Begging Signals in a Mobile Feeding System: The Evolution of Different Call Types

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abstract: In some species, dependent offspring join foraging providers and beg for food. Mobile offspring might benefit from evolving begging signals adapted to the different situations they are exposed to, but this possibility has been ignored. In cooperatively breeding meerkats (*Suricata suricatta*), dependent offspring use a repertoire of several begging calls when joining foraging adults. We found that these calls can be differentiated on the basis of their acoustic structure and that pups adjusted the use of specific call types according to the social context. Pups continuously gave "repeat" calls when they accompanied foraging adults, and playback of these calls increased provisioning by the adults. When pups saw adults with food, they switched from repeat calls to vigorous "high-pitched" calls; adults also preferred to "feed" loudspeakers broadcasting high-pitched calls rather then loudspeakers broadcasting repeat calls. The elaboration of different begging calls might reflect an adaptation to a situation where dependent young must solicit food from potential feeders while at the same time directing feeders to bring the prey item to themselves and not to another begging pup. Here we show that mobile but dependent offspring adapt to different contexts in a mobile feeding system by using a repertoire of begging calls.

Keywords: begging, meerkat, parent-offspring communication, sibling competition, vocal communication.

The behavior of offspring begging for food has received considerable theoretical and empirical interest as a model of animal communication between signalers and receivers

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with conflicting interests (Trivers 1974; Parker and Macnair 1979; Kilner and Johnstone 1997; Godfray and Johnstone 2000). Begging is usually seen as an outcome of conflict over resource allocation between parents and offspring (Godfray 1991). The question of how the parent-offspring conflict may be resolved evolutionarily has led to the development of honest-signaling models and scramble-competition models, both predicting that begging reflects offspring need (Royle et al. 2002). Honest-signaling models assume that begging is costly and resource allocation is under parental control (Godfray 1991, 1995), whereas sibling scramble-competition models assume that food allocation is under offspring control (Rodriguez-Girones et al. 2001; Parker et al. 2002).

Most of the current understanding of offspring begging behavior derives from studies of altricial birds in a stationary, competitive environment—the nest with several young. In these cases, providers bring food to dependent young at a stationary place (Budden and Wright 2001; Wright and Leonard 2002), and begging behavior of offspring is often confined to the short period when providers are present (but see Roulin et al. 2000). Although offspring are still dependent after leaving the nest, previous studies have mainly focused on their short time at the nest and ignored subsequent parent-offspring communication after the offspring have left the nest. In contrast to the nest-bound phase of development, mobile offspring are exposed to various different contexts during the postfledging phase. Thus, other constraints may have shaped acoustic begging signals, which might have led to the evolution of a repertoire of acoustic begging signals. For example, during the mobile phase, dependent young have to ensure that adults feed them instead of a sibling, but they also have a chance to dissuade the adult from eating the food item by constantly begging for food, whereas nest-bound nestlings can do this only during the restricted time when providers are at the nest.

In meerkats (*Suricata suricatta*), a cooperatively breeding mongoose, pups begin to follow the foraging group when they are 1 month old, and until they can find their own food independently (at around 3 months), they solicit

food from nearby group members, including both parents and helpers. Adults forage in the sand, preying on invertebrates and small vertebrates (Doolan and Macdonald 1996), which they either eat themselves or donate to a pup. Pups follow foraging adults rather than waiting at one location to be fed, and they produce a repertoire of different vocalizations in different contexts (fig. 1). Pups constantly give one type of call, a "repeat" call, over long periods while following foraging adults; however, whenever a pup observes that an adult has a food item, it switches to another call type, the "high-pitched" call (Manser and Avey 2000). When pups attempt to forage for themselves, they emit what we term the "digging call." Finally, during aggressive interactions between pups for food, they either growl or snap at an approaching pup (Hodge et al., forthcoming).

To understand why such an elaborate begging behavior has evolved, we investigated whether calls differ in their acoustic structure. We then conducted experiments to determine whether the use of calls by offspring depends on different social contexts (i.e., whether a pup was alone, with a helper, or with another pup). Finally, we performed a series of playback experiments that investigated whether helpers adjust food allocation and foraging behavior in response to different call types. We predicted that (1) pup calls emitted in different social contexts can be assigned correctly on the basis of their acoustic structure, (2) pups use different calls according to the context, and (3) food allocation of potential providers depends on the call type a pup emits.

