Calling in the gap: competition or cooperation in littermates' begging behaviour?

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Offspring are frequently raised alongside their siblings and are provisioned early in life by adults. Adult provisioning is stimulated by offspring begging, but it is unclear how each offspring should beg, given the begging behaviour of their siblings. It has previously been suggested that siblings may compete directly through begging for a fixed level of provisioning, or that siblings may cooperate in their begging in order to jointly elevate the level of provisioning by adults. We studied the begging behaviour of meerkat *Suricata suricatta* pups, explored how it changed as the begging behaviour of their littermates altered, and asked how the adults responded to group-level changes in begging. We found conflicting evidence for classic models of competitive and cooperative begging. Pups reared in larger litters begged at higher rates, yet experimentally increasing begging levels within groups caused individual begging rates to decrease. Pups decreased begging rates when close to other begging pups, and pups spaced further apart were fed more. Adults increased their overall level of provisioning as group levels of begging increased, but per capita provisioning decreased. Adults preferred to provision speakers playing back recordings of two pups begging alternately to recordings of the same two pups begging simultaneously. Therefore, we suggest that meerkat pups avoid some of the costs of direct competition imposed by an escalation of begging as other pups beg, by begging in gaps between the bouts of others or avoiding littermates. Such behaviour is also preferred by provisioning adults, thus providing additional benefits to the pups.

Keywords: begging; meerkats; cooperation; indirect competition; coordination

1. INTRODUCTION

Studies of begging by groups of offspring reveal that they usually beg concurrently for limited resources supplied by adults (e.g. Smith & Montgomerie 1991; Godfray 1995; Price 1996; Leonard & Horn 1998; Leonard *et al*. 2000; Neuenschwander *et al*. 2002; Bell 2007), but the strategy by which each individual should beg, given the begging behaviour of other group members, remains unclear. Most simply, individuals may not pay attention to the begging of their peers, but instead beg according to their own level of hunger (e.g. Kilner & Johnstone 1997). However, several lines of evidence suggest that individuals do modulate their begging according to the presence or behaviour of others. Initially, begging behaviour was considered to be an example of direct competition, with offspring immediately exaggerating their signals of need in response to the rising begging levels of others in their group, so as to individually obtain a disproportionate share of the limited resources (Godfray 1995; Leonard *et al*. 2000; Neuenschwander *et al*. 2002 but see Kacelnik *et al*. 1995; Cotton *et al*. 1996). However, in addition to mediating competition, offspring may jointly attempt to maintain overall begging rates at a level that motivates adults to feed them (e.g. Burford *et al*. 1998; Glassey & Forbes 2002; Bell 2007). Strategies of this kind are described as cooperative begging (Johnstone 2004). Competitive

begging holds for aspects of begging that influence the division of food among offspring. If begging influences the total level of provisioning, and particularly if certain young can gain direct control of food allocation or when the costs of extracting additional resources from adults are high, then competitive begging is not stable, but instead, cooperative begging may evolve (Johnstone 2004).

Discriminating between begging strategies is possible depending on the following predictions: first, an individual's begging level relates to the number of offspring raised with it. If offspring are begging in direct competition with one another, individuals in larger broods or litters (and hence more competitors) tend to beg at higher levels than those raised in small broods or litters with few young (Leonard *et al*. 2000; Neuenschwander *et al*. 2002). Conversely, if offspring are begging cooperatively, individuals raised with more collaborators, tend to beg at lower levels (Mathevon & Charrier 2004; Marques *et al*. 2006; Bell 2007). Second, an individual's begging level changes in response to changes in the begging levels in the brood or litter. If offspring are begging in direct competition with each other, an increase in the begging levels within their brood or litter provokes an increase in each individual's begging level. If offspring are begging cooperatively, an increase in the begging levels within their brood or litter allows an individual to decrease their begging level (Bell 2007). Third, adult feeding decisions are expected to vary between strategies. If offspring are begging competitively, adults are expected to feed the young that exhibits the highest level of begging

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(Godfray 1995). If offspring are begging cooperatively, then an adult's provisioning rate rises as the overall level of begging within the brood or litter increases (Johnstone 2004).

