



Offspring competition and helper associations in cooperative meerkats

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In cooperatively breeding vertebrates, helpers commonly vary in how much care they provide. We investigated whether meerkat, *Suricata suricatta*, pups responded to variation in helper feeding rates by associating with the most productive helpers preferentially throughout the period of pup care. Helpers varied widely in how much food they provided, and pup food intake increased with the time spent in exclusive association with productive helpers. Pups spent more time following productive helpers than poor helpers, and we confirmed the causality of this finding by conducting long-term feeding experiments which increased helper productivity and showed that pups spent significantly more time with helpers whose feeding rate had been experimentally raised. Pups aggressively defended helpers from approaches by littermates, but there was no evidence that pups defended productive helpers more strongly, or that larger pups were more likely to gain exclusive access to the most productive helpers. Our results provide evidence that, by associating with particular helpers, meerkat pups can influence how much care they receive during development. These findings highlight the importance of considering the behaviour of offspring, when investigating the way care is distributed in cooperative societies.

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In cooperatively breeding vertebrates, where helpers assist parents in rearing young, helpers commonly vary markedly in how much care they provide (Cockburn 1998; Cant & Field 2001). Although a number of studies have investigated the causes of variation in helping effort (reviewed in Komdeur 2006), less attention has been focused on the consequences that this variation may have for the way care is distributed among offspring in cooperative societies. Offspring are likely to benefit from adopting behaviours that increase their chances of receiving care, such as begging more intensely when a good helper is close by, or competing to monopolize access to the best feeders, which could have important ramifications for the way that resources are divided. As yet, however, we know

little about whether offspring are able to recognize good helpers, or whether they modify their behaviour in response to variation in helper quality.

Our understanding of how offspring respond to variation in helper quality is limited, in part, by the difficulties of following offspring once they have left the nest or den. Most studies of cooperative species have been conducted on nesting birds (Stacey & Koenig 1990; Koenig & Dickinson 2004) where helpers usually return to the nest only when they have found a food item, so chicks have little opportunity to take advantage of variation in helper feeding rates. Once offspring have left the nest or den, however, and are able to move freely, it may be beneficial to follow the most productive helpers closely, particularly as helpers commonly provide food to the closest begging offspring (Ostreiher 1997; Brotherton et al. 2001). There is evidence from some cooperatively breeding species that offspring do follow individual helpers closely once they have left the nest or den, forming short-term (e.g. McGowan & Woolfenden 1990; Langen & Vehrencamp 1999) and, in some cases, long-term associations with particular

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individuals (e.g. Byle 1990; Leedman & Magrath 2003; Hodge 2005). However, we know little about how these associations form, or whether offspring preferentially associate with the best helpers. This is unfortunate, as food provisioning during the latter part of development can be higher than when young are confined to the nest or den (McGowan & Woolfenden 1990; Langen 2000; Leedman & Magrath 2003) and offspring behaviour during this period may therefore strongly influence offspring survival and eventual breeding success (Lindstrom 1999).

We investigated associations between meerkat pups and helpers during the period when pups have left the breeding burrow and are able to move freely. Meerkats, *Suricata suricatta*, are small, diurnal cooperative mongooses that live in groups of 2–50 in the arid regions of southern Africa (Doolan & Macdonald 1996; Clutton-Brock et al. 1999a). An average litter consists of four pups (range 1–7), which leave the natal burrow at around 30 days and accompany the group on foraging trips. Until they can feed independently (at around 3 months of age) they move between helpers who supply them with small, nonshareable prey items, mainly burrowing invertebrates (Brotherton et al. 2001). Helpers usually provide food to the closest begging pup (Brotherton et al. 2001) and, as helpers vary in the amount that they feed (Clutton-Brock et al. 2001a), pups are likely to increase their food intake by closely following the most productive individuals and aggressively defending them against approaches from littermates. As early food intake improves survival and subsequent reproductive success (Russell et al. 2007) the benefits of successfully defending the best helpers are likely to be high.

