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Do meerkat (*Suricata suricatta*) pups exhibit strategic begging behaviour and so exploit adults that feed at relatively high rates?

Joah R. Madden · Hans-Joerg P. Kunc · Sinead English · Marta B. Manser · Tim H. Clutton-Brock

Abstract Adults vary in their generosity in provisioning the young and their sensitivity to the need of the young. Do the young modulate their behaviour so as to specifically target more high-provisioning adults? This is especially likely in situations with mobile, nutritionally dependent young. We studied cooperatively breeding meerkats *Suricata suricatta*, in which pups beg to parents and other adults in the group. We found that the young begged differently when next to different adults and that they are consistent in how they beg when next to each adult. Pups next to adults that provision at high rates beg at higher rates and spend longer with them, and these adults are generally more sensitive to increases in begging rate. Such behaviour has adaptive benefits to offspring in terms of increased likelihood of being fed. However, offspring do not appear to be actively seeking out high-provisioning adults or increasing their begging behaviour when they encounter one. Pups did not appear to actively discriminate between adults in their association or begging behaviour. We suggest instead that the relationship between an adult's relative contribution to pup feeding and the behaviour of its accompanying pup is driven by adult behaviour, with responsive adults that feed pups at a relatively higher rate preferentially associating with fast-begging hungry pups.

Keywords Begging · Meerkats · Provisioning · Sexual conflict · Parent–offspring conflict

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Introduction

All adults are not equal, and the mobile young that have a choice of adults can benefit by associating with generous individuals. Adults vary widely in the level of care that they give, partly as a result of differences in their age and sex (e.g. Davies 1976; Moreno 1984; Edwards 1985; Verhulst and Hut 1996; Clutton-Brock et al. 1999; Hunt and Simmons 2002; Lessells 2002). Typically, this has been measured as the generosity of the adult—the relative amount of care that they provide to a group of young compared with that given by their partner. Adults may also vary in their responsiveness to different begging cues (MacGregor and Cockburn 2002; Johnstone and Hinde 2006; Bell 2008). For example, whilst higher rates of begging tend to elicit a general increase in provisioning (e.g. Ottosson et al. 1997; Burford et al. 1998; Halupka 1998; Kilner et al. 1999; Krebs 2001; Glassey and Forbes 2002), there is some evidence that females are more responsive to begging calls than males (Quillfeldt et al. 2004; English et al. 2008). Most previous studies on begging rates have concentrated on nestling altricial birds, in which the young are confined to the nest. However, in situations with mobile begging

systems (e.g. fledgling birds and mammals), there may be additional factors that influence begging behaviour, including the possibility that the young can benefit by associating with generous individuals, and exaggerate their payoffs by elevating their begging when they are close to especially responsive individuals. If generous individuals are also those that are most sensitive to changes in begging rates, the potential payoffs to young for forming the correct association become even greater.

Do the young choose which adult to associate with and what level of begging to exhibit, depending on specific attributes of the adult? Broods of owlets *Tyto alba* beg at higher rates to the arrival of females than they do to males (Roulin and Bersier 2007), but, as in most studies of begging on nestling birds, an individual response by offspring is hard to measure, with young restricted to the nest and as a single nestling's begging being difficult to isolate. Individual responses were seen in blue tit *Parus caeruleus* nestlings, with hungry individuals moving within their nest towards male parents, although their level of begging intensity did not differ with adult sex (Dickens et al. 2007). A more suitable system to investigate this may be one in which the young are spatially independent but still provisioned by adults, for example fledgling birds or nutritionally dependent mammalian young. The question is confounded by whether patterns of association and differential begging arise as results of facultative changes in the behaviour by the young or instead are the inevitable outcomes of differential investment in begging strategies by the young according to their nutritional states. If variation in begging behaviour were facultative, then the young are expected to actively seek to associate with generous adults or, on encountering a generous individual, may be expected to rapidly elevate their begging rate. Alternatively, if variation in begging behaviour depends on differential investment in begging strategies, then hungry offspring, which beg at a higher rate, are more likely to be found next to profitable adults, as they have more to gain by associating closely with them (e.g. Hodge et al. 2007). In both sets of circumstances, strategies determining begging relationships and associations are under the control of the young.