We investigated the begging behaviour of pups of cooperatively breeding meerkats *Suricata suricatta*, which live in groups of 2–50 individuals (Doolan & Macdonald 1999). Meerkat pups follow adults throughout the day emitting 'repeat' calls continuously (Manser & Avey 2000); whenever a pup observes that an adult has a food item, it switches to another call type, the 'high-pitched' call (Manser & Avey 2000). When pups attempt to forage for themselves, they emit a 'digging call' (Kunc *et al.* 2007). Pups are fed discrete invertebrate and small vertebrate prey by both their parents and helpers until they are around three months old (Brotherton *et al.* 2001).

We tested the predictions of competitive and cooperative begging models. First, we ask whether litter size predicts begging rates by observing begging rates at 'natural' litter sizes and then by experimentally manipulating litter size. Second, we ask whether pups adjust their begging rates as the intensity of begging close to them changes, by observing natural pup begging rates and distance to other pups and then by playing back begging calls next to focal pups and measuring the change in their own begging behaviour. Third, we record adult feeding behaviours towards different begging behaviours, depending on the overall begging level in the litter. We then ask whether this feeding behaviour alters per capita food intake for individual pups. Finally, we test whether adults differ in their feeding behaviour according to the different begging strategies, with pups begging simultaneously with each other, or with pups begging synchronously so as to fill in gaps between individuals.

2. MATERIAL AND METHODS

(a) *Study site and general methods*
We studied free-ranging meerkats around the Kuruman river in the southern part of the Kalahari Desert in South Africa (26°58′ S, 21°49′ E) from March 2004 to June 2006. Meerkats live in groups with a dominant breeding pair and a number of related and unrelated helpers who do not commonly breed. Litters of up to six pups are produced two to four times per year and raised cooperatively by the group (Clutton-Brock *et al.* 1998). Pups remain at the sleeping burrow with a babysitter for their first four weeks, before they accompany the group foraging. All animals were habituated to close observation (<1 m) and marked for individual identification with hair dye. The study was conducted under the permission of Northern Cape Conservation Service and the ethical committee of Pretoria University, South Africa.

(b) *Do individual's begging level relate to group size?*
(i) *Do natural begging rates of pups vary with litter size?*
We recorded pup vocalizations of 124 pups of 34 litters in 13 different groups. Recordings were made for 20 min while the pup was foraging with the group at a distance of approximately 50 cm using a Sennheiser ME66/K6 microphone connected to a Marantz PMD670 (WAV format, sample frequency: 44.1 kHz, resolution: 16 bit). During this period, all behaviours of the pup and its association with other members of the group (distance to and identity of nearest adult and pup) were spoken on the second channel of the

recorder. Therefore, pup calling could be related to its activity and proximity to other meerkats. Calls were transferred to a PC and spectrograms (spectrogram: sample frequency = 22.5 kHz, fast Fourier transform = 1024, overlap = 93.75, time resolution = 2.9 ms) were generated with the software package AVISOFT SASLab Pro 4.38 (R. Specht, Berlin). We distinguished different call types on the basis of their acoustic structure and focused on the 'repeat calls' given continuously while begging alongside adults (cf. Manser & Avey 2000; Kunc *et al.* 2007). We counted the total number of repeat calls given over the 20 min period, and calculated the mean number of calls 10 s^{-1}. Litter size was taken to be the number of pups foraging with the focal pup on the day of recording. We constructed a linear mixed model (LMM) to explain mean repeat call rate with litter size; litter identity was included as a random factor.

(ii) *Does call rate vary with a change in group-level begging?*
We manipulated the levels of begging in 13 groups by subjecting each group to three treatments: control—no changes were made to pup number; removal—two pups, one of each sex (or one if there were only two pups in the group) were removed; addition—two speakers each playing back the repeat calls of a similarly aged pup from another group were carried in haphazard patterns within the spread of foraging adult meerkats in a group by two observers, one playing calls of a male pup and one playing calls of a female pup. This attempted to mimic the foraging and begging behaviours of meerkat pups. Although it would have been preferable to match the temporary removal of pups from groups with the temporary addition of pups (rather than speakers mimicking pups) to groups, we had ethical concerns that pups added to foreign groups may not be accepted or even attacked. However, adults responded to speakers broadcasting begging calls in the same way that they responded to real pups, and repeatedly brought food items to the speaker (see also Manser & Avey 2000; Kunc *et al.* 2007; Manser *et al.* 2008). Treatments were presented on a consecutive day at a group, and in a random order. There was a 15 min habituation period starting after the group had started foraging, before the treatment started. Each treatment lasted for 1 hour. A treatment was paused if foraging was interrupted for more than 2 min by alarm calls, inter-group encounters or the presence of roving individuals. The behaviour of one female pup at each group aged between 35 and 50 days was recorded by one observer. Repeat calls were counted from spectrograms as above and calling rate was calculated by counting repeat calls in the first 10 s of each minute and taking a mean value for the 60 min. Two more observers recorded all feeds made to pups and the speakers, refusals (defined as an adult physically blocking a pup from accessing a food item) and successful pup forages. Playbacks were made using the equipment described above. Amplitudes were set to match the natural begging levels, which varied between groups (Manser & Avey 2000; Kunc *et al.* 2007; Manser *et al.* 2008). Response variables were analysed with repeated-measures ANOVA.

