

## 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,

FFT = 1024, overlap = 93.75, time resolution = 2.9 ms) were generated with the software package Avisoft SASLab Pro 4.38 (R. Specht, Berlin, Germany). We took 10 examples of repeat begging calls for each individual at each of the two age periods, and from these we then measured five call parameters (using the automatic parameter function in Avisoft) for each begging call: duration, peak frequency, minimum frequency, maximum frequency and bandwidth. We performed a discriminant function analysis (DFA) using all five parameters to separate calls given by pups and juveniles.

#### Do juveniles increase begging when adults resume feeding?

During the three playback periods described above we recorded the vocalizations and behaviour of a focal (female) juvenile. During this recording period, all behaviours were recorded on one channel of a digital recorder as above, while the vocalizations of the juvenile were recorded on the other channel. Therefore, we could simultaneously record the total time spent begging and the rate of repeat begging calls made by the juvenile. Because of technical problems, these recordings were only conducted at nine of the 11 groups tested.

#### Adult response to calls of pups and juveniles

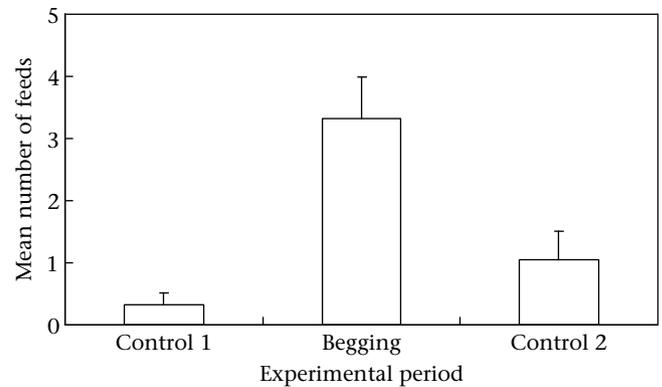
We asked whether adults fed youngsters differentially after begging calls given by pups and juveniles. We carried out a playback experiment at eight groups in which two loudspeakers broadcast begging calls. One speaker played calls of an individual recorded during the peak begging period (aged 40–60 days) while the second speaker played calls of the same individual recorded during the postbegging period (aged 100–120 days). Playbacks comprised loops of 10 s made up of an equal number of begging calls (12), and matched for peak amplitude. The individual was from a different group to that in which the playback was made. Recordings of a different individual were used for each group. Loudspeakers moved around the group, carried by field assistants who followed young subordinate helpers at a distance of 4–5 m in a constant orientation as they moved among the group, thus simulating a moving pup in the group, with no experimenter bias as to where speakers were positioned. We recorded all feeds made by adults to speakers over a 1 h experimental period. All test groups contained pups during their peak begging period, and experiments started at least 15 min after the group had started foraging after leaving their sleeping burrow. A feed to a speaker was classed as occurring when an adult approached within 1 m of the speaker carrying a food item, and no pup was within 1 m of the speaker. The numbers of feeds made to the speaker playing calls of the individual, when either young or old, were compared using a Wilcoxon signed-ranks test.

The study was conducted under permits issued by Northern Cape Conservation Service and the ethical committee of Pretoria University, South Africa.

## RESULTS

#### Do Adults Cease Responding?

Feeding by adults increased dramatically when begging was experimentally added to the group and continued above control levels after playback of begging calls ceased (Friedman test:  $\chi^2_2 = 14.0$ ,  $N = 11$ ,  $P = 0.001$ ; Fig. 1). Juveniles did somewhat reduce time spent foraging during the playback of begging calls, compared with the preplayback period, but they also tended to increase their foraging to a level above both periods after playback ceased ( $\chi^2_2 = 5.091$ ,  $N = 11$ ,  $P = 0.078$ ). The rate of digging calls given by juveniles did not vary significantly between periods ( $\chi^2_2 = 2$ ,  $N = 9$ ,



**Figure 1.** Mean + SE numbers of feeds made by adults in 11 groups to loudspeakers broadcasting either begging calls of pups or control background noise. Each experimental period lasted 20 min and all playbacks followed the same order of control 1–begging–control 2.

$P = 0.368$ ). Juveniles did not alter the time that they spent close to (<2 m) adults across periods ( $\chi^2_2 = 1.273$ ,  $N = 11$ ,  $P = 0.529$ ).

