Animal Behaviour 86 (2013) 893–900

Contents lists available at ScienceDirect

Animal Behaviour

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

Individual recognition in a wild cooperative mammal using contact calls

Lynda L. Sharpe, Amy Hill, Michael I. Cherry*

Department of Botany and Zoology, University of Stellenbosch, South Africa

ARTICLE INFO

Article history:
Received 27 March 2013
Initial acceptance 20 May 2013
Final acceptance 16 July 2013
Available online 15 September 2013
MS. number: 13-00273R

Keywords:
contact call
cooperation
dominance hierarchy
dwarf mongoose
Helogale parvula
individual recognition
relative rank
vocalization

Many of the mechanisms advanced to explain the evolution of intraspecific cooperative behaviour, such as reciprocity or social prestige, hinge on an animal's ability to recognize individual group members. However, 'true' individual recognition, between adult group members, has never been demonstrated in a cooperatively breeding bird or mammal species. We tested whether a wild cooperative mammal, the dwarf mongoose, *Helogale parvula*, could recognize individual group members from their vocalizations. We provided test subjects with a large, desirable food item and then simulated the approach of another group member using playbacks of its contact calls. Mongooses were more vigilant after hearing the calls of individuals of higher rank than themselves (that could steal their food) compared with individuals of lower rank than themselves (that could not). We showed that the mongooses were not simply responding to age-related cues that conveyed potential information on rank, and provide some evidence that they were associating the unique characteristics of the call with an individually specific characteristic of the caller (i.e. its relative rank). We conclude that dwarf mongooses exhibit 'true' individual recognition, and this finding supports the potential validity of mechanisms that rely on individuals monitoring the behaviour of others to explain the evolution of cooperative behaviour.

Many of the mechanisms advanced to explain the evolution of intraspecific cooperative behaviour hinge on an animal's ability to recognize individual group members. Reciprocity (Trivers 1971; in which individuals exchange help) and social prestige (Zahavi & Zahavi 1997; in which individuals accrue status from helping) cannot exist unless animals are able to keep track of the behaviour of specific individuals. Similarly, the punishment or bribing of noncooperators, which underlies the strategies of 'pay to stay' (Gaston 1978; Kokko et al. 2002) or 'pay to breed' (e.g. Reyer 1990; Creel & Waser 1991), relies upon an animal's ability to recognize and monitor the cooperative contributions of other individuals. Likewise, indirect reciprocity by image scoring (Nowak & Sigmund 1998), in which individuals assess interactions between third parties, requires sophisticated recognition of multiple individuals. Although cooperative behaviour can exist in the absence of individual recognition, models show that the presence of individual recognition greatly facilitates its evolution (Hammond & Axelrod 2006). Despite this, 'true' individual recognition, between adult group members, has never been demonstrated in a cooperatively breeding bird or mammal species.

Individual recognition, which consists of one animal identifying another by its individually distinctive characteristics (Dale et al. 2001), has been reported in a wide range of taxa (Tibbetts & Dale 2007). However, in many of these instances it remains unclear whether the animal is identifying a single individual or has simply learned to associate the individual's unique and distinctive characteristics with a class of individual (e.g. one of my neighbours, one of my rivals, one of my offspring). When an animal genuinely associates an individual's cues with only one specific individual it is exhibiting 'true' individual recognition (Beecher 1989; Tibbetts & Dale 2007); and it is 'true' individual recognition that is required if members of social groups are to monitor one another's cooperative behaviour.

There is considerable debate over the best way to define and identify 'true' individual recognition. Some researchers believe that it is necessary to demonstrate that an animal can recognize multiple individuals within a given class (Thom & Hurst 2004) while others suggest that it is sufficient to show that the animal can recognize a single individual (provided the individual is unique to its class; e.g. a mate in a monogamous pair; Tibbetts et al. 2008). Other researchers argue that the whole concept of 'true' individual recognition is of limited value because the inherent difficulty of

---

* Correspondence: M. I. Cherry, Department of Botany and Zoology, University of Stellenbosch, Private Bag X1, Matieland 7602, South Africa.
E-mail address: mic@sun.ac.za (M. I. Cherry).

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.07.023

identifying an animal's perceptions makes it virtually impossible to test (Steiger & Muller 2008). In this study we follow the definition provided by Tibbetts & Dale (2007) which asserts that in order to demonstrate 'true' individual recognition it is necessary to show that the animal has not only learned the distinctive characteristics of the signaller (such as its calls) but also associates these with information that is unique to the signaller (rather than with class-specific information; Tibbetts & Dale 2007).

Such 'true' individual recognition has been well documented in primates (e.g. captive chimpanzees, *Pan troglodytes*, can select pictures of individual vocalizers after hearing their calls; Kojima et al. 2003) but demonstrating it in other taxonomic classes has proven much more difficult. Nevertheless, it was achieved for paper wasps, *Polistes fuscatus*, by demonstrating that the wasps associate the facial characteristics of nestmates with the nestmate's specific position in the dominance hierarchy (Tibbetts 2002; Tibbetts et al. 2008) and for hooded warblers, *Wilsonia citrina*, by showing that the birds associate the songs of specific neighbours with particular territories (Godard 1991). That 'true' individual recognition has never been demonstrated in a cooperatively breeding species may simply reflect the difficulty of devising appropriate experiments (Steiger & Muller 2008; Townsend et al. 2012) or that studies on these species have focused on kin and group recognition. However, we cannot dismiss the possibility that members of cooperative groups are not able to recognize one another, invalidating many of the proximal mechanisms that have been proposed for the evolution of cooperation.