(c) *Do pups adjust their begging levels as local begging intensity varies?*
(i) *Does call rate vary with inter-pup distance?*
We used a subset of 20 individuals from those described above (§2b(i)), comprising one male and one female from 10 litters, each from a different group. We collected six 10 s

periods of call rates, clear of background noise, when the pup was more than 2 m away from the nearest adult and when it was begging. These comprised three periods when a pup was 'close' (<2 m) to another pup and three when it was 'distant' (5–10 m) from another pup, and we calculated mean calling rates for each individual in each situation.

(ii) *Does call rate vary with an increase in local begging levels?*
We manipulated begging levels adjacent to specific focal pups and recorded their own immediate change in begging levels. We followed eight focal meerkat pups aged 40–60 days old and recorded their vocalizations as described above. Pups were accompanied by a speaker (broadcasting WAV files from a Zen Touch digital player) at a distance of 1.5–2 m with one of four playbacks: control—no noise; high-pitched calls; digging calls; repeat calls (cf. Manser & Avey 2000; Kunc et al. 2007). Each call type lasted for 1 min and was presented three times in a random order mixed with the other calls, so that each focal pup heard 12 min of playback. Each focal individual heard calls given by a different, single individual, recorded previously in another group. Begging calls given by the focal pup in each minute were counted from spectrograms by an observer who was blind to the identity of the playback in progress. A sum of calls given during the 3 min of each playback was used. The use of three non-begging calls ensured that any effects we observed of pup's response to playback of repeat calls were not simply the result of the pup responding to playback of unusual sounds in close proximity.

(d) **How do adults respond?**
(i) *Does provisioning vary with changes in group-level begging?*
We asked whether the overall provisioning level of adults varied with the overall begging level in the group. During the experiment described above (§2b(ii)), we recorded the total number of feeds made by adults to pups in the group over the 60 min test period. This allowed a comparison of feeding rates on consecutive days at a group in which begging had been increased, decreased or unaltered.

(ii) *Does provisioning vary with local levels of begging?*
We observed 114 pups for a total of over 74 hours. During this time we recorded all feeds to the focal pup, totalling 600 feeds, and recorded the time that the pup spent begging to adults. For both activities, we estimated the distance of the focal pup to the nearest sibling, placing each observation in one of four categories (<2, 2–5, 5–10, and >10 m). We calculated the number of feeds that a pup received in each of the four distance categories, accounting for the time that they spent begging in each of the four categories.

(iii) *Does per capita food intake increase with increased begging?*
We tested whether a pup received more food, or at least did not reduce the amount of food that it obtained, when it reduced begging in response to increased begging by 'littermates'. During the experiment described above (§2b(ii)), we recorded the number of feeds made by adults to the focal pup from whom we had collected measures of begging rate over the 1 hour test period. We compared the feeding rates made to the pup on consecutive days at a group in which begging had been increased, decreased or unaltered.

