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# Signals of need in a cooperatively breeding mammal with mobile offspring

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In many bird species with biparental care for young in the nest, hungry chicks beg repeatedly and parents adjust their feeding rate to the call rate of young. Repetitive calling also occurs in fledglings and in some mammals where offspring follow provisioners. It is not yet clear whether, in mobile systems with dispersed young where adults cannot compare the vocal behaviour of all young simultaneously, the calls represent a signal of need. We investigated repetitive begging by cooperatively reared meerkat, *Suricata suricatta*, pups that foraged with the group. Pups produced two types of begging calls: repeat calls over long periods and high-pitched calls mainly confined to feeding events. Food-deprived pups stayed closer to feeders, and begged for longer and more intensely by calling at a higher rate. Hungry pups increased both the rate of repeat calls, which were given continually, and the number of high-pitched bouts, but adults increased their food allocation only in relation to the rate of repeat calls. Our study indicates that hunger may lead to several changes in vocal behaviour, only some of which may be used by adults to assess need.

*Keywords*: begging; call rate; cooperative breeder; meerkat; mobile begging system; signal of need; *Suricata suricatta*

In many species, adults adjust their provisioning rate to the begging intensity of offspring, whereby increased begging elicits increased food allocation (Ottosson et al. 1997; Krebs 2001; Glassey & Forbes 2002; Wright & Leonard 2002). Begging intensity has been shown to vary with offspring need (Hofstetter & Ritchison 1998; Sacchi et al. 2002), the presence and behaviour of littermates (Johnstone 2004) as competitors (Leonard & Horn 1996) or cooperators (Bell 2007), the presence of brood parasites (Kilner et al. 1999) and the receiver to whom the signal is addressed (Bell 2008). The relative influence of these factors on begging behaviour may depend on the social system and how offspring are spatially distributed. To understand the underlying mechanisms in parent–offspring communication, we not only have to measure the effect of these factors on the begging behaviour of offspring (signaller), but we also need to identify the specific signals affected, and how variation in these signals influences the provisioning rate of adults (receivers).

A close linkage between the behaviour of begging offspring and provisioning adults is expected where offspring honestly signal need and adults benefit by responding to such honest signals with increased feeding (Kilner & Johnstone 1997; Royle et al. 2002). Although offspring may be expected to demand as much food as possible (Trivers 1974; Godfray 1995; Mock & Parker 1997), their begging carries costs, not only immediately in terms of increased energetic expenditure (e.g. Chappell & Bachman 2002) or predation risk (Leech & Leonard 1997), but also indirectly through reduced fitness of parents and siblings, both current and future (Trivers 1974; Lessells & Parker 1999). Therefore, a stable signalling strategy is reached

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when the benefits obtained by an offspring increasing its begging display are matched by the costs that an exuberant display imposes (Godfray 1995). Continued exaggeration of begging is prohibited by such costs, and so honesty is imposed on the signal to which the adult attends.

Begging behaviour in systems where the young are mobile and dispersed during foraging with the group may differ from that in stationary systems. In spite of the brief interaction time between parents and offspring in a stationary feeding system, adults can compare the begging intensity of all offspring simultaneously, and decide how often and whom to feed accordingly. In contrast, in the dispersed feeding systems of some fledglings (Smith et al. 2005; Draganoiu et al. 2006) and some mammals (Manser & Avey 2000; Bell 2007), dependent offspring follow adults closely while they search for food. Group members are spread out and only one or a few of the offspring follow the same adult (Manser & Avey 2000; Gilchrist 2004). Adults are not able to monitor the begging behaviour of all the offspring simultaneously, although vocal cues might be perceived from individuals further away. As adults have information on begging intensities of only one or a few offspring in their immediate vicinity, they may simply feed the nearest offspring (Manser & Avey 2000; Brotherton et al. 2001) rather than assessing relative signals of need among dispersed young. Consequently, feeding events are spatially unpredictable for the young and it may be more important for them to ensure a close spatial position to the best feeders, to influence the food allocation rate of that particular individual by honestly signalling their hunger.