Using data from our long-term meerkat study, we asked five specific questions. (1) How much do helper feeding contributions vary during the pup-feeding period? (2) Are pups likely to benefit from associating with productive helpers? (3) Do pups spend more time with productive helpers? (4) Do pups compete for access to productive helpers? (5) Are larger pups more likely to secure access to productive helpers?

METHODS

Study Site and Population

We collected data between June 1999 and May 2005 from a free-ranging population of meerkats living in 16 social groups on ranchland in the South African Kalahari (26°58'S, 21°49'E). A detailed description of habitat and climate at the study site is provided elsewhere (Russell et al. 2002). All individuals in our study population were habituated to close observation and could be followed on foot from less than 1 m (Clutton-Brock et al. 1998). Individuals could be easily identified in the field by a combination of unique dye marks, which were applied while the meerkats were sunning in the morning without the need for capture. Groups were visited approximately every 3 days to collect behavioural and life history data and, as a result, the ages of most pups (>98%) were known within 5 days. Pups were sexed soon after emergence from the natal burrow

(at approximately 30 days). Most group members were trained to step on to a portable electronic balance from a young age, in return for a small reward of hardboiled egg (Clutton-Brock et al. 1998), and we were therefore able to collect regular weights for over 95% of the study population. All weights used in this study were collected in the morning prior to foraging. Individuals were classified as pups until they were 3 months of age and could forage independently. We refer to all subordinate group members over the age of 3 months as helpers, although contributions by individuals of less than 6 months are generally small (Clutton-Brock et al. 2001a, b). All research protocols were approved by the University of Pretoria Ethics Committee.

Data Collection

We refer to the period when dependent pups are foraging with the group as the 'pup-feeding period'. During the pup-feeding period we assessed variation in helper feeding rate by conducting continuous 20-min focal watches on helpers, in which we recorded all food items found and all food items fed to pups. Full details of the types of prey items eaten by pups are provided by Brotherton et al. (2001). Focal watches were paused if the focal individual engaged in behaviours other than foraging, and therefore provide an absolute rate of pup feeding while foraging. We conducted 3712 focal watches on 303 helpers in 98 litters in 12 groups between June 1999 and November 2001. From March 2004 to May 2005, we also conducted 478 continuous 20-min focal watches on 72 pups from 25 litters in 13 groups in which we recorded the time that the focal pup spent within 2 m of each helper and within 2 m of each littermate, all food items given to the focal pup and the identity of the feeder, and all aggressive interactions involving the focal pup. For each aggressive interaction, we noted the identity of both pups, the severity of the interaction, the cause of aggression (food or helper) and the identity of the winner, if known. Aggressive interactions fell into two main classes of severity: 'mild' aggression, where the aggressor either growled, piloerected or briefly snapped at an approaching pup; and 'severe' aggression where two pups actively fought and grappled with one another. The winner was defined as the pup that remained within 1 m of the cause of competition at the end of the interaction. If the winner was known, we also recorded whether the winner was the original owner (i.e. the pup that was following the helper/eating the food item before aggression took place). We included data only from litters where more than one pup foraged and excluded litters where more than one female gave birth; all littermates therefore had the same mother and were born on the same day. In addition to focal watches, we recorded all occasions when an adult fed a pup, and all incidences of aggressive competition between pups ad libitum (Altmann 1978). Ad libitum data were collected from 580 pups from 140 litters in 16 groups between June 1999 and May 2005. As not all types of data were available for all litters, sample sizes vary between analyses.