(iv) *Do adults discriminate between begging strategies?*
We mimicked these competitive and cooperative begging strategies through playback experiments and observed during

which playback the adults provisioned loudspeakers and pups with the most food items. As defined here, pups begging competitively vocalize at the same time as each other (simultaneously) such that if one pup starts to beg, another also begins begging and two or more pups are heard at any time, interspersed by periods of silence when no pup begs. As defined here, pups begging cooperatively 'fill in the gaps' when a littermate ceases or reduces begging, such that the pups beg in sequence and a constant level of begging from the group as a whole is maintained, despite individuals stopping or starting. Playbacks were made by moving a single speaker in a haphazard manner within each of nine groups, in order to mimic the behaviour of a begging pup. Playbacks started 90 min after foraging had started, and were paused if foraging was interrupted (see above). The playbacks were either (i) two pups begging for 3 min each sequentially to each other, each for 3 min, for five repeats, such that there was continuous begging noise from a single pup for 30 min, mimicking cooperative begging or (ii) the same two pups begging simultaneously for 3 min followed by 3 min of silence and repeated five times, such that there was a total of 15 min of two pups begging together interspersed by a total of 15 min of silence, mimicking competitive begging. Therefore, there was the same total amount of sound presented to the group over the 30 min. The same calls were used in both the sequential and simultaneous playbacks and consisted of cuts from one male and one female littermate from a different group to that being tested. The order that the playbacks were presented was randomized. All pup feeds, successful pup forages and refused food items were recorded, as were feeds to the speakers. This allowed us to conduct a matched-pair comparison on the rates of behaviour occurring within each group under each of the two playbacks.

(e) *Statistical analyses*
All LMMs were constructed using GENSTAT 8.1 (Lawes Agricultural Trust, Rothampstead, Harpenden, UK). Variance components of LMMs were estimated with the restricted maximum-likelihood method. Residuals were checked for normality. All other analyses, including repeated-measures ANOVAs, were carried out using SPSS v. 13.

3. RESULTS
(a) **Do individual's begging level relate to litter size?**
(i) *Does natural begging rates of pups vary with litter size?*
Pup begging rate increased with the size of the litter that they were raised in (LMM: Wald $\chi_1^2 = 9.72$, $p = 0.002$; figure 1). Pups that were raised alone begged at a mean rate of approximately 55 per cent of that uttered by pups that were raised in litters of five.

(ii) *Does call rate vary with a change in group-level begging?*
The begging rate of the focal pup changed with group-level begging (repeated-measures ANOVA: $F_{2,24} = 10.51$, $p = 0.0005$; figure 2). When group begging was increased, the focal pup's begging decreased by a mean of 18 per cent, but increased by a similar amount (15%) when begging was reduced. Although pups responded to playbacks, their own change in begging rate did not fully compensate for the gain or loss of total begging noise produced in the group following our manipulation. Mean apparent litter size varied from 2 (removal), through 3.85
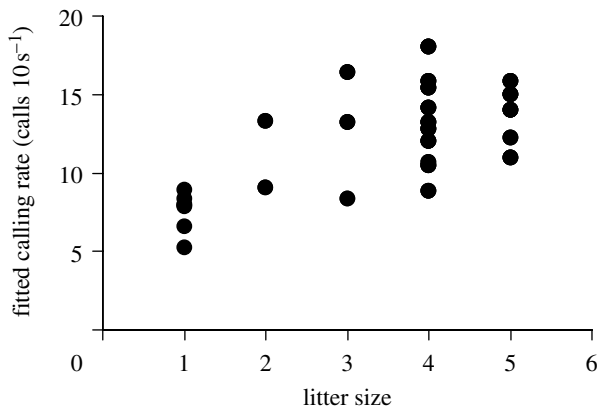
Figure 1. Relationship between the begging rate of pups and the size of the litter that they are raised in. Calling rate is the fitted values taken from a model that includes group and litter identity. Points represent individual litters.
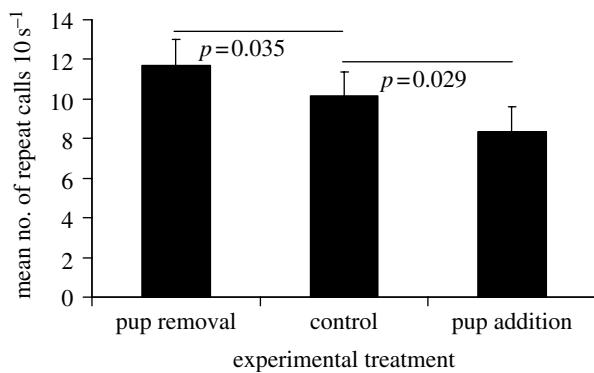

Figure 2. Mean rates ($+1$ s.e.) of repeat begging calls given by a focal meerkat pup under three different treatments. For all treatments, $n = 13$. The *p*-values indicate the results of *post hoc* least significant difference (LSD) tests between the treatments.