However, young may not have complete control over food allocation, and adults can maintain influence over which young they feed. Such favouritism can be explained by both sexual conflict, with differences between parents in the benefits of caring for a particular type of offspring and parent–offspring conflict, with costs of caring for particular offspring (Trivers 1974; Lessells 2002). This may result in long-term feeding preferences for particular juveniles, or classes of juveniles, within the brood (Brotherton et al. 2001; Draganoiu et al. 2005). The relative role of sibling competitions and adult control appears to differ depending

on the spatial distribution of offspring (Sasvàri 1990), a factor most obvious in mobile begging systems (but see Tanner et al. 2007 for an example in an apparently static, nest-based begging system). If, by begging at a higher rate, the young attract the attention of more generous adults, then the young need not facultatively change their begging, and any relationship between a generous adult and a rapidly begging offspring is most likely under the control of the adult, with generous adults seeking out hungry pups.

Meerkats offer an excellent opportunity to test whether individual offspring beg strategically, facultatively adjusting their begging behaviour according to adult identity, and whether by doing so, they can gain increased benefits from such fine-tuned behaviour. Meerkat pups behave like fledgling birds, continuing to beg and be fed by adults after having left the natal den, as well as starting to forage for themselves (Manser and Avey 2000; Brotherton et al. 2001). Pups forage with the group when about 25 days old and are fed in response to begging calls by parents and other helper adults in the group for a further 3 months (Manser and Avey 2000; Brotherton et al. 2001). Meerkat pups do not associate with a single adult but, instead, move freely between them, with adults typically feeding the closest pup to them (Manser and Avey 2000; Brotherton et al. 2001). Specifically, adults preferentially feed hungry pups that utter high rates of begging calls (Manser et al. 2008), with adult females being more responsive to changes in begging rate than adult males (English et al. 2008).

First, we establish whether adults consistently differ in their relative rates of feeding pups. Second, we test whether pups beg differently when next to different adults. Third, we conducted a playback experiment to ask whether adults that fed pups at high rates are also more sensitive to increases in begging rates. Finally, we used a series of feeding and displacement experiments to differentiate between three alternative explanations for differences in begging behaviour. In the first two, begging behaviour is under pup control and either explained by facultative changes in a pup's behaviour driven by the identity of the adult that the pup is begging next to, or is the result of differential investment in begging strategies, depending on the pup's nutritional state. In the third, adults control the patterns of association by responding differently to pup behaviour, with adults that fed pups at high rates preferentially approaching hungry pups begging at high rates.

Materials and methods

Study site, species and observational data

We studied wild meerkats around the dry Kuruman riverbed in the southern part of the Kalahari Desert in South Africa

(26º58′ S, 21º49′ E). Meerkats live in groups of two to 50 individuals with a dominant breeding pair and a number of related and unrelated helpers of both sexes 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. 1999). From about 4 weeks, pups accompany the group as they forage, being fed invertebrate and small vertebrate prey by adults (Clutton-Brock et al. 1999). All animals were habituated to close observation (<1 m) and marked for individual identification with hair dye. All animals were known from birth, so their age, sex and other important life history events were known.

We examined the feeding efforts of 108 adults from six different groups, each group caring for one litter. For each group, we took 10 days when a large number of feeds were recorded (mean=33.83; range=16–43). Ad libitum data were collected from the groups that were visited for at least three mornings each week between March 2005 and February 2006 during peak periods of pup begging when the pup was between 40 and 60 days old. During these sessions, all feeds made by adults to pups were noted. We chose a 10-day period, as this was certain to include all of the time following the start of the pups foraging with the group. From these feeding measures, we could calculate the mean relative contributions to pup feeding made by the adult. The relative contribution to pup feeding was determined by the number of feeds given by each adult divided by the total number of feeds given by the group. Adults who contributed relatively high levels of feeding effort to pups could be described as high provisioning, whereas those that contributed relatively low levels could be described as low provisioning. We tested whether adults differed in their relative contribution to feeding pups and calculated how repeatable this measure was between days. We used the long-term (10 day) measure of relative contribution to pup feeding rather than a measure of relative contributions to feeding on the day of the recordings or experiments because, although the two measures are strongly and positively related ($r=0.74$, $n=61$, $p<0.001$), measures on the day of recording or experiment may have been disrupted by our activities at the group, and measures over a longer term provided a much larger sample size and so a more accurate measure. All measures of an individual's contribution to pup feeding were calculated after all of the experiments had been completed and derived from observations made by people other than the experimenters, so experimenters did not know what contributions to pup feeding an adult had made over the previous 10 days.

