cooperative behaviour should be highly dependent upon the ratio of costs and benefits of doing so [1,2]. While costs vary primarily upon internal characteristics (e.g. body condition [17]), the benefits of helping others varies according to recipient identity and associated attributes (e.g. kinship [1,2]). As miners attend to individual differences in call structure, this suggests that fine-scale differentiation is important within this society, in contrast to some other systems [6]. Other potential benefits of differentiating between individuals exist, such as the ability to respond more efficiently to unreliable callers [15,18,19]. In the bell miner (Manorina melanophrys), despite neither familiarity nor spatial proximity reliably encoding relatedness [13,20], kin are still preferentially aided and identified using acoustic cues [8,21]. Thus, differences in individual acoustic signals between noisy miners are also highly likely to influence subsequent cooperative behaviour.

While it is unclear from this study whether or not miners are capable of so-called ‘true’ individual recognition [7,18], this remains a distinct possibility. Determining if habituation to a given call type extends to other functionally distinct call types of a given individual would be useful in this regard. Either way, the acoustic differentiation capabilities of miners ([13,14], herein) closely resemble those of animals traditionally viewed as having more cognitively challenging communication systems [19]. HDP clearly demonstrated the level of information decoded by

Miners decode individuality in calls  P. G. McDonald 3

miners, with unequivocal tests of cooperative hypotheses requiring individual-level responses now able to be undertaken.

Research was approved by the Macquarie University Animal Ethics Committee (AEC2007/010).

Simon Griffith provided access to facilities and Nina Svedin assisted with fieldwork.

8 McDonald, P. G. & Wright, J. 2011 Bell miner provisioning calls are more similar among relatives and are used by helpers at the nest to bias their effort towards kin. Proc. R. Soc. B 278, 3403–3411. (doi:10.1098/rspb.2011.0307)