(control) to 5.85 (addition), so that even if the two remaining individuals in a group undergoing a removal treatment both increased their calling rate by 15 per cent, the total output would only match that of 2.3 pups rather than the 3.85 that would naturally be calling. Moreover, we found no difference in the number of food items found by the focal pup in any of the three treatments (repeated-measures ANOVA: $F_{2,24} = 0.11$, $p = 0.90$).

(b) *Do pups adjust their begging levels as local begging intensity varies?*

(i) *Does call rate vary with inter-pup distance?*
Individual pups had lower calling rates when they were close to another pup than when they were farther away from another pup (repeated-measures ANOVA: distance $F_{1,18} = 8.86$, $p = 0.008$; figure 3). Begging rate decreased by almost 25 per cent when a pup moved from 5 to 10 m away from a pup to within 2 m of a pup.

(ii) *Does call rate vary with an increase in local begging levels?*
An experimental increase in begging next to a pup drove individuals to decrease their own rate of begging (repeated-measures ANOVA: $F_{3,21} = 7.27$, $p = 0.0016$; figure 4) with the greatest decrease during the playback of repeat calls.
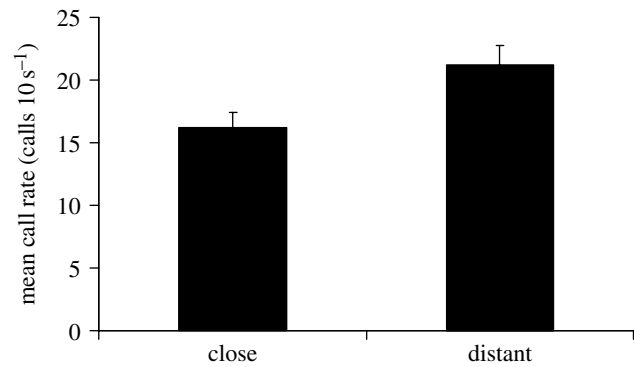
Figure 3. Mean rates ($+1$ s.e.) of repeat begging calls given by a focal meerkat pup when either close to (<2 m) or distant from ($5–10$ m) another littermate, while engaged in begging and more than 2 m from the nearest adult. For each distance, $n = 20$.
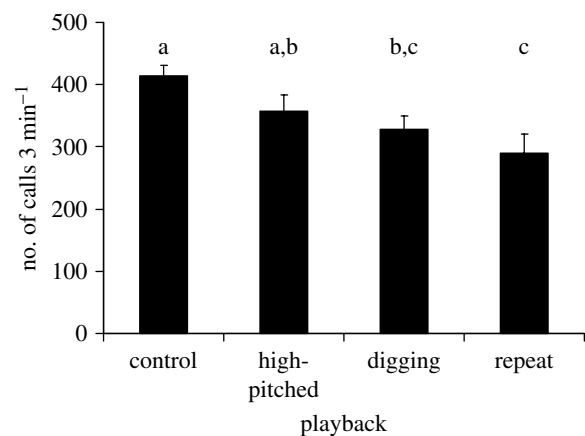

Figure 4. Mean number ($+1$ s.e.) of begging calls given by eight focal pups in response to playback in their immediate vicinity of three begging call types and a silent control. Letters indicate playbacks that do not differ from each other in pair-wise *post hoc* LSD tests (control versus high-pitched $p = 0.069$; control versus digging $p = 0.013$; control versus repeat $p = 0.010$; high-pitched versus digging $p = 0.196$; high-pitched versus repeat $p = 0.042$; digging versus repeat $p = 0.201$).

(c) *How do adults respond?*
(i) *Does provisioning vary with changes in group-level begging?*
Experimental variation in the level of begging calls within the group explained the variance in the amount of feeding recorded under the three treatments. When overall begging levels in the group were increased, the total feeding rate within the group increased, despite the begging rate of the focal individual decreasing, whereas when overall begging levels in the group were reduced, so too was the total feeding rate, despite the begging rate of the focal individual increasing (repeated-measures ANOVA: $F_{2,24} = 4.60$, $p = 0.02$; figure 5).