We used identical methods to calculate the relative contributions of each adult made over 10 days before the day on which recordings of the pup's begging vocalisations

were made or the feeding or association experiments were conducted (see below).

Focal recordings of pup vocalisations and observations of associative behaviour

Recordings of pup vocalisations were made from 29 pups from 16 litters, between March 2005 and June 2006, when pups were 40–60 days old. Recordings lasted 20 min and were collected whilst pups were foraging with the group at a distance of approximately 50 cm using a Sennheiser ME66/K6 directional microphone connected to one channel of a Marantz PMD670 digital recorder (wav-format, sample frequency, 44.1 kHz; resolution, 16 bit). During this period, all behaviours of a pup and its association with other members of the group (distance to and identity of nearest adult and pup) were simultaneously recorded on a second channel of the recorder. Therefore, a pup's vocalisations could be related to its activity and proximity to other meerkats. In order to measure how pup begging varied depending on adult identity, we collected measures of begging rates from pups next to 21 adults, each of whom had three or more 10-s begging bouts recorded from pups next to them that were separated by at least 5 min. Calls were transferred to a PC and spectrograms (spectrogram: sample frequency=22.5 kHz, fast Fourier transform=1,024, overlap=93.75 and time resolution=2.9 ms) were generated with the software package Avisoft SASLab Pro 4.38 (R. Specht, Berlin). We focused on the repeat calls, given continuously whilst begging alongside adults (Fig. 1; cf. Manser and Avey 2000). We counted the number of repeat calls given in the 10-s period at the start of each minute over the 20-min period and calculated the mean number of calls/10 s to give us a measure of begging rate.

We investigated what attributes of the adult predicted the begging rate of the pup next to them by taking the first
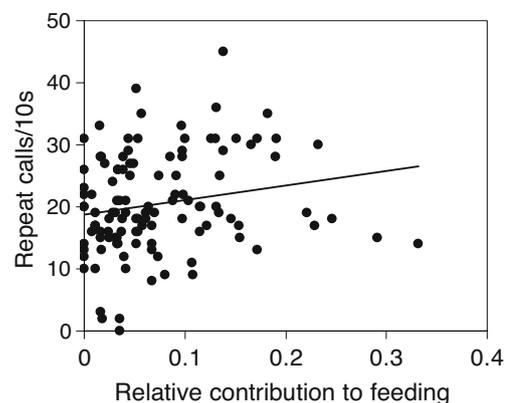

Fig. 1 Relationship between the rate of repeat calls given by a focal pup when next to an adult and the contribution to pup feeding by that adult over the previous 10 days

recorded measure of begging from a pup next to each adult that it begged to. We constructed a linear mixed model (LMM) explaining variation in begging rate that included adult dominance (subordinate or dominant, with dominant adults being the pup's likely parents), adult sex, adult contribution to feeding over the previous 10 days, adult mass, presence of lactation, total time that the pup spent next to the adult during the 20 min recording session and pup sex. Pup identity and group were entered as a random term.

We investigated what attributes of the adult predicted how long each pup spent next to each adult during a 20-min recording period. We constructed a generalised LMM (GLMM) explaining variance in time spent next to a specific adult controlling for the time that a pup spent next to any adult, which included adult dominance (subordinate or dominant), adult sex, adult contribution to feeding over the previous 10 days, adult mass, presence of lactation and pup sex. Pup identity, adult identity and group were entered as random terms.

Experimental manipulation of pup associations

First, we tested whether pups actively discriminated between adults depending on the adult's sex, dominance, mass or contribution to feeding. We separated factors of adult identity from their immediate past feeding record and confounding spatial factors that may act on pup decisions by conducting a displacement experiment. Pups were picked up and lifted from their current nearest adult and placed next to a new adult, at least 5 m from where they had previously been foraging. Their subsequent behaviour was observed for 1 min, during which time we recorded the time that it spent within 1 m of an adult and the adult's identity, as well as the total time that it spent >1 m from any adult. We conducted 104 displacement experiments on 26 pups, 13 of each sex, from eight groups, each moved three to five times and interacting with 93 adults. Experiments were conducted between January and February 2006.