Statistical Analysis

For analyses we used Minitab 13 (Minitab Inc., State College, PA, U.S.A.) unless multivariate statistics were required, in which case we used Genstat 5.4.2 (Lawes Agricultural Trust, Rothamsted, Harpenden, U.K.). As most multivariate analyses involved repeated sampling of individuals, litters or groups we used linear mixed models (LMMs). These are similar to general linear models, but allow both fixed and random terms to be included. In all mixed models, variance components were estimated with the restricted maximum likelihood (REML) method, and random terms were retained in the model unless the variance component was found to be zero. In each model, all potential explanatory terms were entered and dropped sequentially until only those terms that explained significant variation remained. Each dropped term was then put back into the minimal model to obtain its level of nonsignificance and to check that significant terms had not been wrongly excluded. All two-way interactions were tested, but results are presented only if found to explain significant variation. All statistical tests were two tailed. Unless otherwise stated, means are quoted ± 1 SE.

Helper feeding contributions

To assess variation in the contribution of helpers to feeding pups within a litter, we used helper focal watches to investigate (1) the rate at which helpers fed pups/h in each litter and (2) the proportion of food items found that helpers gave away per litter. This analysis included focal watches conducted when pups were 40–60 days of age, as during this period, pup age has no significant influence on the rate at which pups are fed (LMM controlling for pup identity: $\chi^2_1 = 0.07$, $N = 105$ focal watches on 61 pups, $P = 0.79$).

Benefits of associating with productive helpers

We began by investigating whether the proportion of time pups spent with a helper influenced the overall rate of food intake during the feeding period. We calculated the mean number of food items that each pup received/h during pup focal watches conducted between 40 and 60 days of age. The feeding rates of 43 pups from 12 litters in nine groups were log transformed and fitted as the normally distributed response term in an LMM. To investigate whether the ‘time spent alone with a helper’ (i.e. when no other pup was within 2 m) was more important than the ‘time spent with a helper per se’ (i.e. including times when other pups were also within 2 m) we fitted both terms separately into two identical LMMs. In each model, rainfall during the peak feeding period (mm), mean helper-to-pup ratio, pup sex and pup weight at emergence relative to the litter mean were included as potential explanatory terms. Litter and group identity were included in the model as random terms. To assess whether pups were fed more when alone with productive or with poor helpers, we calculated the average rate that pups were fed when alone with productive or with poor helpers per focal watch. The values for multiple focal watches on the same pup were averaged and compared.

Time with productive helpers

To obtain a measure of the relative productivity of each helper in litters where pup focal watches were conducted, we used ad libitum pup feed data to calculate the total number of times each helper fed a pup a food item in the 7 days prior to the day of the pup focal watch (which provides a proxy for helper quality on the day the focal watch was conducted). This was subtracted from the mean feeding rate of all helpers of that group in that week. Helpers were classified as ‘productive’ if their feeding contribution was above average in the previous week and ‘poor’ if their feeding contribution was below average in the previous week. Relative feeding contributions were calculated only for helpers that were present in the group on all observation days in the week prior to the day of the pup focal watch, and were collected only in litters where helpers did not differ in habituation levels (to avoid biases arising from variation in the ease with which different individuals could be observed).

To investigate whether pups spent more time with productive helpers during the pup-feeding period, we conducted three separate analyses. First, for each focal watch, we compared the average time that pups spent within 2 m of productive and poor helpers before switching (‘association bout duration’). Second, we compared the proportion of each focal watch that pups spent within 2 m of the most productive helper (i.e. the helper that fed the most in the previous week) and least productive helper (i.e. the helper that fed the least in the previous week). For both analyses, the values for multiple focal watches on the same pup were averaged and compared.

