Animal Behaviour 104 (2015) 51–57

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Chestnut-crowned babblers show affinity for calls of removed group members: a dual playback without expectancy violation

Jodie M. S. Crane [a,*], Joel L. Pick [b], Alice J. Tribe [c], Ernő Vincze [d], Ben J. Hatchwell [a], Andrew F. Russell [e]

[a] Department of Animal & Plant Sciences, University of Sheffield, Sheffield, U.K.
[b] Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Zurich, Switzerland
[c] Fowlers Gap Arid Zone Station, School of Biological, Earth & Environmental Sciences, University of New South Wales, Sydney, Australia
[d] Department of Limnology, University of Pannonia, Veszprém, Hungary
[e] Centre for Ecology & Conservation, College of Life & Environmental Sciences, University of Exeter, Penryn Campus, Penryn, U.K.

ARTICLE INFO

Article history:
Received 10 September 2014
Initial acceptance 17 October 2014
Final acceptance 17 February 2015
Available online 9 April 2015
MS. number: 14-00730R

Keywords:
contact calls
cooperative breeding
group discrimination
group living
individual recognition
sociality
vocal communication

Cooperative breeding typically evolves within discrete, stable groups of individuals, in which group members derive direct and/or indirect fitness benefits from cooperative behaviour. In such systems, strong selection on group discrimination should emerge. Despite this prediction, relatively few studies have investigated the mechanism of group discrimination in cooperative vertebrates, and the results of many may be confounded by 'expectancy violation', since test individuals from which stimuli were derived remained in the group during experimentation. Here, we used a novel experimental protocol that eliminates this confounding effect in a test of group discrimination in cooperatively breeding chestnut-crowned babblers, *Pomatostomus ruficeps*, using long-distance contact calls. Long-distance contact calls were found to be individually specific, but to lack obvious group level signatures. Using dual playbacks of removed group and nongroup members, we found that these calls allow effective discrimination: groups unanimously approached the speaker broadcasting calls of group members and concomitantly increased their contact call rates. Together, our results suggest that group discrimination emerges from individual recognition. Additionally, the affiliative behaviour of group members towards playbacks of removed members contrasts with the aggressive responses towards nongroup members found in all other studies. One explanation for these differences stems from our elimination of expectancy violation, but further studies are required to verify this.

Cooperative breeders live in discrete groups of individuals characterized by stable long-term associations. In vertebrates, these groups are typically composed of nuclear or extended family units that arise from delayed dispersal of offspring (Emlen, 1995; Hatchwell, 2009), reinforced by low levels of promiscuity (Cornwallis, West, Davis, & Griffin, 2010; Lukas & Clutton-Brock, 2012). Within such groups, kin selection is an important driver of cooperative behaviour (Cornwallis, West, & Griffin, 2009; Dickinson & Hatchwell, 2004) and recognition of group members often suffices to ensure that helpers direct care to relatives and gain indirect fitness benefits as a consequence (Queller, 1992). However, in many species, groups may also contain a substantial proportion of unrelated individuals (Riehl, 2013) and both relatives and nonrelatives may benefit directly through their group membership (Cockburn, 1998; Kokko, Johnstone, & Clutton-Brock, 2001). For example, as most cooperative breeders coordinate foraging behaviour, territorial defence and/or predator evasion (Koenig, Pitelka, Carmen, Mumme, & Stanback, 1992), the ability to discriminate group members from nongroup members will help maintain group integrity, with potential associated survival benefits (Clutton-Brock, 2002). Given that group discrimination may enhance both indirect and direct fitness benefits, it is perhaps surprising that relatively few studies have attempted to identify, and experimentally verify, the group discrimination mechanisms in cooperative vertebrates.

Across taxa, a number of sensory modalities may facilitate group level discrimination (Dietemann, Peeters, Liebig, Thivet, & Hölldobler, 2003; Leclair et al., 2013; Mateo, 2003; Tibbetts, 2002). In cooperative vertebrates, olfactory (Jordan, Mwanguhya, Kyabulima, Ruedi, & Cant, 2010; Leclaire, Nielsen, Thavarajah,

* Correspondence: J. M. S. Crane, Department of Animal & Plant Sciences, University of Sheffield, Sheffield S10 2TN, U.K.
E-mail address: jodie.m.s.crane@gmail.com (J. M. S. Crane).

http://dx.doi.org/10.1016/j.anbehav.2015.02.022

Manser, & Clutton-brock, 2013; Mares, Young, Levesque, Harrison, & Clutton-Brock, 2011) and auditory (Table 1) cues are primarily considered. Among the latter, a total of eight studies in seven species have identified potential vocalizations that may enable group (or kin) discrimination and used experiments to test group responses to playbacks of group versus nongroup members (or kin versus nonkin). For example, four studies have verified that group members can be discriminated on the basis of calls (Hopp, Jablonski, & Brown, 2001; Keen, Meliza, & Rubenstein, 2013; Price, 1999) or song (Payne, Payne, & Rowley, 1988). Further, three studies of two species show that familiar kin can be discriminated from familiar nonkin on the basis of calls (Hatchwell, Ross, Fowlie, & McGowan, 2001; Sharp, McGowan, Wood, & Hatchwell, 2005) or songs (Akçay, Swift, Reed, & Dickinson, 2013), and presumably so too can group members be discriminated from nongroup members (but this was not verified). Finally, only Townsend, Hollén, and Manser (2010) failed to find a differential response to playbacks of calls of group versus nongroup members. Interestingly, in all those cases in which differential responses were observed, groups approached the vocalizations of nongroup members aggressively rather than approaching group members amicably (Table 1). Why this should be is not obvious, but one explanation is provided by expectancy violation (Kondo, Izawa, & Watanabe, 2012): in all those experiments showing significant responses, the familiar call stimulus was recorded from an individual that was present in the group during the experiment.