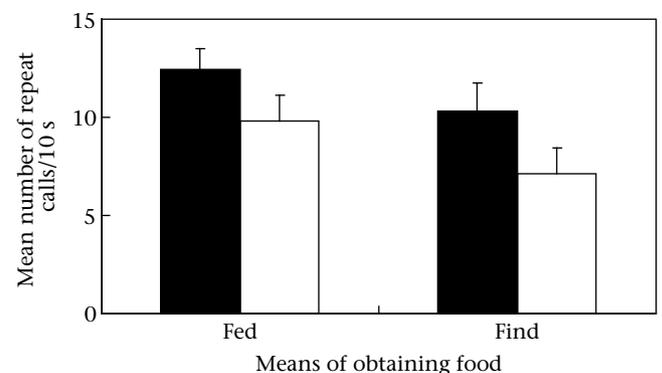
#### Does Behaviour Depend on Experience?

Overall begging levels (rate of repeat begging calls) decreased after a food item was eaten, regardless of means of acquisition (repeated measures ANOVA: before versus after:  $F_{1,17} = 8.29$ ,  $P = 0.010$ ; Fig. 2). However, pups did not change their behaviour depending on how they obtained their last food item (interaction between before/after and finding food/being fed: time spent digging:  $F_{1,17} = 2.23$ ,  $P = 0.15$ ; time spent begging:  $F_{1,17} = 0.074$ ,  $P = 0.79$ ; time spent >2 m from adult:  $F_{1,17} = 0.21$ ,  $P = 0.65$ ; rate of repeat calls:  $F_{1,17} = 0.14$ ,  $P = 0.71$ ; Fig. 2).

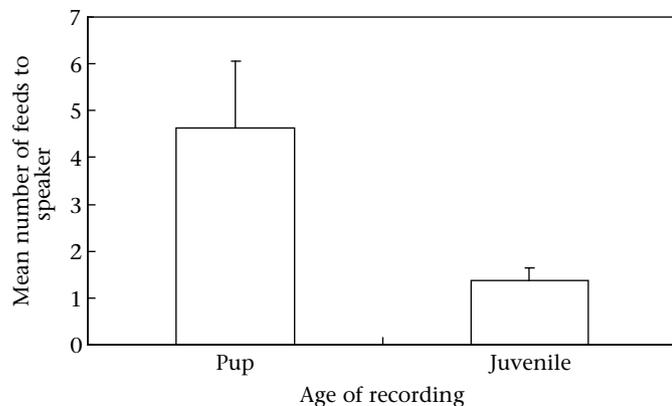
#### Do Physiological Constraints Affect Calls?

##### Comparison of begging call structure

The begging calls of pups could be separated from those of juveniles using a DFA. A measure of the peak frequency at the centre of the call was strongly related ( $r = 0.994$ ) to a function that separated calls of pups and juveniles ( $\lambda = 0.78$ ,  $\chi^2 = 43.4$ ,  $P < 0.0001$ ), assigning 69% of pup calls and 73% of juvenile calls to their correct category. Pups had calls of a mean peak frequency of 1231 Hz, whereas those of juveniles had a mean peak frequency of 953 Hz.



**Figure 2.** Mean + SE begging rates of 18 pups in the 5 min before (black bars) and after (white bars) obtaining food either by being fed by an adult or finding it themselves while foraging.



**Figure 3.** Mean + SE numbers of feeds/h at eight groups to loudspeakers broadcasting calls of an individual meerkat when a pup (40–60 days old) and when a juvenile (100–120 days old).

#### *Do juveniles increase begging when adults resume feeding?*

A resumption of provisioning by adults induced by our experimental playback of pup begging calls did not cause a change in the juveniles' begging behaviour. We observed no differences in time spent begging across the three periods (Friedman test:  $\chi^2_2 = 0.722$ ,  $N = 11$ ,  $P = 0.697$ ), nor did juveniles alter the mean rate at which they gave repeat begging calls between the three periods ( $\chi^2_2 = 1.226$ ,  $N = 9$ ,  $P = 0.542$ ).

#### *Adult response to calls of pups and juveniles*

Within groups, adults delivered more food to loudspeakers broadcasting the calls of an individual recorded when it was a pup than to those broadcasting calls recorded when the same individual was a juvenile (Wilcoxon signed-ranks test:  $Z = 2.25$ ,  $N = 8$ ,  $P = 0.024$ ; Fig. 3).

## DISCUSSION

Meerkat young effectively cease producing begging calls that stimulate adult provisioning after around 100 days (Manser & Avey 2000). Our experiments demonstrate that this cessation of begging does not appear to be the result of adults not responding to begging calls after a certain period of time. Neither does it appear to be the result of pups voluntarily ceasing begging as they switch to foraging as their success at foraging increases. Instead, the acoustic structure of pups' repeat begging calls changed with age, and adults discriminated between the begging calls of individuals at different ages, reducing their rate of feeding to begging calls of juveniles compared with those of pups. It appears that this change cannot be avoided, such that even when adults were artificially induced to resume provisioning in groups containing nonbegging juveniles, the juveniles did not resume production of pup-like begging behaviour.