A correlation between pup association patterns and helper productivity does not necessarily mean that pups preferentially associate with productive helpers, however, as this correlation could also arise if helpers simply feed more when pups are close by for other reasons. To test the causality of any correlation, we conducted a manipulation experiment in which helper productivity was experimentally raised by supplemental feeding throughout the period of care. Meerkats eat bird and reptile eggs naturally when available, and feeding individuals with boiled hens’ eggs substantially increases the amount of care that they provide (Clutton-Brock et al. 1999b, 2000, 2001a). We fed 17 helpers with 25 g of hardboiled egg per day throughout the pup-feeding period which significantly increased the proportion of food items fed to pups in comparison to unfed matched controls (paired t test: $t_{16} = 2.40$, $N = 17$ pairs, $P = 0.029$). When experimental animals had been fed for at least 2 weeks, we conducted instantaneous scans on all pups in the litter every 5 min in which we recorded whether the pup was within 2 m of either the experimental or control individual. Scans were collected until pups were 60 days old and were collected only when experimental and control individuals were actively foraging. A minimum of 40 scans were collected on each pup in each experiment. To investigate whether pups spent more time associating with helpers whose productivity had been experimentally increased, we compared the proportion of scans that pups spent with experimentally fed helpers with that spent with unfed controls.

We also considered the factors that influenced the average association bout duration during each focal watch by fitting the log-transformed association bout duration as the response term in an LMM in which pup age, helper-to-pup ratio, rainfall in the previous 30 days, pup sex and pup weight relative to the litter mean on the day of the focal watch were included as potential explanatory terms. Pup and litter identity were included in the model as random terms, but group identity was excluded as the variance component was zero. This analysis was based on a sample of 101 focal watches on 25 foraging pups in seven litters.

Competition between pups

To investigate whether pups competed more for productive helpers, we compared the number of times that pups competed over productive helpers per focal watch, with the number of times they competed over poor helpers. The values for multiple focal watches on the same pup were averaged and compared.

Advantages of pup size

To investigate whether larger pups were more likely to win aggressive interactions, we considered all cases of aggression within pup dyads in which a full fight developed. Minor aggressive interactions were excluded as one pup might not have been actively competing (for example, if it was snapped at while walking past a littermate). For 57 pup dyads in 16 litters in 11 groups in which severe aggression occurred, we tested whether the proportion of interactions in which the heaviest pup won was significantly greater than 0.5, using a one-sample *t* test.

To investigate whether pup size influenced the time they spent with productive helpers, we classified pups as 'large' or 'small' according to their relative size in relation to the rest of the litter at first emergence from the natal den (i.e. before they began foraging with the group). Pups that were >5 g heavier than average at emergence were classified as 'large' and pups that were >5 g lighter than average at emergence were classified as 'small'. The mean proportion of time that large and small pups spent with productive helpers and the mean food intake of large and small pups throughout the pup-feeding period were averaged and compared within litters. We also calculated the growth rate (g/day) of pups by taking the gradient of the linear regression between pup weight and pup age during the pup-feeding period. Growth rates were calculated only if pups were weighed more than four times during this period. The growth rates of large and small pups were compared within litters. As weight data were available for pups from 1999, while pup-feeding and association data were available only from 2004, the sample size of litters with large and small pups differs between analyses.

RESULTS

Helper Feeding Contributions

The contribution that different helpers made to pup feeding was highly variable both within and between

litters. The average feeding rate per litter ranged from 0.16 to 6.18 food items/h with a mean \pm SD of 1.29 ± 1.32 , and the average percentage of food items found that were fed to pups ranged from 1.30 to 19.45% with a mean \pm SD of $5.74 \pm 5.32\%$. Within each litter, some helpers did not feed pups at all, while the contribution of the best helper per litter was over seven times higher than average. The best helpers in each litter fed a mean \pm SD of 8.09 ± 5.99 food items/h and gave away a mean \pm SD of $41.94 \pm 30.38\%$ of food items found.

Benefits of Associating with Productive Helpers

The average rate at which pups were fed was not significantly influenced by the time they spent with helpers per se (LMM: $\chi^2_1 = 1.99$, $P = 0.16$), but increased significantly with the time they spent alone with a helper (i.e. when no other pup was within 2 m; Fig. 1, Table 1). None of the other terms included in the model had any significant influence on the rate at which pups were fed (Table 1). Pups were fed at a significantly higher rate when they were alone with a productive helper than when they were alone with a poor helper (paired *t* test: $t_{73} = 3.35$, $N = 74$ pups, $P < 0.001$; Fig. 2).