Methods

Study Site and Animals

We studied free-ranging meerkats along the dry bed of the Kuruman river in the southern part of the Kalahari Desert in South Africa (26°58′S, 21°49′E) from March 2004 to February 2006 (for details of the study site, see Russell et al. 2002). Meerkats live in groups with a dominant breeding pair and up to 50 helpers. Litters of up to seven pups are produced up 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. All animals were habituated to close observation (<1 m) and marked for individual identification with hair dye or haircuts applied to their fur. These marks were small and applied noninvasively during sunning at the morning sleeping burrow. The study was conducted under the permission of the Northern Cape Conservation Service and the ethical committee of Pretoria University, South Africa.

Recording Protocol and Call Analysis

We collected data from 40 foraging pups (23 females, 17 males) from 11 litters and 11 groups between days 14 and 21 after leaving the burrow. On one audio channel, we recorded all vocalizations given by the focal pup during a 20-min focal watch at a distance of approximately 50 cm, using a Sennheiser ME66/K6 directional microphone connected to a Marantz PMD670 (.wav format, sample frequency: 44.1 kHz, resolution: 16 bit). On the other audio channel, we described the context in which the pup was giving the vocalization. Calls were transferred to a personal computer and spectrograms (spectrogram: sample frequency = 22.5 kHz, fast Fourier transformation = 1,024, overlap = 93.75, time resolution = 2.9 ms) were generated with the software package Avisoft SASLab Pro 4.38 (R. Specht, Berlin). We classified calls according to the context in which they were given and distinguished between the following contexts: begging, when a pup follows feeders
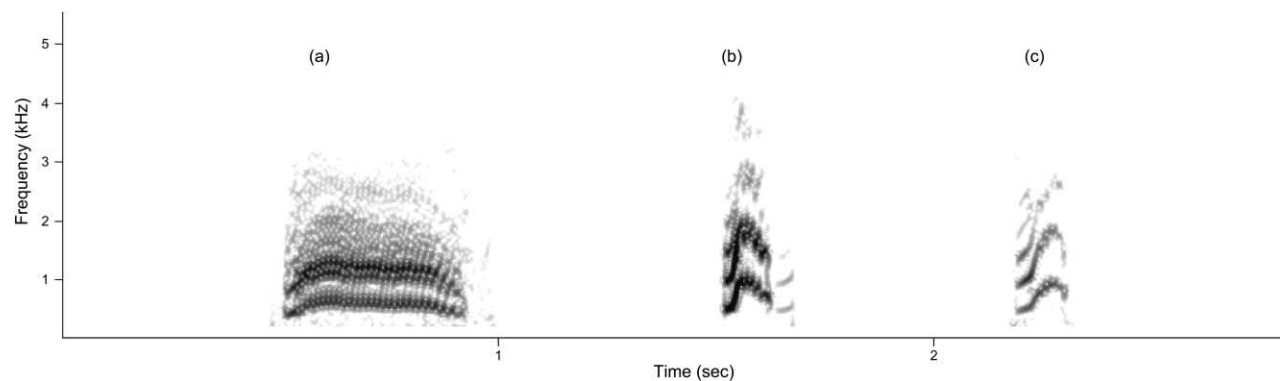
Figure 1: Spectrogram of the three types of begging calls of a meerkat pup: *a*, repeat call; *b*, high-pitched call; and *c*, digging call.

and emits repeat calls; excited, when a pup approaches a potential feeder and emits high-pitched calls; and digging, when a pup digging for food by itself emits digging calls.

To analyze differences in call structure between the call types given in different contexts, we used discrimination analysis and aimed to extract five high-quality calls with a high signal-to-noise ratio for each of the three call types for each pup. We analyzed a total of 514 calls (mean = 13.3 calls per pup); sample sizes varied because the quality of recordings was sometimes compromised by background noise from wind or tall grass. For each call, we measured (1) duration (s); (2) peak frequency at start (Hz); (3) fundamental frequency at start (Hz); (4) bandwidth at start (Hz), that is, the difference between maximum and minimum frequency; (5) difference in fundamental frequency in the end minus fundamental frequency at start (Hz), as a measure of modulation; and (6) the mean entropy, which allowed us to quantify the pureness of sound.