Cessation of begging in meerkats and the accompanying cessation of provisioning does not appear to be enforced by adult resistance. This contrasts with one study of black kites, *Milvus migrans*, where adults reduced their approaches towards begging young over time, despite the frequency of begging by young remaining unchanged (Koga & Shiraiishi 1994), and another of herring gulls, *Larus argentatus*, in which even though chicks increased begging, parental investment was reduced just prior to fledging (Graves et al. 1991). Despite the cessation of calls, adult meerkats within the group were still willing to provide food when they heard the experimentally broadcast begging calls of pups, suggesting that they still responded to begging calls, and did not

simply stop feeding pups following a set period after pup birth. Pup begging provokes changes in circulating cortisol levels in adult meerkats and this appears to initiate adult provisioning behaviour (Carlson et al. 2006). This hormonally mediated mechanism may explain why adults continued provisioning, albeit at a much lower level than during playback, in the control period following playback, rather than ceasing such behaviour as soon as playback of begging calls stopped.

Young meerkats did not alter their begging behaviour depending on how they obtained their last substantial food item. Begging and foraging are mutually exclusive, with foraging young having their head down in a foraging hole and expending energy on digging behaviours. Foraging individuals produce 'digging calls' (Manser & Avey 2000) which provoke far lower levels of adult provisioning than begging calls (Kunc et al. 2007). A young meerkat that gained a substantial food item by successful foraging may be expected subsequently to invest more heavily in foraging, whereas a young meerkat that gained a substantial food item by successful begging may be expected subsequently to invest more heavily in further begging. Although our mimicry of these two conditions provoked reduced overall levels of begging calls, as previously demonstrated when pups are fed a large food item (Manser et al. 2008), the young did not subsequently differentially invest in either foraging or begging depending on whether they had 'found' or been 'fed' the food item. Meerkat pups that are successful foragers when young become more efficient foragers as adults (Thornton 2008), suggesting that they learn and develop foraging skills from early in life. Similarly, young white-winged coughts, *Corcorax melanorhamphos*, that depend on food gained by begging lack foraging experience and so are poorer foragers throughout winter (Heinsohn 1991). Despite this, we found no evidence that pups strategically exchanged begging for foraging over short timescales following an apparent increase in their foraging success.

Begging calls across a range of taxa change as offspring get older (see also Jurisevic 1999; Leonard & Horn 2006; Sawhney et al. 2006). Typically, calls became lower in peak frequency with age. In meerkats, such changes may be explained by an increase in body size, with juveniles weighing about twice that of pups. Body size explains similar changes in call structure, with larger individuals producing calls of lower pitch across taxa (Davies & Halliday 1978; August & Anderson 1987; Pfefferle & Fischer 2006). It is possible that as individuals get older, their motivation to beg decreases as they gain more food and this may explain the change in call structure. However, the calls of fed meerkat pups differ from those of hungry pups in their rate and duration, and not in other acoustic parameters, specifically peak frequency, that we found to be effective for discriminating between individuals of different ages in this study (Manser et al. 2008). Juvenile meerkats did not revert to producing pup-like calls, even if by doing so they could gain benefits from provisioning adults. Instead, when adults were induced to provision by our experimental playback of pup begging calls, juveniles ran over to adults with food and took the food from them (J. R. Madden, H.-J. P. Kunc & S. English, personal observation), rather than attracting adults towards them by producing begging calls.

Adult meerkats discriminated between the calls of pups and the calls of juveniles. Under natural circumstances this could be caused by juveniles calling at much lower rates than pups (J. R. Madden, unpublished data), with adults provisioning at a rate proportional to begging rate (Manser et al. 2008). However, we controlled for this in our playbacks, matching the rates of pups and juveniles, yet adults still provisioned food at lower rates to playbacks of juvenile calls than those of pups. We observed that the discrimination by adults is not perfect, and in almost all our playbacks, adults fed at least occasionally to the speaker broadcasting the juvenile calls.

Young meerkats appear to stop begging, and so cease to be fed by adults, because they produce calls of a structure that fail to promote high levels of adult provisioning behaviour. This may be caused by physiological processes such as increased body size. We found no evidence to support the idea that adults have an inherent propensity to cease provisioning young after a defined time period, suggesting that the cessation of begging is not driven by temporal factors acting on adult behaviour. Nor did we find evidence that young meerkats strategically abandoned begging in favour of practising foraging, following an improvement in their apparent foraging skills. Instead, the conflict of interest between the offspring and the adults over the duration of the begging period and attendant food supply (Trivers 1974) appears to be mediated by adults paying attention to an uncheatable signal of offspring age, the acoustic structure of their begging calls. When young meerkats are unable to produce the call, adults stop providing food. At this point, energetically costly, but acoustically ineffective begging ceases to provide any benefits, and so young meerkats stop begging.

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