Second, we examined whether pups discriminated between adults based on their immediate feeding experience. Adults, selected haphazardly, were presented with a scorpion (genus *Opisthophalamus*) whilst within 2 m of a begging pup. Adults could either feed the pup the scorpion or eat it themselves. After the adults had either fed the scorpion to a focal pup or had refused it, by physically blocking the pup from reaching the food item, we separated the pup from the adult and placed it next to a random adult at least 5 m from where the food encounter had occurred. We then observed the behaviour of the pup for the following minute, recording the time that it spent within 1 m of an adult, and the adult's identity, as well as the total time that it spent >1 m from any adult. We conducted 52

displacement experiments on 24 pups from eight groups that were either fed by a focal adult who had been experimentally provisioned with a scorpion ($n=27$) or who had been refused a provisioned scorpion by a focal adult ($n=25$).

Scorpion feeding experiment

We tested what factors determined whether adult meerkats donated food items to begging pups after we had controlled for the cost of acquiring the food item by giving adults a scorpion as they were foraging. A total of 128 scorpions (genus *Opistophthalamus*) weighing 1–3 g were experimentally delivered to 73 adults from eight groups whilst within 2 m of a begging pup (29 individuals). Adults could either feed the pup the scorpion or eat it themselves. All experiments were carried out in January and February 2006. We constructed a GLMM with a binomial error structure (fed/not fed) and a logit link, explaining whether the scorpion was fed to a pup, which included adult dominance (subordinate or dominant), adult sex, adult contribution to pup feeding over the previous 10 days, adult mass, pup sex and pup mass. Pup identity, adult identity and group were included as random terms to account for repeated presentations to the same adult, sometimes in the presence of the same pup.

Measuring adult sensitivity to pup begging rates

We tested how much adults increased their rate of feeding, given a standard increase (tripling) in the rate of begging played next (2 m) to them. We played back 30 min of low rate and 30 min of high rate begging (only repeat calls), presented in a random order, to four focal individuals in each of ten groups between December 2005 and May 2006 (see English et al. 2008). Playback cuts were made from recordings of female pups from another group by either adding or removing periods of background noise between calls to create the low (40 calls/minute) and high (120 calls/minute) treatments, respectively (values within the natural range). Within each group, the experiment was made over two consecutive days. The first playback experiment in each session was preceded by a 20-min habituation period of calls at an intermediate begging rate. In order to avoid habituation to the playbacks, no more than two experiments were played consecutively to a group in one session. During the playback, we recorded data on the foraging behaviour of the focal individual. Sensitivity was calculated as the change in the percentage of found food items that were provisioned between the low- and high-rate begging playbacks. We used a GLMM to test whether an adult's contribution to pup feeding was related to their sensitivity,

entering group as a random factor, and with the response variable being generosity, that is, the number of feeds that each individual made during observation visits over the preceding 10 days, with the total number of feeds made within the group as the denominator.

Statistical analysis

Models were constructed using Genstat 8.1 (Lawes Agricultural Trust, Rothampstead, Harpenden, UK). Random terms were nested with pup and adult identity within group. Variance components of LMMs were estimated with the restricted maximum likelihood method. For predictive models, we sequentially dropped all potential explanatory terms until only terms explaining significant variation remained. We then tested each dropped term in the minimal model to obtain its level of non-significance. We tested all two-way interactions but only present those explaining significant variation. In the case of LMMs, residuals were checked for normality. Repeatability from unbalanced samples were calculated using the method of Lessells and Boag (1987), and we tested whether these were significantly higher than expected by running randomisation tests, conducted using PopTools v.2.7.1. (Hood 2005). All other analyses were carried out using SPSS v. 13. Means are shown ±1 SE.

All work was conducted under the permission of the Northern Cape Conservation Service and the ethical committee of Pretoria University, South Africa.

Results

Do adults consistently differ in their contributions to pup feeding?