(ii) *Does provisioning vary with local levels of begging?*
The numbers of feeds that a pup received in each of the four distance categories relative to their siblings were disproportionate to the time that they spent begging in each category ($\chi^2_3 = 30.00$, $p < 0.001$; figure 6). Pups more than 10 m from another pup were fed at a rate almost
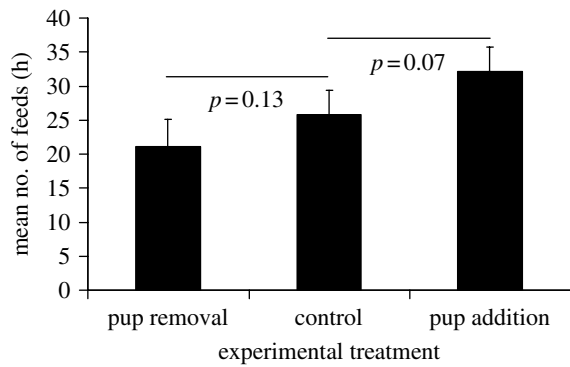
Figure 5. Mean number (+1 s.e.) of the total feeds made by adults within a group under three different treatments. For all treatments, $n=13$. The p-values indicate the results of *post hoc* LSD tests between the treatments.
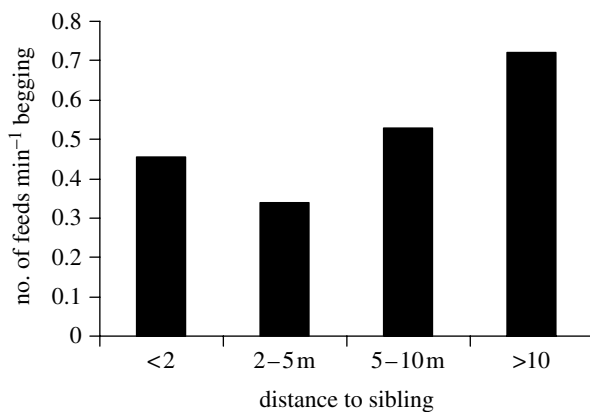

Figure 6. The number of feeds given per minute spent begging to pups at different distances from their siblings.

60 per cent higher for the time that they spent begging than pups less than 2 m from another pup, and at a rate over 110 per cent higher than pups 2–5 m from another pup.

(iii) Does per capita food intake increase with increased begging?

Increasing the perceived number of begging pups by playing back begging calls did not offer a marginal benefit to littermates. Although the total number of feeds made by adults in the group increased with increased begging in the group, the amount of increase did not compensate for the number of begging pups present. Pups in treatments, where one or two littermates were removed, each gained a mean of 10.54 feeds h^{-1}, whereas those in control treatments and begging addition treatments gained a mean of 6.71 and 5.50 feeds h^{-1}, respectively.

Although the overall level of feeds increased in groups in which begging was increased, despite the decrease in begging rate by focal pups, the rate of food given to that focal pup revealed a different pattern (repeated-measures ANOVA: $F_{2,24}=6.52, p=0.005$; figure 7). When the litter mates were removed and overall begging rates were decreased, focal pups increased their own begging rate (see above) and experienced a higher per capita feeding rate (*post hoc* least significant difference (LSD) test: pup removal versus control $p=0.007$). When overall begging rates were increased by playback alone, and the focal pup reduced its own begging rate, the focal pup did not obtain
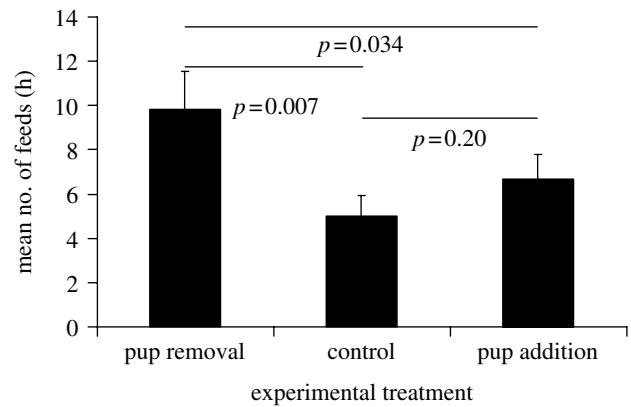
Figure 7. Mean number (+1 s.e.) of feeds to a focal meerkat pup under three different treatments. For all treatments, $n=13$. The p-values indicate the results of *post hoc* LSD tests between the treatments.
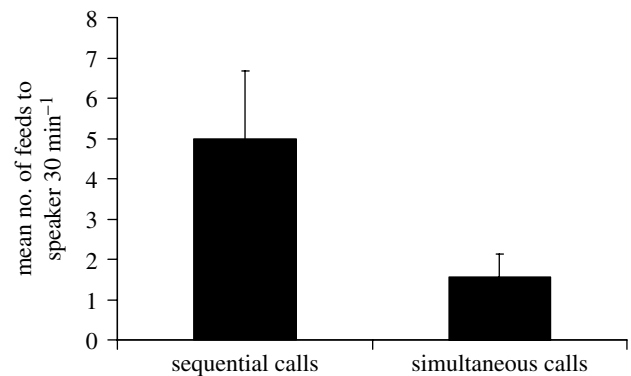

