

Meerkat close calls encode group-specific signatures, but receivers fail to discriminate

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A great deal of variation is known to underlie the vocalizations of animals. Calls can for example vary between individuals or between social and behavioural contexts. Calls also have the potential to vary between groups. Many group-living animals are known to produce stereotyped group-specific calls and such group signatures are thought to play a role in territory defence or indeed mate choice. Group signatures are generally found in long-distance call variants that work to maintain contact between group members, sometimes referred to as 'contact calls'. Cooperatively breeding, territorial meerkats, *Suricata suricatta*, also use contact calls, potentially to maintain social organization during foraging. However, these contact calls are generally quieter than long-distance calls in other species, and better described as 'close calls'. We investigated whether these similar call types also possess group-specific signatures and whether any such variation is used by receivers. We recorded close calls from 71 individuals belonging to 10 meerkat groups. We found that such close calls indeed possessed group signatures, but that this underlying variation did not appear to be used by receivers, possibly because meerkats use other sensory systems to identify nongroup members. We stress the importance of conducting playback experiments when investigating group-specific vocal signatures and use our results as a basis for predicting which animals may rely on group information encoded within close calls.

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From over five decades of research a clear picture has emerged which suggests substantial variation underlies the vocalizations of nonhuman animals (Hauser 1996). While variation can occur at a number of discrete levels, much work has focused on acoustic differences between distinct behavioural contexts, primarily because of the cognitive implications associated with such potential semantic communication (Cheney & Seyfarth 1990, 2007). This concentration has ultimately led to a slight neglect for other relevant causes of variation, their perception and the appropriate response, which may in fact require no less sophisticated cognitive processing (Tibbetts & Dale 2007). Calls can, for example, vary considerably at the individual level, a phenomenon documented in numerous species across the animal kingdom (e.g. birds: Sharp & Hatchwell 2005; mammals: Rendall et al. 1996; McComb et al. 2000; amphibians: Ryan et al. 1996), but also variability can result from differential group membership. This may be particularly true for common calls used to maintain group cohesion (Vehrencamp et al. 2003), and may help individuals distinguish between group and nongroup members.

Primates and some cetaceans are known to exhibit group-specific acoustic differences and discriminate between familiar and unfamiliar individuals (primates: Cheney & Seyfarth 1990, 2007; Mitani et al. 1992; Rendall et al. 1996; Mitani & Gros-Louis 1998; Crockford et al. 2004; Herbinger et al. 2009; cetaceans: Ford 1991; Tyack 2000). A number of species of primates and cetaceans live in complex, fission–fusion social groups, and in some cases defend their territories aggressively (Wilson et al. 2001). Hence the selective advantages driving the evolution of group signature calls are likely to include maintenance of social bonds (Tyack & Sayigh 1997; Crockford et al. 2004), negotiation of group decisions (Balsby & Scarl 2008; Scarl & Bradbury 2009) and possibly territory marking (Brown & Farabaugh 1997; Wright & Wilkinson 2001; Crockford et al. 2004).

Group-living birds also provide examples of vocal group signatures. The contact calls of parrots and budgerigars, *Melopsittacus undulatus*, have been shown to vary at the group level and, consequently, this commonly produced social vocalization has been suggested to facilitate group identification (Hile & Striedter 2000; Bradbury 2003; Vehrencamp et al. 2003). From a functional perspective, group signatures in birds may play a role in mating strategies. For example, song sparrows, *Melospiza melodia*, discriminate (in terms of attempted copulations) the songs recorded from distant groups more than those of nearby groups (Searcy et al. 2002), a behaviour previously explained through invoking the

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local adaptation hypothesis. This hypothesis suggests females benefit from mating with local males because such males have genes adapted to local conditions (Baker & Cunningham 1985; Searcy et al. 2002). As such discrimination can have a considerable effect on fitness (e.g. resulting in better adapted offspring), it represents a very plausible selection pressure acting on the evolution of group signatures in birds.

One cross-species commonality that exists for group-specific signatures is their occurrence in the long-distance calls of animals. Chimpanzee, *Pan troglodytes verus*, groups, for example, differ in their pant-hoot vocalizations which can travel over 1 km through dense forest environments and, as previously noted, these signatures probably play a role in signalling territory boundaries to neighbouring communities (Wilson et al. 2001). The contact calls of parrots (Vehrencamp et al. 2003) and the 'screech' contact calls of greater spear-nosed bats, *Phyllostomus hastatus* (Boughman 1997) also appear to show group specificity, keeping contact between individuals over long distances.