Adults differed in their relative level of pup feeding, with individual contributions varying from 0% to 24.6% of feeds within a single group. In all cases, the repeatability that an individual exhibited from day to day was significantly higher than expected from 1,000 randomisations of the data (Table 1).

Do pups beg at different rates to different adults and are these differences consistent?

Pups begged at different rates when next to different adults (LMM: Wald $\chi^2 = 39.91$, $df = 21$, $p = 0.008$). Individual pups increased their mean rate of begging by 79% from the adult to which they begged least (14.55 ± 1.08 calls/10 s) compared to that which they begged most to (26.03 ± 1.30 calls/10 s). The adult that experienced the highest mean begging rate (28.33 ± 1.45 calls/10 s) was begged to at a rate 131% higher than the adult begged to at the lowest rate (12.28 ± 3.66 calls/10 s).

Pups begged relatively consistently when next to specific adults. We derived a repeatability measure of within adult variation in received begging rate of 0.189. Despite this repeatability being rather low, it was still significantly better than that achieved by 1,000 randomisations of the begging rate data ($p = 0.022$).

What attributes of the adult predict the begging rate and time spent in association of pups next to them?

Pups begged at a higher rate when next to high-provisioning adults (Table 2; Fig. 1) and spent longer next to these adults (Table 3; Fig. 2). No other attribute of the adult had an effect on pup behaviour. No two-way interactions were significant in either model.

Are adults that provision at high rates especially sensitive to begging rates, and do they discriminate between pups?

Adults that provisioned at high rates were also individuals that most strongly increased their percentage of provisioning when pup begging rates were experimentally increased (GLMM: Wald $\chi^2 = 5.79$, $df = 1$, $p = 0.016$; Fig. 3).

High-provisioning adults discriminated in favour of light pups when feeding an experimentally provisioned

Table 1 Variance and repeatability in adult generosity from six groups

Group	Adults	Feeds	df	F value	p value	Rpt	P Rpt
Lazuli	18	496	17, 179	6.30	<0.001	0.35	0.001
Moomins	17	498	16, 169	3.82	<0.001	0.22	0.001
Rascals	14	443	13, 139	15.6	<0.001	0.59	0.001
Vivian	19	450	18, 199	5.62	<0.001	0.32	0.001
Whiskers	33	591	32, 329	4.68	<0.001	0.27	0.001
Young Ones	10	308	9, 99	3.03	0.003	0.17	0.001

Variance calculated using ANOVA. Repeatabilities derived using methods of Lessells and Boag (1987). Probability of repeatability exceeding that of chance randomisation of the data, based on 1,000 randomisations

Table 2 LMM of how variables relate to the rate of begging when next to a specific adult

	Wald (χ^2)	df	p value	Effect size	SE
Explanatory term					
Provisioning level	3.82	1	0.05		
Adult sex	0.06	1	0.81		
Adult mass	2.37	1	0.13		
Adult status	0.23	1	0.63		
Lactating	1.48	1	0.23		
Time next to adult	2.54	1	0.11		
Pup sex	0.50	1	0.49		
Minimal model					
Constant				20.28	1.21
Provisioning level				21.52	11.11

Response variable is number of repeat calls given in the first 10-s period that an adult was begged to. Analysis was conducted on data from 89 adults and 31 pups. Pup, adult and group identity were entered as random terms

scorpion, whereas low-provisioning adults did not (Table 4, Fig. 4). No other observed feature of pups or adults explained the probability of adults to feed the scorpion to pups (Table 4).

Do pups seek out adults that provision more?

Pups were not more likely to leave adults that did not provision at relatively high rates. Pups that stayed with one adult for the entire minute were not those that had been placed next to adults that provisioned at relatively higher rates compared with those that visited other adults in the population ($N_{\text{stayed with their given adult}}=13$, $N_{\text{left their given adult}}=54$, t test, $t_{65}=0.40$, $p=0.69$). Pups did not move from low-provisioning adults to high-provisioning ones. The adults to which pups had moved to by then end of the minute did not provisioned at a higher rate than those they had been placed next to at the start (paired sample t test $t_{53}=0.35$, $p=0.73$). Pups did not spend more time next to high-provisioning adults compared to low-provisioning adults. There was no relationship between the proportion of time that displaced pups spent with an adult and their contribution to pup feeding (GLMM: Wald $\chi^2=0.09$, $df=1$, $p=0.77$).