In the cooperatively breeding meerkat, *Suricata suricatta*, pups accompany the group foraging from about 25 days and continuously produce begging calls to solicit food from adults (Manser & Avey 2000). Pups are fed invertebrate and small vertebrate prey by both parents and helpers until nutritional independence at around 3 months old (Brotherton et al. 2001). Helpers typically include full or half sibs of both sexes and unrelated immigrant males (Clutton-Brock et al. 2001). Pups disperse around the group and follow foraging adults, with each pup following an individual adult closely for several minutes, but moving regularly between them (Hodge et al. 2007). Pups are typically several metres away from siblings. In 95% of pup feeds, the pup closest to the adult with food receives the food item (Brotherton et al. 2001). Experimentally fed pups spend less time than control pups begging close to potential feeders (Brotherton et al. 2001). Pups produce a repertoire of different vocalizations in different begging contexts (cf. Manser & Avey 2000; Kunc et al. 2007; Fig. 1). While the group is foraging, pups give continuous ‘repeat calls’ (Fig. 1) at the rate of 60–90 per min (Manser & Avey 2000). However, when pups observe an adult finding or carrying food, they typically switch briefly to the louder ‘high-pitched call’ (Manser & Avey 2000; Fig. 1). With increasing age, foraging pups beg less and dig more for food by themselves, producing digging calls (Manser & Avey 2000; Kunc et al. 2007). Playback experiments revealed that adults base their feeding decisions on the call amplitude (Manser & Avey 2000) and preferentially try to feed a loudspeaker playing high-pitched calls rather than repeat calls in the crucial moment of food allocation (Kunc et al. 2007). Thus variation in the production of repeat or high-pitched calls may be used as a signal of need.

In this study we investigated how begging in dispersed young with multiple feeders varies according to hunger, and how variation in specific signals affects the rate at which adults bring food to dependent young. We compared food-deprived and experimentally fed meerkat pups in relation to (1) their spatial location relative to the closest feeder, (2) their begging rate and their use of specific call types, and (3) differences in the acoustic structure of their calls. We then tested (4) whether adults discriminated between the vocalizations of hungry and fed pups, and (5) how adults responded to increased rates of the different types of begging calls. Thus, we asked whether begging vocalizations of offspring in a dispersed system with cooperative care serve as signals of need, and in particular which aspects of the vocal behaviour indicate the nutritional state of the young and are used by adults to assess their need.

## METHODS

### Study Population

Data were collected on a wild but habituated meerkat population at the Kuruman River Reserve, South Africa (26°58′S, 21°49′E), between 2002 and 2007. Details on habitat, climate and study population are provided elsewhere (Clutton-Brock et al. 1998). All animals were individually marked and habituated to close observation (within 0.5 m). Experiments were conducted during the peak provisioning period when pups were 40–60 days old (Brotherton et al. 2001).

### Effect of Hunger on Begging Behaviour

We used three experiments to test how begging behaviour changed with hunger. In experiment 1, we tested whether pups changed their call rate after having received a single large prey item. In experiment 2, we investigated whether the same pup called at a lower rate after a period of natural foraging in the group than immediately after it had been deprived of food for 1 h. In experiment 3, we compared several aspects of begging behaviour between fed and hungry siblings treated in the same way, since parameters other than call rate also appear to correlate with feeding rate (Brotherton et al. 2001). We measured the following behaviours of the pups: distance to feeder, proportion of begging versus other behaviour by pups, use of the different begging call types, call rate and the acoustic structure of the repeat calls.

#### *Experiment 1: supplementary feeding and begging rate*

The vocalizations of 18 pups from eight groups were recorded before and after the pups ate a supplementary food item. The pup was allowed to forage naturally with its group for at least 15 min after the start of the day’s foraging. Its vocalizations were then recorded with a Marantz