Time with Productive Helpers

Pups changed helpers frequently, typically remaining with each helper for 88 s on average, although this was highly variable, ranging from a few seconds to over 6 min. The duration of each association bout was related to helper quality and the number of helpers available per pup. Pups remained longer with relatively productive helpers than with relatively poor helpers (productive helpers: median \pm IQR = 1.23 ± 0.37 , 0.80 min; poor helpers: 0.97 ± 0.18 , 0.45 min; Wilcoxon signed-ranks test: $W = 2659.0$, $N = 83$ pups, $P < 0.001$) and when the number of helpers per pup was high, pups moved rapidly between helpers, spending less time with each one (LMM: Fig. 3, Table 2). None of the other terms included in the model

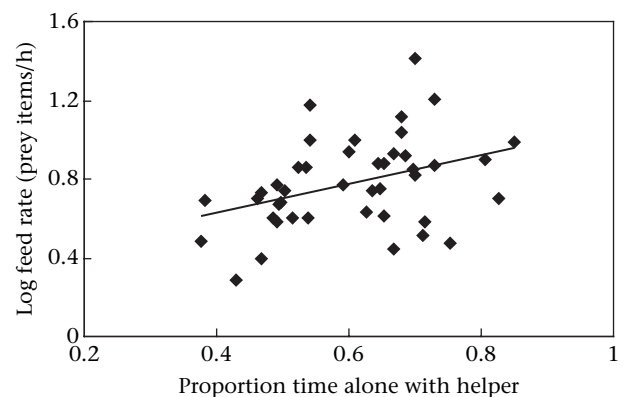


Figure 1. The influence of the proportion of time that pups spent alone with a helper on the rate at which they were fed throughout the pup-feeding period. $N = 43$ pups.

Table 1. Factors affecting the mean rate at which pups were fed during the peak pup-feeding period (linear mixed model)

Explanatory terms	Log mean rate of food intake (feeds/h)		Wald statistic (χ^2)	P
	Effect size	SE		
Mean time alone with helper	0.63	0.25	6.06	0.014
Rainfall	0.0043	0.0034	1.59	0.21
Pup sex				
Female	0	0	0.66	0.42
Male	-0.046	0.057		
Relative weight*	-0.0028	0.003	0.61	0.44
Helper-to-pup ratio	0.017	0.024	0.50	0.48
Constant	0.78	0.050		

Significant P value is highlighted in bold. Litter and group identity were included as random terms.

*Relative weight refers to the weight of the pup at first emergence from the natal den, relative to the litter mean.

had any significant influence on association bout duration (Table 2).

Overall, pups associated with the most productive helper in the group for a significantly greater proportion of foraging time than with the least productive helper (paired t test: $t_{69} = 3.63$, $N = 70$ pups, $P = 0.001$; Fig. 4a). Experimentally increasing the productivity of helpers confirmed this finding and showed that pups spent a greater proportion of scans associating with fed helpers than unfed controls ($t_{16} = 3.10$, $N = 17$, $P = 0.007$; Fig. 4b).

Competition Between Pups

Pups competed aggressively for access to helpers. Of 3591 observed aggressive interactions, 96% involved a pup defending a helper, and only 4% were over access to a food item. Most aggression over helpers was ‘mild’ (57%), but 43% of interactions involved a full fight and were classified as ‘severe’. Pups were involved in

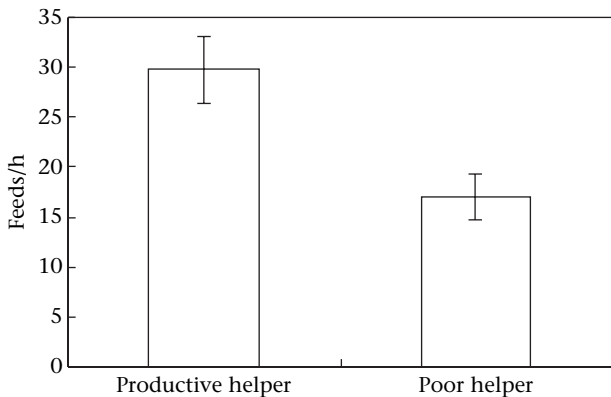


Figure 2. The mean rate \pm SE at which pups were fed when foraging with productive and poor helpers. $N = 74$ pups.