Pups that had been fed a scorpion spent proportionately less time next to the focal adult that had just fed them than pups that had been refused food spent next to their refuser, despite the scorpion having been already eaten (GLMM: Wald $\chi^2=4.65$, $df=1$, $p=0.031$; effect=1.23, SE=0.57; constant=−2.79, SE=0.52; Fig. 5). Pups that were fed or refused did not differ in the overall amount of time that they spent with any adult (GLMM: Wald $\chi^2=0.99$, $df=1$, $p=0.32$) and did not differ in the time that they spent next to the random adult to which they had been displaced (GLMM: Wald $\chi^2=1.59$, $df=1$, $p=0.21$).

Discussion

Adult meerkats can be described as either contributing a relatively high number of feeds to pups or a relatively low number. Within groups, adults differ in this measure, but their relative pup-feeding effort remains consistent from day to day within a single litter. We did not investigate predictors of contribution to pup feeding in meerkats in this paper, but such differences in other species have been predicted by the adult's sex (Davies 1976; Moreno 1984; Edwards 1985; Verhulst and Hut
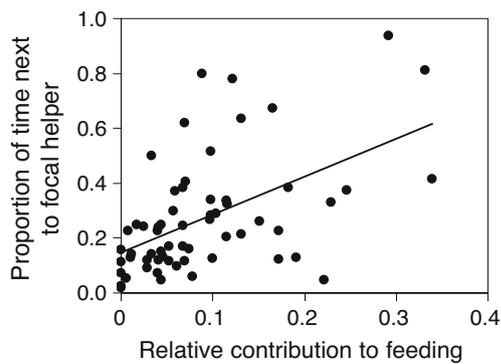
Table 3 GLMM of how variables relate to the time that a pup spent next to an adult, controlling for the total time that the pup pent next to any adult

	Wald (χ^2)	df	p value	Effect size	SE
Explanatory term					
Provisioning level	19.65	1	<0.0001		
Adult sex	1.23	1	0.25		
Adult mass	0.10	1	0.73		
Adult status	0.52	1	0.48		
Lactating	1.08	1	0.30		
Pup sex	0.56	1	0.46		
Minimal Model					
Constant				−0.99	0.13
Provisioning level				7.14	1.46

Analysis was conducted on data from 52 adults and 28 pups. Pup identity, adult identity and group were entered as random terms

Fig. 2 Relationship between the time that a focal pup spent next to an adult as a proportion of the total time it spent next to any adult and the contribution to pup feeding by that adult over the previous 10 days

1996; Hunt and Simmons 2002), condition (Bell 2008) or age, breeding status and presence of helpers (MacColl and Hatchwell 2003; Gilchrist 2004; Woxvold et al. 2006) and may not depend on the relatedness of the adult to the offspring (Briskie et al. 1998; Wright et al. 1999; Canestrari et al. 2005). Differences in care may be related to differences in sensitivity to offspring need (MacGregor and Cockburn 2002; Mock et al. 2005; English et al. 2008), adult condition (Sasvàri 1990; Bell 2008) or informational asymmetry (Johnstone and Hinde 2006).

The begging rate of meerkat pups varies depending on the identity of the adult they are begging next to, and this is consistent over multiple encounters with the same adult. Pups do not appear to discriminate between adults based on sex, dominance or size, unlike nestling birds (Roulin and Bersier 2007; Dickens et al. 2007). Instead, the best predictor of the begging rate of a pup and the time that it spends next to an adult is the relative contribution to pup feeding of the adult who they are begging next to. Pups begging at higher rates tend to be those next to adults who have contributed a relatively high rate of pup feeds in the previous 10 days. These adult meerkats are also those that appear to be most sensitive to changes in the begging rate
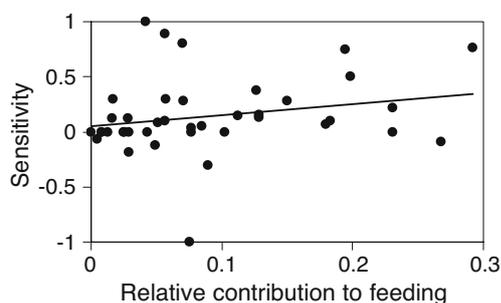

Fig. 3 Relationship between the sensitivity of a focal adult to pup begging calls (how much it changes its percentage of food fed given a tripling of pup begging rate) and the contribution to pup feeding by that adult over the previous 10 days

of pups. This could provide pups with an opportunity to optimise the return for their investment in begging by targeting specific, high-provisioning adults.