The aim of this study was to quantify variation in the acoustic structure of long-distance contact calls of chestnut-crowned babblers, *Pomatostomus ruficeps* (Fig. 1a), and to investigate their role in permitting discrimination of group members from nongroup members. Chestnut-crowned babblers are ca. 50 g cooperatively breeding passerines endemic to arid regions of southeastern Australia. They live in relatively large groups (range 3–23 individuals in adult plumage, mean = 11 when not breeding) in open habitat in which predation is a common threat, particularly in small groups (Sorato, Gullett, Griffith, & Russell, 2012). Therefore, maintaining contact with members of the group is likely to be important for survival. First, we conducted acoustic analyses to investigate whether long-distance contact calls, chiefly used to locate group members out of visual contact (Crane, 2014), are individually specific and/or carry signatures of group identity (Fig. 1a). Second, we used a novel dual playback experiment to test whether groups are able to discriminate between the vocalizations of a group member and a member of another unfamiliar group (Fig. 1b). The novelty of this experiment in the context of cooperative breeding is twofold: (1) before the onset of the experiment we removed the group member whose vocalization we presented; and (2) we broadcast the vocalization of the focal group member simultaneously with that of the focal nongroup member, from separate speakers. If the focal individual is not removed, groups experience an expectancy violation through hearing the call of a group member that is already present within the group; potentially generating unnatural responses (Kondo et al., 2012; see Discussion). Dual playbacks not only represent a more ecologically realistic scenario (Rogers et al., 2004), but also force groups to make a direct 'choice', thereby removing any ambiguity in their response.

METHODS

The study was conducted in September and October 2011 at the University of New South Wales Arid Zone Research Station at Fowlers Gap in far western New South Wales, Australia (31°05′S, 141°43′E). The study population has been monitored closely since 2004, so we know the origin of most individuals (Rollins et al., 2012). The habitat is characterized by sparse, open, low-lying shrubland intersected by a network of dry drainage channels with short, linear stands of tall shrubs and trees. Babblers have a natural tendency to move along these drainage channels, as within them both prey availability and vegetation are more abundant and contiguous (Portelli, Barclay, Russell, Griffith, & Russell, 2009). The sparseness of vegetation allowed accurate measures of group responses to playbacks to be determined.

Removals and Recordings

The experimental procedure was carried out over 2 consecutive days in each group (or 3 days in two cases). On the morning of the first day of the procedure, a social group ($N = 19$ groups) was captured during nonbreeding using standard mist nets (under licence from the Australian Bird and Bat Banding Scheme) and the total number of group members noted (range 6–19, mean ± SD = 12.2 ± 3.3). Most members of the group were released at the capture site but between one and four birds (mean ± SD = 2.7 ± 0.9), depending on the size of the group, were selected and removed to an aviary (under UNSW animal care and ethics committee licence number 06/40A). Multiple birds were

Table 1
Experimental tests for auditory mechanisms of group (or kin) discrimination in cooperative birds and mammals

Species	Vocalization	Comparison	Protocol	Results	Reference
Splendid fairy-wren, *Malurus splendens*	Long song	Group member versus nongroup member	Alternating calls (N=19 groups)	>Approach to nongroup member >Aggressive to nongroup member	Payne et al., 1988
Stripe-backed wren, *Campylorhynchus nuchalis*	Contact call	Group member versus nongroup member	Alternating calls (N=16 groups)	=No differences in approach >Aggressive to nongroup member	Price, 1999
Long-tailed tit, *Aegithalos caudatus*	Contact call	Familiar kin versus familiar nonkin	Alternating calls (N=8 groups)	>Approach to nonkin >Aggressive to nonkin	Hatchwell et al., 2001
Mexican jay, *Aphelocoma wollweberi*	Primary call	Group member versus nongroup member	Alternating calls (N=10 groups)	>Approach to nongroup member >Aggressive to nongroup member	Hopp et al., 2001
Western bluebird, *Sialia mexicana*	Dawn song	Kin versus nonkin (equal familiarity)	Alternating calls (N=13 groups)	=Approach >Aggressive to nonkin	Akçay et al., 2013
Superb starling, *Lamprotornis superbus*	Flight call	Group member versus nongroup member	Alternating calls (N=9 groups)	>Approach to nongroup member	Keen et al., 2013
Chestnut-crowned babbler, *Pomatostomus ruficeps*	Contact call	Group member versus nongroup member	Dual playback (N=11 groups)	>Approach to group member >Contact calls to group member	This study
Meerkat, *Suricata suricatta*	Contact call	Group member versus nongroup member	Alternating calls (N=12 groups)	=No differences in approaches =No differences in time by speaker	Townsend et al., 2010

Alternating calls (under 'Protocol') refers to playbacks consisting of a single vocalization type presented at a time, whereas 'dual playback' refers to both test vocalization types being presented simultaneously. Under 'Results': >signifies greater or increased response; =signifies no difference. Most studies recorded various aspects of approach behaviour (e.g. closest distance, time spent within a certain radius), and accompanying vocalizations (e.g. aggressive or contact).