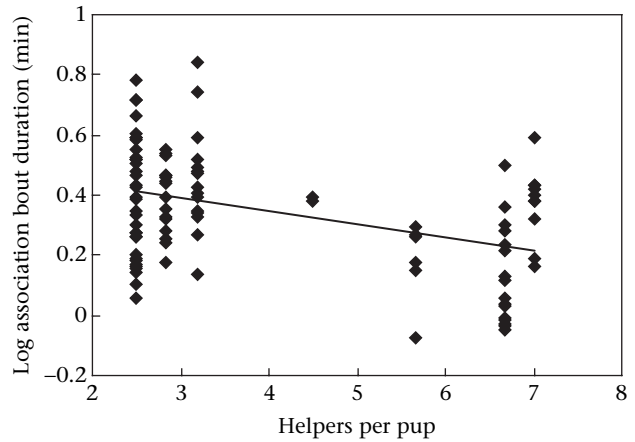


Figure 3. The influence of helper-to-pup ratio on mean association bout duration per focal watch. Data are from 101 focal watches on 25 foraging pups in seven litters.

a mean \pm SD of 3.39 ± 4.10 aggressive interactions/h during the peak pup-feeding period (range 0–23.47). There was no evidence that pups defended productive helpers more strongly than poor helpers (productive helpers: median \pm IQR = 0.00 ± 0.00 , 14.7 interactions/h; poor helpers: 3.28 ± 2.51 , 6.73 interactions/h; Wilcoxon signed-ranks test: $W = 533.0$, $N = 63$ pups, $P = 0.16$).

Advantages of Pup Size

Within litters, large pups were no more likely to initiate aggressive interactions than small pups (large pups: median \pm IQR = 0.38 ± 0.38 , 1.47 interactions/h; small pups: 0.86 ± 0.86 , 1.24 interactions/h; Wilcoxon signed-ranks test: $W = -26.0$, $N = 13$ litters, $P = 0.72$). Within each pup dyad, on average, heavier pups won severe aggression on $50.5 \pm 1.1\%$ of occasions, which does not differ significantly from the number of wins that would be

Table 2. Factors affecting the mean association bout duration per focal watch (linear mixed model)

Explanatory terms	Log mean association bout duration (min)		Wald statistic (χ^2)	P
	Effect size	SE		
Helper-to-pup ratio	-0.043	0.021	4.08	0.045
Rainfall	-0.00038	0.0055	0.47	0.49
Pup sex				
Female	0	0	0.42	0.52
Male	-0.025	0.039		
Relative weight*	-0.00074	0.0018	0.17	0.68
Pup age	-0.00044	0.0012	0.13	0.71
Constant	0.35	0.040		

Significant P value is highlighted in bold. Pup and litter identity were included as random terms.

*Relative weight refers to the weight of the pup on the morning of the focal watch, relative to the litter mean.