Are pups in control of this pattern of begging and association? If so, pups may be facultatively adjusting their begging rates as they encounter different adults and choosing to spend longer with them, depending on the adult's provisioning rate. In this situation, we predict that any pup encountering a high-provisioning adult will rapidly elevate its begging rate and stay with that adult for a long time. This remains to be tested explicitly. Alternatively, this relationship between begging and an adult's contribution to pup feeding may be explained by differential investment: Hungry pups spend longer next to adults overall, having a greater need to be fed, and because they continue to compete more strongly for adults, they tend to be more likely to be observed with high-provisioning adults (Hodge et al. 2007). Hungry pups typically beg at a higher rate than well-fed pups (Manser et al. 2008); therefore, if hungry individuals are more willing to invest in competition for certain adults than well-fed pups, we expect to observe hungry pups, who are begging at a high rate, next to high-provisioning adults who they have monopolised. Well-fed pups may chose to forgo begging and feeding in exchange for the opportunity to practice foraging (Thornton 2007), and so they invest less in competition for specific, high-provisioning adults and are therefore found next to them less often or more often next to low-provisioning adults, who are not competed for so strongly.

Separating the explanation of facultative adjustment from the explanation of differential investment is difficult. Evidence against a fine-scale facultative adjustment is provided by our displacement experiments, which revealed that pups did not actively seek out high-provisioning adults nor did they discriminate between high- and low-provisioning adults, at least over a short time period. Pups were not more likely to leave low-provisioning adults when they had been placed next to them than when placed next to an adult that provisioned at a higher rate; pups did not 'trade up' adults by moving from low- to high-provisioning adults; finally, pups did not spend longer with high- than low-provisioning adults overall. It is possible that our experiment was too brief, lasting only 1 min, so that pups were still sampling different adults before committing to spending time with just one. Additionally, by moving pups, we may have disturbed them and caused unnatural behaviours. However, we noticed no qualitative differences in a pup's behaviour following its brief handling (JRM, SE and HJK, personal observation). Further evidence against the facultative adjustment explanation is provided by our displacement scorpion feeding experiment. If pups facultatively spend more time with high-provisioning adults, then we predicted that an adult that had just fed a food item to a

Table 4 GLMM of variables relating to the probability that adults will feed pups a scorpion that they have been experimentally provisioned with

	Wald (χ^2)	df	p value	Effect size	SE
Explanatory term					
Provisioning level × pup mass	4.02	1	0.048		
Provisioning level	1.17	1	0.28		
Adult sex	0.05	1	0.82		
Adult mass	0.43	1	0.52		
Adult status	0.04	1	0.85		
Pup sex	0.09	1	0.77		
Pup mass	0.53	1	0.47		
Minimal model					
Constant				−1.55	0.57
Provisioning level × pup mass				−0.60	0.30

Analysis was conducted on data from 128 presentations to 71 adults with feeds to 29 pups. Pup identity, adult identity and group were entered as random terms