Figure 8. Mean number (+1 s.e.) of the total feeds made by adults within a group, accompanied by playback of either sequential (low intensity and continuous) or simultaneous (high intensity and interrupted by periods of silence) begging calls. For all playbacks, $n=9$.

significantly more feeds than during the control period (*post hoc* LSD test: 'pup addition' versus control $p=0.20$). Moreover, we found no difference in the number of refusals by adults in any of the three periods (repeated-measures ANOVA: $F_{2,24}=0.67, p=0.52$).

(iv) Do adults discriminate between begging strategies?

Playback of begging calls that mimicked pups begging competitively provoked a lower rate of feeding by adults than playback of begging calls that had pups begging cooperatively (Wilcoxon signed-rank test: $n=9, Z=2.55, p=0.011$; figure 8). A similar pattern was seen in the number of feeds given within the group as a whole (Wilcoxon signed-rank test: $n=9, Z=1.76, p=0.078$). One confounding factor could be that the sequential playback lasted for twice the total time of that of the simultaneous playback (essential in order to control for the total amount of begging experienced by the helpers). Despite this, helpers fed to speakers broadcasting sequential begging at twice the rate of that to speakers broadcasting simultaneous begging (Wilcoxon signed-rank test: $n=9, Z=2.52, p=0.012$) suggesting that the duration of the playback alone could not explain the differential responses of the adults.

Table 1. Predictions derived for each of the three models of begging that are supported by our observations and experiments. (Y, result supports the prediction; N, result refutes the prediction; ~, results do not relate to predictions. Results in parentheses show tentative support or refutation of the prediction.)

		competitive	cooperative	indirect competition
effect of group begging levels	litter size	Y	N	~
	changes in group-wide begging	N	Y	(Y)
effect of local begging levels	inter-pup distance	N	Y	Y
	changes in local begging	N	Y	Y
adult responses	feeding to group-wide begging	(N)	Y	~
	feeding to local begging	(Y)	(N)	Y
	per capita food allocation	~	N	~
	discrimination of begging calls	N	Y	Y

4. DISCUSSION

Our work provided conflicting support for competitive and cooperative begging. Competitive begging was refuted in four of the five sets of results, whereas cooperative begging was refuted in three of the eight sets of results (table 1). Therefore, we consider an alternative begging strategy that the young could practice. Offspring may seek to avoid costs imposed by begging in direct competition with one another (energetic, Kilner 2001; social enforcement, Drummond 2002; exposure to predators, Leech & Leonard 1997). If pups reduce their level of begging when others increase and increase their begging as others decrease, or when others are far away, then their own signal is heard against a lower background level of begging. Offspring effectively fill in the gaps between one another's begging, both spatially and temporally, in order to make their own signal more conspicuous. We suggest that the pups are engaging in indirect competition when begging, choosing to beg at high rates only when littermates are begging at low rates or are far away. We made predictions based on indirect competition, tested them against our results (table 1), and compared these with the two begging strategies that have been suggested previously.

The pattern of changes in pups' begging levels, depending on the level of begging they experienced in their group, provided equivocal support for competitive and cooperative models of begging. Our analysis of how begging rate related to litter size, as has previously been carried out on birds (Leonard *et al.* 2000; Neuenschwander *et al.* 2002; Mathevon & Charrier 2004), suggests that the begging behaviour of meerkat pups could be described as competitive. We found that the pups raised in larger litters begged at a higher mean rate than the pups raised in smaller litters. As Godfray (1995) predicted, a rise in the number of competitors drives an increase in the begging rate uttered by a single young individual. This is surprising, because whereas nestlings are confined in close proximity to brood mates, and in most previous studies are cared for by only two adults, meerkat pups are spread out and cared for by numerous adults, producing conditions in which competition might be less strong. However, our subsequent experiment testing whether pups facultatively adjusted their begging rate in a competitive manner as the perceived number of littermates changed, failed to support the prediction made for competitive begging. In fact, all our results were exactly opposite to what is predicted for pups begging competitively. Instead of increasing their begging as the number of begging littermates was increased, pups actually decreased their begging, and when we reduced