If cooperative species are to monitor the helping behaviour of other individuals, they need to be able to recognize helpers even when visibility is reduced by vegetation or lack of proximity. Audio signals provide the ideal means and cooperative species are known to utter special vocalizations when performing cooperative behaviours, such as the provisioning call given when feeding young (e.g. McDonald et al. 2008) or the 'watchman's song' (Wickler 1985) voiced by sentinels as they guard the group from predators (Manser 1999; Kearn & Radford 2013). We know that group members monitor these vocalizations (altering their own behaviour in response; e.g. Manser 1999; Hollen et al. 2008) but it is unclear whether they also use them to identify helpers.

Many studies have shown that the vocalizations of cooperative species are individually distinctive (Rasa 1986; Payne et al. 1988; Sharp & Hatchwell 2005; McDonald et al. 2007; Schibler & Manser 2007), but we cannot assume that group members are able to discern these differences or associate them with specific individuals. This has been underscored by recent research on meerkat, *Suricata suricatta*, vocalizations (Schibler & Manser 2007; Townsend et al. 2010). Using a habituation–dishabituation playback experiment, McDonald (2012) showed that captive noisy miners, *Manorina melanocephala*, can discriminate between the mobbing calls of different individuals but it remains unknown whether the species uses this ability. Although studies have confirmed that cooperative species show class-level recognition, of kin or group members (Payne et al. 1988; Price 1999; McDonald & Wright 2011; Leclaire et al. 2013), 'true' individual recognition, apart from the recognition of offspring (Muller & Manser 2008) or the group's dominant female (Reber et al. 2013), remains unverified. In an effort to remedy this, Townsend et al. (2012) devised a novel experiment that showed that meerkats increase their vigilance when played a single individual's calls from two different locations. This suggests that the meerkats recognize the incongruity and thus the uniqueness of the call. However, it does not show that they associate the calls with specific individuals.

In this study we examined whether a cooperative mammal, the dwarf mongoose, *Helogale parvula*, exhibits 'true' individual recognition by testing whether wild dwarf mongooses associate the contact calls of individual group members with the caller's relative rank.

Dwarf mongooses are small carnivores that live in close-knit groups of 3–30 individuals. The alpha pair largely monopolizes breeding (Keane et al. 1994) but all group members assist in pup rearing (Rood 1978) and sentinel duty (Rasa 1986). Group members show a linear dominance hierarchy which, although correlated with age, is labile (Creel et al. 1992). Females are the philopatric sex and males exhibit delayed dispersal (Rood 1990). The mongooses forage together by day, maintaining group cohesion using individually distinctive and consistent contact calls (Marquardt 1976; Rasa 1986). They feed on arthropods and the occasional small vertebrate and, when food is scarce during the winter dry season, they steal prey from lower-ranking group members. A mongoose intent on stealing growls before commandeering the victim's foraging hole or snatching a large prey item from its mouth. Subordinates offer little resistance although those in possession of a particularly large item usually try to flee.

Capitalizing on this stealing behaviour, we provided test subjects with a large, desirable food item and documented their reactions to playbacks of the contact calls of socially subordinate and dominant group members. We predicted that if dwarf mongooses can recognize specific individuals from their vocalizations they will respond apprehensively to the contact calls of individuals of higher rank than themselves (that can steal their food) but ignore the contact calls of individuals of lower rank than themselves (that cannot).

METHODS

Study Population

We collected the data at Phuza Moya Private Game Reserve in northeastern South Africa (24°16′10″S, 30°47′46″E) between March and August 2012. Details of the study site's vegetation and climate are provided in Sharpe et al. (2010 electronic supplement). The study population consisted of four wild groups of dwarf mongooses (group sizes = 12, 13, 18, 18) habituated to an observer walking within 1–2 m. Because we have monitored the study population since 2006, the birth dates of most group members were known to within a few days, and all individuals were uniquely marked using Garnier Nutrisse hair dye (applied with a long-handled paintbrush as they were sunning). Only nonalpha adults (i.e. older than 1 year) were included in this study. Our methods were approved by the University of Stellenbosch's ethics committee and conform to the laws of South Africa.

Dominance Rank

To quantify dominance rank, we used critical incident sampling to document displacements at a resource (i.e. food, water or sunning sites), overt aggression or submission (i.e. uttering submissive vocalizations when grooming or approaching another group member; Rasa 1977). We used a handheld computer (Psion organiser II; model LZ64) to record the identity and role of the participants for 1186 dyadic interactions (range 177–432 per group).

To calculate ordinal dominance rank for all individuals, we used the I&SI method (de Vries 1998). For each of the four groups we compiled a 'win/lose' matrix which listed an individual's 'wins' (or assertions of dominance) beside its row name, and its 'losses' (submissions) under its column name (Fig. 1). An individual was considered dominant to another group member if its 'wins'