Effect of Social Context on Call Types Used by Pups

We tested how pups used different call types depending on social context by conducting prey presentation experiments in nine different groups, testing 11 female and 11 male pups. We presented a living, medium-sized scorpion of the genus *Opistophthalamus*, a common prey of meerkats, to each of the focal pups once when (1) it was alone, with no helper or other pup present within 3 m; (2) a helper was within 1 m, but no other pups were present within 3 m; and (3) another pup was within 1 m, with no helpers within 3 m. Following the presentation of the scorpion, we noted which call type the pup emitted. After each scorpion presentation, we suspended experimental activity for at least 30 min.

Playback Protocols

To avoid pseudoreplication, we created for each group a new stimulus tape, using a standardized recording level, from clear recordings of calls given by a female pup in the group one day before the first playback was carried out. Playbacks in the .wav format were broadcast from an IRiver iHP-140 MP3-player connected to a Thomson ASK 145 loudspeaker. The playback volume was adjusted to 68–72 dB at 0.5 m to simulate the normal amplitude of a pup following a potential feeder (Manser and Avey 2000). When conducting a playback experiment, the observer walked behind the focal helper at a distance of 1.5 to 3 m while holding the loudspeaker 5–10 cm above the ground. We conducted one playback experiment per day; all playback experiments were performed in the morning after all group members had left the burrow and at least 50% of the group was foraging. A playback was paused if

foraging by the group or the focal individual was interrupted for more than 2 min by alarm calls, intergroup encounters, or the presence of prospecting males from other groups.

First, we tested whether repeat and digging calls of pups led to different levels of food allocation by adults. We conducted a single-speaker playback experiment in eight different groups, using one female helper older than 6 months as a subject. Playback trials consisted of three treatments: background noise as a control, repeat calls, and digging calls, each lasting 30 min. Moreover, each playback trial included a 20-min habituation period to allow individuals to adjust to the experimental setup. Each playback session started with 30 min background noise, recorded in the same territory the previous day, followed by the habituation playback. Calls for the habituation period consisted of recorded repeat calls that were different from the repeat calls used during the repeat call treatment. This was necessary to ensure that the adults treated the speaker as a begging pup. After the habituation period, we played either the repeat call or digging call treatment first. We are aware that this was not a completely randomized design, but starting with the habituation and then switching to background noise might cause the group to lose habituation, rendering subsequent responses to playback of pup vocalizations hard to interpret. We decided that since background noise was merely a control, randomization was less important than the fact that animals were well habituated during the two randomized call type treatments; that is, we played repeat calls first four times and digging calls first four times. Whenever the focal subject found a prey item, we recorded whether it ate the item or took it to within 1 m of the loudspeaker and/or fed it to a pup. Since the likelihood of feeding a pup is also influenced by the size of the prey (Brotherton et al. 2001), we categorized every prey item found by a subject as either small, medium, or large. Prey items that did not protrude from an adult's mouth and had to be chewed only 1–5 times before swallowing were classified as small. Medium prey items required 5–15 chews and protruded less than halfway from the subject's mouth. All prey items exceeding these measures were considered to be large. We recorded every 30 s whether the subject was foraging, and we also noted when other group members approached to feed the loudspeaker.

Second, we tested whether high-pitched and repeat calls differed in their signal value. We used an experiment where seven female helpers, each from a different group, were offered a choice between two speakers. We simulated two begging pups, one of which was switched to high-pitched calls as soon as we presented the focal adult helper with a prey item (a scorpion, as above), whereas the other speaker continued to emit repeat calls. All calls within each experimental trial were from the same pup to exclude the

possibility that some individuals were preferred recipients of food items. Each of the two speakers was attached to one end of a 4-m pole. Before we started the experiment, we fed the chosen subject half of a boiled chicken egg. This ensured that the focal subject had a full stomach and was therefore more likely to feed the pup rather than eat the food itself, reducing the number of scorpions used in each trial. We waited until the subject was foraging and then followed it at a distance of 1.5–3 m. The person carrying the pole stood behind the subject so that the distance between the subject and each speaker was the same. The trial started with a 30-s playback of repeat calls of the same pup from both speakers. We then presented the subject with a scorpion and immediately switched one loudspeaker to playback of high-pitched calls, leaving the other emitting a new sequence of repeat calls, both recorded from the same pup. We noted whether the subject ate the prey item or approached to within 0.5 m of the loudspeaker carrying the scorpion in its mouth, as if attempting to feed the loudspeaker. Since helpers feed pups only around 20%–45% of found food items (Brotherton et al. 2001), we repeated the experiments until an individual approached and tried to feed one of the loudspeakers.