overall begging in the group, by removing competitors temporarily, focal pups increased their rate of begging. Such a pattern of behaviour matches the predictions made verbally by Wilson & Clark (2002), and following a model by Johnstone (2004), with individual's begging decreasing as the level of begging by siblings increases. This pattern of behaviour contrasts with more common observations of competitive begging, and has been described as cooperative begging (Mathevon & Charrier 2004; Marques *et al.* 2006; Bell 2007). It is possible that even though per capita begging decreases as the total amount of begging increases within a group, the individual begging at the highest level may still receive higher rates of feeding. No explicit predictions relating to begging as indirect competition can be derived relating to these results. However, individuals which increase their own begging levels, when those of the group as a whole decrease, exploit a short term lack of direct competition from other pups. Our experimental results provide tentative support for this, showing that the pups do increase begging when group-level begging is experimentally reduced.

Changes in pup's begging levels depending on the level of begging they experienced in their immediate vicinity contradicted the models for pups begging competitively, but did support models of pups begging cooperatively or in indirect competition. Instead of increasing their begging, as actual or apparent competition from littermates was increased, pups decreased their begging. We observed that the pups reduced their rate of begging when close to another pup. Pups also reduced their rate of calling when an experimental 'pup' started to beg close by them. These results, however, do not discriminate between cooperative begging and indirect competition. Both models predict that the individuals will beg more when the local levels of begging are lowered.

Adult responses to different begging behaviours allow us to better separate these two models. As predicted by models of cooperative begging (Johnstone 2004), an increase in the total amount of begging within a group, owing to an increase in the number of begging pups, provoked a gross increase in the amount of food that adults provisioned. However, contrary to Johnstone's conditions, the per capita amount of food actually decreased. Evidently, the additional increase in begging provided by each pup did not prompt a marginal increase in food being supplied. Adults did not preferentially provide food to sites where begging was locally intense. Adults supplied less food to a speaker broadcasting sporadic bursts of high-intensity begging, given by two

pups simultaneously, mimicking competitive begging, than to a speaker broadcasting low intensity, continuous begging given by two pups sequentially, mimicking two pups begging cooperatively, or in indirect competition. One explanation for this apparent preference may be that the playback of begging provokes enhanced levels of circulating cortisol, a hormone also associated with long-term contributions to pup provisioning (Carlson *et al.* 2006). Continuous aural stimulation by sequential begging may provoke a higher level of secretion of cortisol than occasional playback of vigorous begging. However, this does not explain why adults naturally preferred to feed pups with littermates that were far away. Models of indirect competition through begging predict just this, such that pups do best when there are no other pups around, and that adults do not need to compare two pups simultaneously in direct competition in order to make provisioning decisions. In fact, adults appear to prefer to avoid sites where there may be direct competition between pups for food.

The begging behaviour of mobile young from social, cooperatively breeding species such as meerkats is likely to differ from that of young raised exclusively by their parents at a fixed location, such as is seen in most nestling birds. With the potential for more feeders than offspring (Clutton-Brock *et al.* 1998), disparate levels of relatedness between offspring and helpers (Griffin *et al.* 2003), physical competition between pups for helpers (Hodge *et al.* 2007) and a variety of begging calls being given (Kunc *et al.* 2007), we may expect that the evolution of cooperative begging is favoured in meerkats (Johnstone 2004). However, rigorous testing of explicit predictions fails to support this. Instead, individuals coordinate their actions with those of littermates so as to minimize their own costs, rather than maximize the benefits to others. This may be exhibited by individuals begging in the gaps when littermates fall silent, refraining from begging whenever another pup is begging, or avoiding begging littermates. Therefore, competition between pups is indirect, with individuals trying to separate their begging signals in time and space. This begging strategy of calling in the gaps is also preferred by adults, so the benefits to individual pups are substantial and reinforce the behaviour that superficially appears to meet the criteria for cooperative begging.

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