pup would be especially attractive, and the pup would tend to seek out and spend time with that individual. Instead, we found that pups spent less time with an adult that had just fed them than with an adult that had just refused them a food item. Perhaps this is simply because an individual who has naturally just provisioned a pup with a scorpion is less likely to provision its next food item. Alternatively, this observation could support the differential investment explanation, such that once a pup has been well fed (a scorpion constitutes about 0.5–2% of a pup's body weight), then it is less likely to associate with a high-provisioning adult. We may expect that the well-fed pup actually spends less time next to any adult at all, but instead forages on their own; however, our results did not reveal that, in the minute following the scorpion presentation, fed pups spent longer away from adults overall. Finally, a previous work has revealed that hungry pups spend longer next to adults than when they are well fed (Manser et al. 2008), which again suggests that this simple rule of pup behaviour, that tries to associate with an adult when hungry, may help explain our observation that pups spend longer and beg at a higher rate
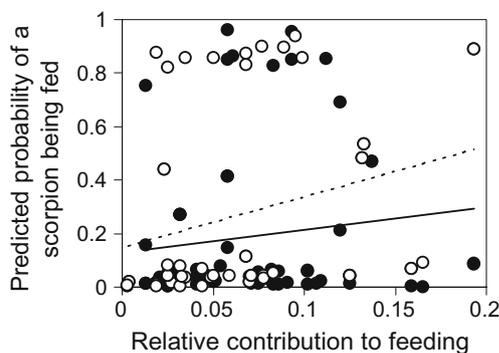
next to high-provisioning adults. On balance, our results suggest that it is less likely that pups facultatively adjust their begging behaviour towards specific adults and more likely that the patterns of difference that we observe are a result of differential investment in strategies to counter hunger.

This distribution of associations may be controlled by adults rather than by pups. Adults that provision at high rates could be seeking out hungry pups begging at high rates (Manser et al. 2008). Adults were discriminating in their feeding behaviour. High-provisioning adults were more likely to feed an experimentally provisioned scorpion to a pup but only if the pup was light. High-provisioning adults were not increasingly likely to feed a heavy pup. This mirrors previous work showing that adults discriminate in their feeding decisions based on an offspring's mass (Sasvàri 1990) or sex (Bell 2008). The ability of pups to move and associate with adults may confound the interpretation of these data, but discrimination of the young can be based on vocal cues alone (Draganoiu et al. 2006). This allows us to separate the effect of pup behaviour from that of adult discrimination. When we recorded the begging calls of a pup when
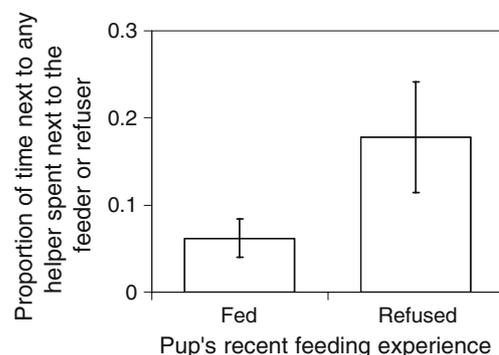

Fig. 4 Relationship between a focal adult's previous contribution to pup feeding and the probability that it will feed a pup, depending on pup mass. For visualisation, pups are dichotomised about the mean, with light pups (<240 g) shown as *white circles/dashed line* or heavy pups (>240 g) shown as *black circles/solid line*

Fig. 5 Mean±1 SE proportion of the time that a focal pup spent <1 m from any adult to that spent <1 m from an adult that had either just fed or refused them an experimentally provisioned scorpion

hungry and fed and broadcast them from randomly moving loudspeakers, adults preferred to feed the calls of the pup when hungry to calls of the same pup when well fed (Manser et al. 2008). Therefore, adult meerkats do discriminate between pups on the basis of their vocalisations, probably because these indicate their nutritional state. This suggests a mechanism by which adults can control the patterns of association between themselves and pups.

Our observations and experiments demonstrate that (1) offspring attended by different adults beg at different rates, (2) that they are consistent in how they beg when next to each adult, (3) that they spend more time with high-provisioning adults and (4) that they give higher rates of begging when next to adults who consistently provision young at a high rate and who are generally more sensitive to increases in begging rate. Such behaviour has obvious benefits to offspring in terms of increased likelihood of being fed. However, we found no evidence to suggest that offspring are facultatively seeking out high-provisioning adults or strategically adjusting their begging behaviour as they encounter one. Furthermore, we did not find evidence for pups discriminating between adults, although hungry pups may compete more strongly for the exclusive access to high-provisioning adults (Hodge et al. 2007). Most probably, the relationship between an adult's contribution to pup feeding and the behaviour of its accompanying pup is driven by adult behaviour rather than pup's strategic begging. Hungry pups signal their nutritional state by begging at a high rate and are especially attractive to high-provisioning adults, who preferentially associate with them, explaining our observation that fast-begging, hungry pups are more often seen, and seen for longer, next to high-provisioning adults.

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