Statistical Analysis

Statistical tests were performed using R 2.2.0 (R Development Core Team 2005) and SPSS 12 (SPSS, Chicago). Mean values of all acoustic parameters for each call type of each individual were calculated and used in the subsequent "stepwise discriminant function analysis" in SPSS, in which we aimed to separate the three call types by minimizing Wilks's λ. In analyses of food allocation during playbacks, we controlled for the repeated sampling of the same individuals and, thus, the nonindependence of data points, using a mixed-effects model with "individual subject" fitted as a random factor (Crawley 2002). The response variable was binary; that is, a focal helper either fed the found food item or did not. Consequently, we fitted a generalized linear mixed model with a binomial error distribution using the "glmmPQL" function in R and fitted "size of found prey item" and "treatment" as explanatory terms and "individual identity" as a random term. Moreover, we investigated how playback treatments influenced the foraging behavior of adult subjects. We fitted "treatment" and "proportion of found food items fed" as explanatory terms and "individual identity" as a random term for each of them separately using the "lme" function in MASS (Venables and Ripley 2002). All interactions were nonsignificant and thus were deleted from the final models (Engqvist 2005). The number of feeds of other group members during the three treatments were analyzed with a Friedman test. All means are given ± 1 SE.

Results

Discriminant Function Analysis of Calls

Repeat, high-pitched, and digging calls all differed acoustically from one another. A stepwise discriminant function analysis using two functions correctly assigned 84.2% (identical results when using cross-validation) of 120 calls to their true type (Wilks's λ = 0.12, χ^2 = 245.1, df = 8, $P < .0001$; fig. 2), which is higher than that expected by chance (33.33%). The first function explained 92.0% of the explained variance and was positively related to call duration ($r = 0.98$), while the second function explained the remaining 8.0% of variance and was positively related to modulation (difference in fundamental frequency [fundamental frequency at end minus fundamental frequency at start]; $r = 0.76$). Repeat calls were most accurately discriminated, with 38/40 (95%) assigned correctly and two classified as high-pitched calls. High-pitched and digging calls were somewhat less accurately discriminated with 33/40 (82.5%) high-pitched calls correctly assigned and 7/40 classified as digging calls, while 30/40 (75%) digging calls were correctly assigned, with one classified as a repeat call and nine as high-pitched calls. Repeat calls were typically of long duration, almost three times as long as high-pitched or digging calls, and had a lower peak frequency,
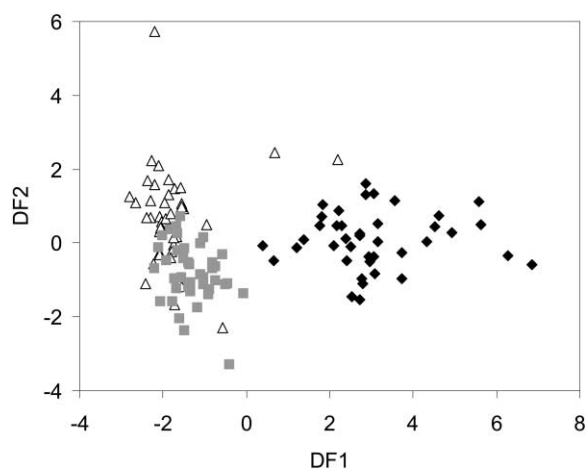
Figure 2: Plot of discriminant function scores of the three call types commonly given by meerkat pups. DF1 is positively related to syllable duration, while DF2 is positively related to modulation (difference in fundamental frequency [fundamental frequency at end minus fundamental frequency at start]). Diamonds = repeat calls; squares = high-pitched calls; triangles = digging calls.

Table 1: Mean values ± SE for the six call parameters used to separate the three call types of meerkat pups (*Suricata suricatta*)

Call Type	Duration (s)	Peak frequency (Hz)	Fundamental frequency (Hz)	Bandwidth (Hz)	Difference (Hz)	Entropy
Repeat	.39 ± .012	621 ± 22	443 ± 10	2,155 ± 66	22 ± 11	.40 ± .007
High-pitched	.14 ± .004	701 ± 25	451 ± 7	2,072 ± 60	60 ± 13	.39 ± .009
Digging	.13 ± .008	668 ± 25	446 ± 12	1,903 ± 80	177 ± 18	.36 ± .006

Note: $N = 40$ pups; 23 females, 17 males. Difference = difference in fundamental frequency (fundamental frequency at end minus fundamental frequency at start).

broader bandwidth, and lower modulation than either of the other two call types (table 1; fig. 2).

