



Why do meerkat pups stop begging?

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Begging by young provokes adults to provide food for them. However, eventually begging by young and provisioning by adults cease and young become nutritionally independent. Why do young cease begging and so forgo food brought to them by adults? Three explanations have been proposed: (1) adults may not respond to begging anymore and cease feeding begging young; (2) young may voluntarily switch from begging to independent foraging as they gain more rewards from this; (3) young may become unable to produce stimulating begging calls. We tested these three explanations using meerkat, *Suricata suricatta*, pups. Playback of begging calls at groups where begging had naturally ceased provoked adults to resume provisioning, suggesting that adults had not stopped responding to begging. Experimental provision of food to pups mimicking either natural pup feeding or foraging success produced no differences in subsequent changes in begging or foraging behaviour, suggesting that pups were not assessing the most rewarding means of obtaining food and switching from begging to foraging accordingly. The begging calls of pups (aged 40–60 days) were acoustically different to those produced when they were juveniles (aged 100–120 days), and adults discriminated between rate-controlled playbacks of the two age classes of calls, delivering less food to calls of a juvenile than to the same individual's calls recorded when a pup. Adult meerkats paid attention to the acoustic structure of begging calls, and ceased provisioning when the call structure changed. We suggest that older pups are unable to produce stimulating begging calls. © 2009 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Begging provides offspring with benefits in the form of 'free food' (reviewed in Wright & Leonard 2002). Such benefits to offspring occur at a cost to the adults that provide the food (Pugesek 1990; Wheelwright et al. 2003). This produces a conflict of interest between the offspring and the adults (Trivers 1974), such that offspring are expected to benefit from extending their begging period and attendant food supply, while adults benefit from stopping providing food to begging offspring. Eventually, all offspring cease demanding 'free food' and stop begging. Why do individuals stop begging, and so lose a low-cost source of nutrition? Three mechanistic explanations have been suggested, and these could apply to either vocal or nonvocal begging displays.

First, adults stop responding to begging, and so cease feeding offspring, despite continued offspring begging (Graves et al. 1991; Koga & Shiraiishi 1994). Thus, adults have control over offspring behaviour and offspring might cease begging because it ceases to

provide any benefits. Second, if begging and foraging are mutually exclusive, offspring may switch from begging to foraging as they become more proficient and so gain increased benefits from foraging themselves (Davies 1976; Yoerg 1994; Hirose & Balsam 1995; Smiseth & Moore 2004). Hence, offspring cease begging to concentrate on a more profitable foraging strategy. Third, offspring may become unable to produce stimulating begging signals as their signal structure changes with age (Jurisevic 1999; Leonard & Horn 2006; Sawhney et al. 2006; Thornton & McAuliffe 2006). Hence, offspring have no control over extending begging, owing to physiological constraints. These three mechanisms may not be exclusive, but instead act in concert; however, it is only by testing each explicitly that we can understand the process of ceasing begging.

Meerkats, *Suricata suricatta*, provide an excellent model system in which to test these three explanations for the cessation of begging. Meerkats live in cooperative breeding groups in southern Africa in which free-ranging pups are provisioned with food items, in response to a vocal begging display, for about 100 days after birth (Manser & Avey 2000; Brotherton et al. 2001). Pups follow adults within the group throughout the day, giving continuous 'repeat' begging calls (Manser & Avey 2000). Repeat begging calls elicit more feeds to pups than other calls, including 'digging' calls given while the pup is foraging for itself (Manser & Avey 2000; Kunc et al. 2007). Experimentally fed pups spend less time begging and less

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time in social foraging than control pups (Brotherton et al. 2001). However, by the time that pups are 120–150 days old they have ceased giving begging calls and gain food exclusively by foraging for themselves (Manser & Avey 2000; Brotherton et al. 2001).

We tested the three explanations for why offspring may cease begging. First, if adults no longer respond to pup begging, we predicted that the artificial introduction of begging calls into a group will not induce adults to provision food to young. Second, if juveniles switch their behaviour from begging to foraging depending on prior experience, then we predicted that juveniles who have just been successful in finding food would subsequently spend more time foraging, while juveniles who have just been fed by an adult would subsequently spend more time begging. Third, if juveniles become incapable of producing begging calls, then we predicted that: (1) juveniles' begging calls will sound different to those of pups; (2) when making feeding decisions adults will discriminate against playbacks of the begging calls of an individual when it is a juvenile compared to when it is at its peak begging period; and (3) increasing adult propensity to feed within a group will not cause juveniles to resume giving correct begging calls.