But what about species that also use calls for group coordination and exhibit territorial behaviour towards extragroup members, yet exist together in cohesive foraging parties? Do these calls, typically given to close-by group members, also exhibit group signatures and what adaptive function would they have in this social setting? To address these questions on group signatures and their adaptive function, we investigated both the variation that underlies meerkat, *Suricata suricatta*, close calls and whether any information in these calls is used by receivers. Close calls are the most commonly given meerkat call type, being produced during social-foraging contexts every 5–20 s. Acoustically, close calls can be described as short, pulsated, medium-frequency (600–1000 Hz) calls which can travel up to 20 m (see Fig. 1) and, similarly to contact calls in other animal species (Vehrencamp et al. 2003), are probably important for the maintenance of group cohesion and spacing between group members (Manser 1998). To date, many studies investigating group-specific signatures have either focused on their production (Mitani et al. 1992; Smolker & Pepper 1999; Crockford et al. 2004; Nousek et al. 2006) or their discrimination by receivers (McComb et al. 2000; Searcy et al. 2002; Vehrencamp et al. 2003) and have not necessarily integrated both signalling aspects together. This is a crucial perspective to take if we are to understand the adaptive function and relevance of such variation.

Meerkats are diurnal, cooperatively breeding, desert-adapted mongooses that live in social groups of 3–50 individuals (Clutton-Brock et al. 2008). Breeding is generally restricted to the dominant pair (Griffin et al. 2004) and all other subordinates help in rearing the offspring through partaking in various cooperative behaviours (Clutton-Brock et al. 2001). They possess a correspondingly complex vocal system with an integrated urgency-based and functionally referential alarm call system (Manser 2001) and other context-specific call types used to coordinate group behaviour (e.g. sentinel calls, lead calls, moving calls, Manser 1998; C.A.H.

Bousquet, personal communication). Meerkats spend most of their time socially foraging in groups on the ground digging for invertebrate prey (Doolan & Macdonald 1996), where their vision is somewhat obstructed. Furthermore, at different times of the year, their natural habitat can become densely vegetated, again restricting vision even more. Vocalizations therefore play a crucial role in keeping individuals continually informed of changes in the social and ecological environment. Meerkats are also highly territorial, occupying defined home ranges and defending their territory boundaries aggressively against foreign individuals, such as roving or intruding males (Young & Monfort 2009). When spotting foreign meerkats, an individual typically interrupts foraging and focuses on them, alerting the rest of the group. Often the group then adopts a stereotyped 'raised tail' posture and moves rapidly towards the other group, a behaviour otherwise known as the 'war dance'.

Given the territorial nature of meerkats, being able to recognize continually that they are surrounded by conspecific group members could be advantageous, reducing additional territorial defence costs against intruders, roving groups of males or evicted females, looking for reproductive opportunities. Combining this with the critical role played by the vocal medium in meerkat daily lives, we investigated whether meerkats might produce group-specific close calls, and whether receivers can differentiate between close calls produced by members from other groups in comparison to their own. In addition, because it has been indicated that discrimination between own and foreign-group calls can be influenced by the relationship residents have with surrounding groups, the so-called 'dear enemy' or 'nasty neighbour' effect (Wilson 1975; Muller & Manser 2007; Akcay et al. 2009), we further differentiated 'foreign group' close calls into neighbouring and stranger groups.

METHODS

Study Populations

Sound recordings and playback experiments were carried out on two populations of free-living meerkats: at the Kuruman River Reserve (KRR population), which lies 30 km east of Van Zylsrus (Clutton-Brock et al. 1998), and in the Kalahari Gemsbok National park (park population) along the dry Nossob riverbed. As part of the Kalahari Meerkat Project's long-term data collection, all animals in both populations were tagged with subcutaneous transponders (Clutton-Brock et al. 2001) and with haircuts or dye markings for individual identification. All subjects were habituated to a level that allowed recordings and observations within 0.5 m. The study was carried out under licences issued by the Northern Cape Conservation Service and ethical committee of Pretoria University, South Africa.

Individual and Group Differences

Because individual variation may explain some of the underlying variation between groups, we investigated first whether meerkats have individually distinctive calls and then whether, when we controlled for this variation, group differences persist with a high fidelity. We used calls from 4–10 individuals from 10 meerkat groups all belonging to the KRR population. All individuals included in the analyses were adults over 1 year of age of mixed sexes and status. The number of calls included for each individual varied between six and 10 (most groups had 10 different calls per individual) totalling 688 calls (range 36–98 per group). All calls were recorded between 2003 and 2006, apart from one group, Avatar, which was recorded in 1996. To exclude any possible differences in recording conditions between the two recording

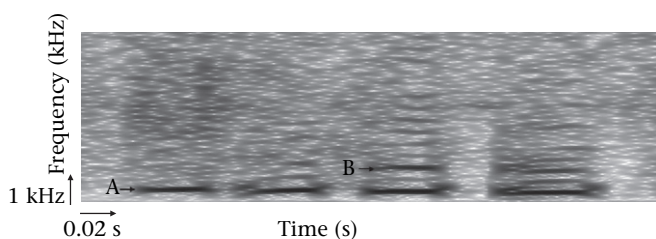


Figure 1. Time–frequency spectrogram illustrating a meerkat contact call produced during foraging. 'A' indicates the lowest visible band representing the fundamental frequency (F0) and 'B' the harmonic overtone of the F0.

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