Effect of Social Context on Call Types Used by Pups

The use of the three call types by pups differed significantly between the different social contexts in which food was presented (fig. 3; χ^2 test: $\chi^2 = 62.76$, df = 4, $P < .001$). When the pups were alone, they mainly gave repeat calls; when a helper was close by, pups mainly emitted high-pitched calls, and when another pup was close by, they typically emitted an aggressive growl or engaged in a short physical competition.

Food Allocation during Repeat and Digging Call Playback

Adult subjects provided significantly more of their prey items to pups when hearing the repeat call than the digging call or background noise playback (fig. 4; $F = 16.32$, df = 1, 15, $P < .001$). Our results confirmed previous findings (Brotherton et al. 2001) that larger prey items were more likely to be fed than small items ($F = 10.72$, df = 1, 15, $P = .0013$). Furthermore, not only did the focal subject donate more food during the repeat call playbacks, but other group members also provided significantly more food items to the loudspeaker during the repeat call treatment than during the digging call and background noise treatments (mean number of feeds to repeat calls: 4.13 ± 1.5; digging calls: 1.13 ± 0.74; background noise: 0 ± 0; Friedman test: $N = 8$, df = 2, $\chi^2 = 8.82$, $P = .012$).

Adult subjects spent more time foraging during the repeat call treatment than during the background and digging call treatments (repeat call: 78.33% ± 5.37%; digging call: 59.58% ± 6.11%; background noise: 66.04% ± 5.83%; $F = 4.44$, df = 1, 13, $P = .034$). However, the amount of time that an individual spent foraging was not influenced by the proportion of food fed to a pup ($F = 1.78$, df = 1, 13, $P = .20$), suggesting that helpers are stimulated to increase foraging when a pup is constantly emitting repeat calls.

### Food Allocation during Repeat and High-Pitched Call Playback

In the seven successful choice tests, all females "fed" the loudspeaker broadcasting high-pitched calls rather than the one broadcasting repeat calls (mean ± SE of scorpions presented to individuals per experimental trial: 3.7 ± 0.64, range: 1–6; binomial test, 7 trials, $P = .016$).

Discussion

Meerkat pups utilize a repertoire of begging calls that differ in their acoustic structure, and they give these different calls according to the social context in which they find themselves. Furthermore, potential providers vary food allocation according to the specific call type that a pup emits.

One possible explanation for the evolution of a repertoire of begging calls in meerkats is that it reflects an adaptation to their mobile feeding system (Manser and Avey 2000). In contrast to stationary systems, where the young are fed in the nest, the young in a mobile system can receive food not only when a potential feeder with food approaches them but also when they follow a potential feeder. In stationary systems, the offspring have only marginal immediate influence on the feeding decision when the feeder finds food, because the offspring cannot follow the feeder physically. However, a feeder's decision might well be influenced by the experience of begging during the last visit to the nest. In a mobile system, however, the adult that discovers a food item can either eat the item or donate it to begging young. A pup therefore benefits from (1) persuading the adult to refrain from eating the food item at the crucial moment when a prey item is found, (2) indicating its own current location to the adult, and, in addition, (3) ensuring that itself, rather than another littermate in the vicinity, is fed by the adult.