METHODS

Study Site and Species

We studied free-ranging meerkats along the dry bed of the Kuruman river in the southern part of the Kalahari Desert in South Africa between December 2005 and July 2007. Meerkats live in groups with a dominant breeding pair and up to 50 helpers. Litters of up to seven pups are produced one to four times per year and raised cooperatively by the group (Clutton-Brock et al. 1999). Meerkat pups remain at the sleeping burrow with a babysitter for their first 4 weeks before accompanying the group as they forage, when they beg for food and are fed by all adults in the group. All animals were habituated to close observation and marked for individual identification with hair dye or haircuts applied to their fur while the animals were sunning themselves.

Do Adults Cease Responding

We introduced pup begging calls using playbacks from loudspeakers in 11 groups in which no individuals were normally begging and the youngest group members were classed as juveniles (aged 100–120 days). We performed playbacks for three consecutive periods in each group, during which field assistants moved loudspeakers around the group, following young subordinate helpers at a distance of 4–5 m simulating a moving pup in the group. We established the control levels of behaviour for group members prior to playback of begging calls by performing a 20 min control playback period, during which time the loudspeakers were playing back ambient noise (bird song, cicadas, etc.) recorded in the territory of another group and matched by peak amplitude to the begging calls (Manser & Avey 2000; Kunc et al. 2007; English et al. 2008). This was immediately followed by a playback lasting for 20 min, during which time each loudspeaker broadcast the begging calls of one of two pup littermates from another group, which were recorded while they were 40–60 days old and at the peak of their begging period. Recordings of a different pair of pups were used for each group. We then immediately performed a postplayback control, using a second 20 min control playback period during which the loudspeakers were again playing back ambient noise as previously described.

During the three playback periods, we recorded the vocalizations (see below) and behaviour of a focal (female) juvenile, as well as all feeds made by adults to the juveniles within the group. During

this recording period, all behaviours of the focal juvenile and its association with other members of the group (distance to and identity of nearest adult and other juvenile) were recorded on one channel of a Marantz PMD660 digital recorder and from this we could subsequently record the total time spent digging, the total time spent less than 2 m from an adult, the size and identity of food items found by the juvenile, and the size and identity of food items fed to the juvenile (see Brotherton et al. 2001).

Does Behaviour Depend on Experience?

We asked whether pups changed their foraging behaviour depending on how they had obtained their last food item. We observed the behaviour of 18 pups aged around 60 days from eight groups before and after either 'finding' a scorpion (genus *Opisotophthalmus*) while foraging themselves or being 'fed' a scorpion of matched size by an adult in the group. Pups were experimentally allowed to 'find' a scorpion by means of an experimenter dropping the scorpion into a hole in which the pup was foraging. Pups were experimentally 'fed' a scorpion by means of the experimenter selecting a nearby adult and presenting the adult with the scorpion while within 2 m of the begging focal pup, which it then gave the scorpion as with a natural pup feed, frequently processing the scorpion to remove its sting, dropping it on the ground and watching while the pup ate it. Therefore, in both treatments, the pup received the same food item, but acquired it in two different ways: first, as an apparent result of its own digging effort; second, as an apparent result of its own begging effort. Pups obtained a scorpion only after at least 5 min during which time they had neither found any food (with the exception of ants or tiny larvae) nor been fed any food by adults. After having eaten the scorpion, the pup was followed for a further 5 min, again during which time they neither found food nor were fed. A longer period may have yielded clearer results, but we found in preliminary studies that it was likely that a pup was fed a substantial food item after 5 min by an adult group member, making it hard to maintain controlled conditions. The order in which the pup found food or was fed was randomized. Food presentations were separated by at least 20 min.

During the recording periods, all behaviours of the focal pup and its association with other members of the group (distance to and identity of nearest adult and pup) were recorded on one channel of a Marantz PMD660 digital recorder using a hand-held microphone (wav-format; sample frequency: 44.1 kHz; resolution: 16 bit), while the vocalizations of the pup were recorded on the other channel, using a Sennheiser ME66/K6 microphone. Therefore, pup calling could be related to its activity and proximity to other meerkats. From these we could record the total time spent digging, the total time spent begging, the total time spent less than 2 m from an adult, the number of repeat begging calls made by the pup, and the number of digging calls made by the pup (Kunc et al. 2007). We used repeated measures ANOVAs to ask whether pups differed in any of these five measures both before and after having obtained food, and whether the means of food delivery affected the pups' subsequent begging or foraging behaviour.

Do Physiological Constraints Affect Calls?

Comparison of begging call structure

We asked whether the structure of begging calls given by pups changed as they got older. We collected recordings of nine pups begging when aged 40–60 days, at the peak of their begging period, and again when they were aged 100–120 days when begging had virtually ceased. Pups were recorded as above with the microphone held approximately 50 cm from the pup. Calls were transferred to a PC and spectrograms (spectrogram: sample frequency = 22.5 kHz,

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