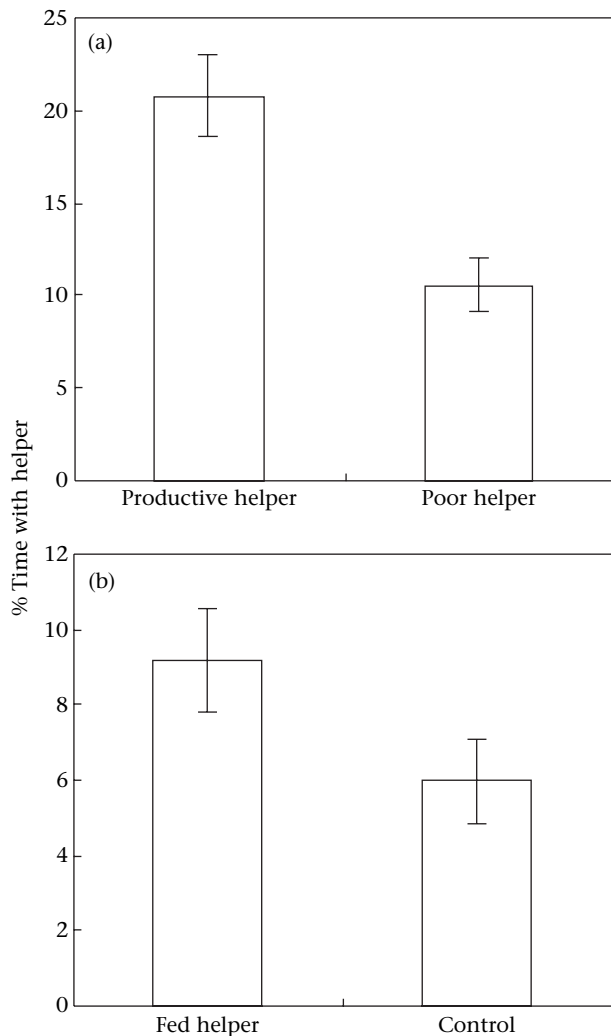


Figure 4. Comparison of (a) mean % of focal time \pm SE that pups were within 2 m of productive and poor helpers ($N = 70$ pups) and (b) the mean % of scans \pm SE that pups were within 2 m of experimentally fed helpers and unfed matched controls ($N = 17$ pairs).

expected by chance (one-sample t test: $t_{56} = 0.31$, $N = 57$, $P = 0.76$). Instead, the probability of winning a competitive interaction was influenced by whether the winner was the original owner; original owners won serious aggressive interactions in 88.6% of cases. The proportion of feeds won by original owners did not differ when there were more than two helpers per pup (16.9%) or when there were fewer than two helpers per pup (15.0%; chi-square test: $\chi^2_1 = 0.32$, $P = 0.57$).

There was no significant difference in the proportion of observation time that relatively large and small littermates spent with productive helpers (large pups: 0.23 ± 0.05 ; small pups: 0.20 ± 0.05 ; paired t test: $t_{13} = -1.0$, $N = 14$ litters, $P = 0.34$). Larger pups did not receive more food/h than their smaller littermates (large pups: median \pm IQR = 14.16 ± 4.72 , 13.74 feeds/h; small pups: 14.55 ± 5.94 , 9.56 feeds/h; Wilcoxon signed-ranks test: $W = 49.0$, $N = 13$ litters, $P = 0.83$) and they grew at similar rates to relatively small pups within the litter (large

pups: 3.28 ± 0.10 g/day; small pups: 3.27 ± 0.11 g/day; paired t test: $t_{55} = 0.18$, $N = 56$ litters, $P = 0.86$).

DISCUSSION

Our results show that meerkat helpers varied widely in the amount they fed to pups, and pups responded to this variation by following productive helpers closely throughout the period of dependence. Pups aggressively defended helpers from approaches by littermates and pups that spent more time alone with productive helpers received more food during the pup period. These findings suggest that meerkat pups are able to respond to variation in helper productivity by adopting tactics that maximize their food intake during development, which is likely to have important consequences for their survival and future breeding success (Lindstrom 1999).