Why do these three functions require different types of begging calls? One explanation is that the adults are fine-tuned in their response to pup begging as a result of ongoing adult-offspring conflict over the level of care expended on pups. Honest signaling models predict that providers should base provisioning decisions on honest information provided by pups, preferentially feeding hun-
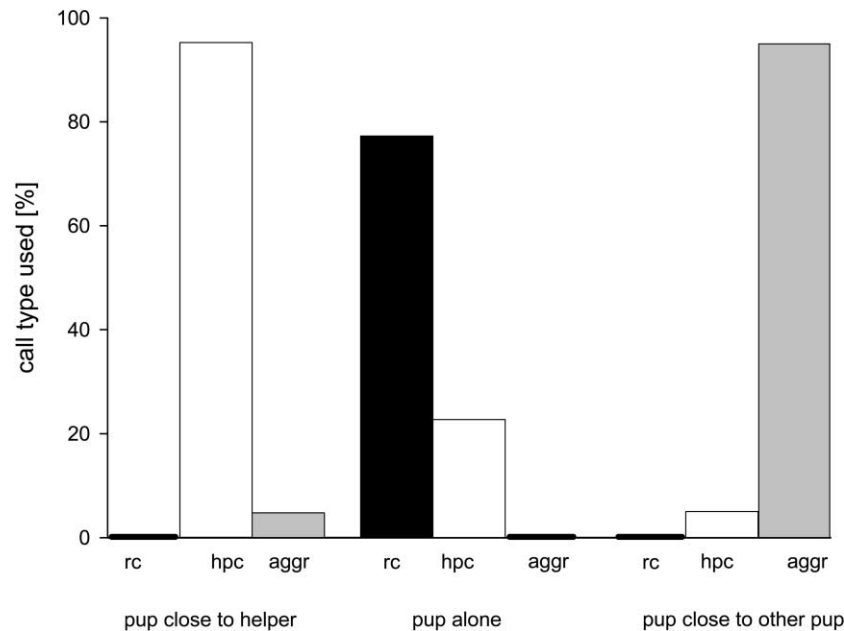
Figure 3: Call type emitted by meerkat pups after presenting them a scorpion in three different contexts: when a helper was close by, that is, within a range of <1 m but with no other pup within a range of 3 m; when it was alone, that is, no helper or other pup was present within a range of 3 m; and when another pup was close by, that is, within a range of <1 m but with no helper within a range of 3 m (rc = repeat call, hpc = high-pitched call, aggr = aggressive growl; $N = 22$ for each presentation).

grier pups and eating the food item if no pup is sufficiently hungry. The honesty of begging calls could be maintained by the physiological cost of giving or exaggerating the call. Such costs could be manifested in a change in begging rate, with calls given at a faster rate being energetically more costly to produce. A relationship between hunger levels and begging intensity has been found in several species of birds (Wright and Leonard 2002). The high-pitched calls of meerkat pups involve the rapid production of calls in a quick series with only short intervals between single calls. Consequently, call rates of high-pitched calls might be higher than those of repeat calls (Kalahari Meerkat Project, unpublished data; http://www.kalahari-meerkats .com).

The question arises of why meerkat pups do not continuously emit high-pitched calls. High-pitched calls might be potentially energetically expensive; this could be the case, because watching the meerkat pups, it is possible to see their chests vibrating violently as they give these calls (H. P. Kunc and J. R. Madden, personal observation). Therefore, given that feeding events occur only a few times per hour, a pup may not be able to sustain such high-pitched calling between events. Instead, pups give such conspicuous but potentially costly calls only when they observe that an adult found a food item. When we mimicked this situation, we found that pups presented with a food item in the presence of a helper were most likely to give high-pitched calls, suggesting that high-pitched calls were particularly attractive to adults. Furthermore, pups may also use additional strategies to ensure that food is delivered to them rather than to littermates; when focal pups were presented with food in the presence of a littermate, they stopped giving begging calls and instead gave an aggressive growl and engaged in direct competition over access to the helper and food (see also Hodge et al., forthcoming).

Adults providing prey to a pup are more likely to feed the offspring emitting high-pitched calls than the offspring emitting repeat calls, yet repeat calls are given almost continuously by begging pups. We showed that repeat calls are given when the pup is not close to another pup and that repeat calls induced adults to engage in higher levels of foraging than the playback of digging calls and background noise. Repeat calls can induce an elevation of cortisol levels in adult male meerkats, and individual contributions to pup feeding were positively correlated with levels of plasma cortisol (Carlson et al. 2006). By giving repeat calls, pups may influence adult physiology such that they provision pups at a high rate.

Repeat calls may serve a second function. They provide a constant aural cue to the location of the pup. While pups usually follow one adult for prolonged periods, there are
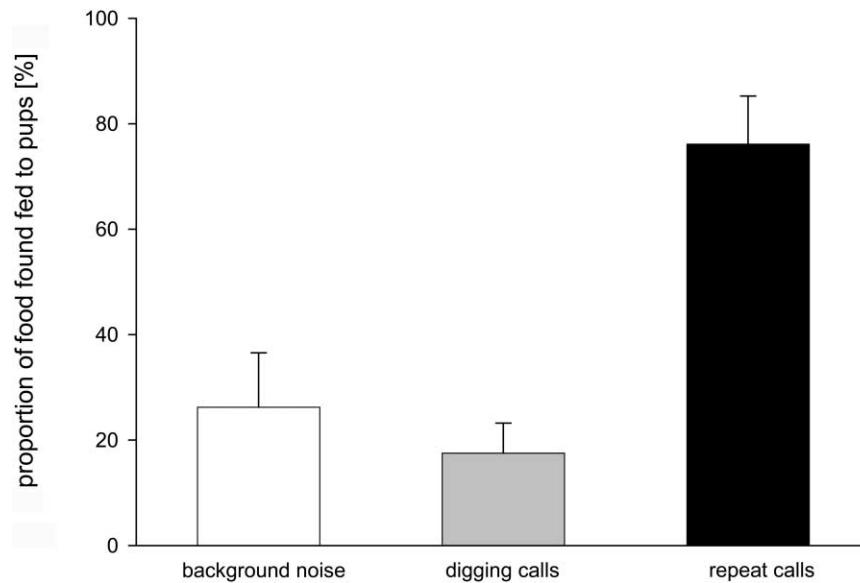
Figure 4: Mean ± SE percentage of found food by a helper fed to pups during 30 min of broadcasting background noise, repeat calls, and digging calls (eight subjects from eight different groups).

often other foraging adults within the group who do not have a pup in attendance. These adults can also provision pups if they find a food item, and they will benefit from reduced search costs and thus be more likely to donate an item if they can easily and rapidly locate a pup. Adults typically feed the nearest pup (Brotherton et al. 2001), suggesting that they seldom make a comparative assessment of pup need but instead simply deliver food to the first pup that they encounter. If the pup gives constant conspicuous calls, it increases its chance of being located by an adult with a food item.

Digging calls do not induce adults to increase their levels of foraging nor do they attract as high levels of provisioning as repeat calls do. So why do meerkat pups continue to give digging calls? We suggest that, like repeat calls, digging calls indicate a pup's presence. Digging calls did not provoke levels of provisioning as high as those seen during playback of repeat calls, but they did provoke higher levels of provisioning by other group members than that provoked by background noise. Therefore, foraging pups may be able to attract the attention of helpers and obtain some level of feeding by producing digging calls. However, if this is the case, why would foraging pups not give repeat calls? We suggest that the action of digging might prevent pups from giving the more beneficial repeat calls, and instead, pups, digging vigorously with their faces oriented downward, are able to produce only the shorter digging calls. By placing themselves close to a potential feeder and digging for food, a pup may optimize its food

intake. It may find its own prey but remain audible to a nearby feeder, attracting the adult toward it if the adult finds food.

Are meerkats unusual in having a range of different begging calls that are adapted for different scenarios? We may expect that in any scenario in which offspring begging both drives parental foraging and mediates competition by determining the individual allocation of food, offspring will face two different selection pressures driving the evolution of begging calls. This can be resolved in one of two ways: either a single call type both provokes parental foraging and provides sufficient information to allow adults to decide where to allocate the food, or different begging calls develop that are more effective than others in a specific context. We expect that these conditions apply in any species in which the young are found alongside foraging adults and are dependent on them for food.

To conclude, we found that begging meerkat pups adjusted their use of different call types depending on context, and potential receivers adjusted their food allocation in response to the call type. Pups gave the most vigorous high-pitched calls when they saw adults in the presence of food, and the adults preferred to "feed" speakers broadcasting these calls. Pups continuously gave repeat calls when they accompanied foraging adults, and this induced increased provisioning by the adults in general and deterred other pups from approaching. Pups also foraged for themselves, digging for food items, and while doing so, produced digging calls, which were less efficient at solic-

iting feeding than the other call types. If a pup was close to another pup and in the presence of a food item, it ceased giving begging calls and instead vocalized aggressively toward the other pup and frequently engaged in violent conflict. The evolution of a repertoire of begging calls in a mobile feeding system might reflect an adaptation to a situation where dependent young must solicit food from potential feeders while at the same time directing feeders to bring the prey item to themselves and not to another begging pup. Therefore, we predict that in cases with mobile feeding systems, such as precocial birds or in postfledging feeding of altricial birds, offspring will give a wider repertoire of food solicitation calls than seen in commonly investigated nest-based begging systems.

Acknowledgments

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