As meerkat pups received more food when following productive helpers, it is surprising that they did not form long-term associations with the best feeders; instead they switched helpers frequently, spending only a few minutes with a helper in each association bout. One possible explanation is that, as there are many helpers in meerkat groups, pups receive more food overall by exploiting multiple feeders than by following one productive individual continuously. The costs of switching helpers (such as increased predation risk and reduced feeding rate when alone) are also likely to be relatively low if pups are likely to find another helper quickly. The idea that switching helpers is beneficial when multiple helpers are present is supported by the finding that meerkat pups remained longer with each helper when the number of helpers in the group was low. This may also explain why 'brood division', where offspring form permanent associations with one individual (Harper et al. 1993), is common in species with biparental care, but seems to be less widespread in cooperative societies with multiple helpers (McGowan & Woolfenden 1990; Stacey & Koenig 1990). However, in at least one cooperative species with multiple helpers (the banded mongoose, *Mungos mungo*), pups commonly form long-term associations with particular individuals (Hodge 2005). In this species, some helpers appear to be able to meet the nutritional needs of both themselves and a pup, so pups are unlikely to benefit from switching between helpers (Hodge 2003). Thus, we might predict that offspring in cooperative societies will form short-term associations with helpers when the number of helpers is high, or when individual helpers are unable to meet the nutritional needs of offspring alone, but form long-term associations if there are few helpers in the group or if helpers are particularly productive.

The amount of food that pups received during development depended not on how much time they spent with a helper per se, but on how much time they spent with a helper when no other pups were close by. This suggests that it is not enough simply to follow the best helpers; pups must also ensure that no littermate is close by or risk a food item being given to a littermate rather than themselves. Pups aggressively attacked any littermate that approached their current helper, suggesting that

aggression is important for facilitating spacing between pups. However, we found no evidence that pups were more aggressive when following a productive helper than when following a poor helper. This may be because, although helpers usually feed the closest pup, they occasionally carry food items large distances (>20 m) if no pup is close by (Brotherton et al. 2001). Pups may therefore be fed by individuals in the group other than their current helper, so tolerating a littermate in close proximity may be costly, even when the closest helper is unlikely to feed them.

As pup competition is important for helping pups secure exclusive access to helpers, we might expect larger pups to have a competitive advantage over their smaller littermates. In nestling birds, larger chicks commonly out-compete their siblings for access to food (Mock & Parker 1997; Ostreiher 1997; Legge 2000; Wright & Leonard 2002) and in species with brood division, there is some evidence that larger offspring associate with the most productive feeders (Leedman & Magrath 2003). However, we found no evidence that larger pups were more likely to win competitive interactions; instead, competitive interactions were almost invariably won by the pup that was originally associating with the helper. Size advantages in competition may be difficult to detect if smaller pups avoided larger pups as a result of subtle aggressive behaviours, or because they were 'trained' to accept a subordinate role through losing previous interactions (Drummond 2006). However, this is unlikely to be the case in meerkats, as we found no evidence that larger pups spent more time with productive helpers, which we might expect if larger pups had an advantage in competition. Theory predicts that original owners will win competitive interactions when the costs of fighting are higher than the benefits of winning (Maynard Smith & Parker 1976). This may explain the lack of size advantage in competition in meerkats, as contesting pups are unlikely to remain long with helpers even if they win, so the benefits of successfully taking over a helper who already has a pup (and has therefore been 'depleted') are likely to be low in relation to the costs of fighting. Size advantages in competition may be more common in species where the benefits of winning are very high, such as those where food limitation commonly results in brood reduction (Lack 1947).

Our results show that by associating with productive helpers, meerkat pups can increase their food intake during development. These findings highlight the importance of considering the tactics that offspring use to maximize the amount of care they receive in cooperative societies. It is likely that helper tactics also influence the distribution of resources, as helpers are likely to gain differential fitness benefits depending on which offspring they care for. For example, helpers may derive greater inclusive fitness benefits from preferentially caring for close relatives (Hamilton 1964) or by helping the sex with which they are most likely to associate in the future (Woolfenden & Fitzpatrick 1984; Clutton-Brock et al. 2002). Further exploration of the tactics that both helpers and offspring use to influence the way care is allocated, and the conflict between them, may prove a rewarding area of future research in cooperative societies.

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