

Food limitation increases aggression in juvenile meerkats

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Both the rate and severity of sibling aggression are predicted to be higher when food availability is low. Although there is now good evidence that food availability influences sibling aggression in facultatively siblicidal species, where aggression commonly results in the death of a competitor, little is known about the proximate causes of aggression in nonsiblicidal species, where aggression rarely results in serious injury. Here, we investigated patterns of aggression between juvenile meerkats (*Suricata suricatta*), a species where littermate aggression is common, but never lethal. We show that the frequency of aggression between littermates increased when rainfall and helper number, both predictors of the amount of food available to pups, were low. Short-term feeding experiments demonstrated that reducing pup hunger by provisioning them before a foraging session significantly reduced their frequency of aggression in comparison to unfed controls. There was no evidence that offspring sex or weight influenced either the rate at which pups were aggressive, or which littermates they were aggressive to. These results suggest that food availability is an important factor affecting the severity of aggressive competition between offspring, even in the absence of lethal aggressive attacks. *Key words:* aggression, agonism, competition, dominance, food amount hypothesis, siblicide, sibling rivalry, *Suricata suricatta*. [*Behav Ecol* 20:930–935 (2009)]

Where offspring are reared together siblings commonly compete for access to limiting resources (Mock and Parker 1997). This usually takes the form of intense begging displays or scramble competition for lucrative feeding positions (Wright and Leonard 2002; Kilner and Drummond 2007; Hudson and Trillmich 2008), but in some species can involve physical aggression between offspring, such as pecking or biting (Frank et al. 1991; Mock and Parker 1997; Drummond 2001a; Drake et al. 2008). In siblicidal species, where such aggression commonly results in the death of a sibling, rates of aggression are predicted to increase when food availability is low, and the benefits of outcompeting close kin are correspondingly large (the “Food Amount Hypothesis”; Mock et al. 1987; Drummond 2001b). Several studies have demonstrated correlations between sibling aggression and food availability (reviewed by Mock and Parker 1997) or offspring growth (e.g., hyenas *Crocuta crocuta*; Golla et al. 1999) and good experimental evidence is also available for some facultatively siblicidal birds (e.g., black guillemot, *Cephus grille*, Cook et al. 2000; blue-footed booby, *Sula nebouxi*, Drummond and Chavelas 1989; and osprey, *Pandion haliaetus*, Machmer and Ydenberg 1998).

In contrast, we know little about the proximate causes of aggression in species where attacks between offspring are common but rarely result in serious injury (Drummond 2001a). Sibling aggression of this kind occurs in some birds with precocial young, where chicks scramble for lucrative feeding patches (e.g., Canada goose, *Branta canadensis*, Radesater 1976; Japanese Quail, *Coturnix coturnix*, Boag and Alway 1980) and there is also evidence of aggression in some cooperative species, where offspring aggressively defend helpers who provide them with food (e.g., banded mongoose,

Mungos mungo, Hodge et al. forthcoming; meerkats, *Suricata suricatta*, Hodge et al. 2007; and pied babblers, *Turdoides bicolor*, Raihani et al. 2008). As in facultatively siblicidal species, aggression may allow offspring to outcompete their litter or broodmates for food items and may therefore be expected to increase when food availability is low. However, as aggression toward close kin is likely to involve smaller indirect fitness costs for the aggressive offspring if it does not cause serious injury to a close relative, aggression in these species may also occur when food is not limiting if it is associated with other benefits, such as establishing future dominance relationships (Drummond 2006). This could have important consequences for both the frequency and direction of aggression, as offspring might be expected to target aggression toward individuals with whom they will compete in the future. Fully understanding the function of aggression in nonsiblicidal species therefore requires detailed investigation of patterns of aggression between offspring, looking particularly at the influence of food availability and individual offspring characteristics on both the frequency and direction of aggressive attacks.

In this study, we investigate patterns of aggression between meerkat pups, a species where aggression between offspring is common, but not lethal (Sharpe and Cherry 2003; Hodge et al. 2007). Meerkats are cooperative mongooses living in groups of up to 50 individuals across the drier regions of southern Africa (Doolan and Macdonald 1996; Clutton-Brock et al. 1999). Reproduction is largely monopolized by one female in each group (Griffin et al. 2003; Clutton-Brock et al. 2006; Hodge et al. 2008) who produces 3–4 litters of pups per year, each litter containing 4 pups on average (range 1–7) (Russell et al. 2003; Hodge et al. 2008). Pups spend the first month of life in an underground burrow, during which time they are reliant on their mother’s milk. They then begin to accompany the rest of the group on foraging trips where they move between older group members begging for food items (usually small invertebrates) until they can forage independently at around 3 months of age (Manser and Avey 2000; Brotherton et al. 2001; Clutton-Brock, Brotherton, et al. 2001). Helpers usually provide food to the closest begging pup (Brotherton et al. 2001) and the

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amount of food that pups receive during this period increases with the amount of time they spend with older group members when no other pups are close by (Hodge et al. 2007). As pup food intake has important consequences for future survival and reproductive success (Russell et al. 2007), pups are likely to gain substantial advantages from maintaining exclusive access to helpers. Pups achieve this by aggressively attacking littermates who approach their current helper during the period of peak pup care (between 40 and 70 days of age) (Sharpe and Cherry 2003; Hodge et al. 2007). This aggression takes the form of lunges, snaps, and occasional full fights, usually resulting in the loser moving away from the vicinity of the winner. The influence of this competition between offspring on early life mortality has not been investigated directly in meerkats, but there is some evidence that pups born in groups with few adult helpers show reduced survival when litter size is large (Hodge et al. 2008). Meerkat pups rarely display submissive behavior and there is no consistent dominance hierarchy among littermates (Sharpe and Cherry 2003).

This study has 2 main objectives. First, we investigate the factors that influence variation in rates of aggression between meerkat pups. Specifically, we investigate the relationships between natural rates of offspring aggression, food availability and individual characteristics such as offspring sex, age, and weight. We also test the causality of any relationship between offspring aggression and food availability, using supplemental feeding experiments to manipulate pup hunger levels. Second, we investigate patterns of aggression between littermates in more detail and ask whether offspring differ in which siblings they are aggressive to within their litter. Specifically, we ask whether pups are more aggressive toward pups of the same sex (with whom they will compete more strongly when they reach adulthood for reproductive opportunities; Clutton-Brock et al. 2006) and whether the direction of offspring aggression is influenced by the relative size of competing pups (as size differences are likely to influence whether or not pups are likely to win an aggressive interaction and hence the value of competing (Drummond 2001a).

MATERIALS AND METHODS

Study site and population

The data presented in this study were collected 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). Detailed descriptions of habitat and climate at the study site are provided elsewhere (Clutton-Brock et al. 1998; Russell et al. 2002). All individuals in our study population were habituated to close observation (from <1 m) and could be easily identified in the field by unique dye marks placed on their fur. Dye marks were applied while meerkats were sunning in the morning without the need for capture. Groups were visited approximately every 3 days to collect behavioral and life history data so the ages of most pups (>98%) were known to within 5 days. Pups were sexed soon after emergence from the natal burrow (at ca. 30 days). Most group members were habituated to step onto a portable electronic balance from a young age, and we were therefore able to collect regular weights for more than 95% of the study population. All research protocols complied with the ASAB Guidelines for the use of Animals in Research and were approved by the University of Pretoria Ethics Committee.

Data collection

Individuals were classified as pups until they were 3 months old and able to acquire most of their food independently. We refer to the period when dependent pups were consistently foraging

with the group (between 40 and 90 days of age) as the “pup feeding period.” During the pup-feeding period, we conducted continuous 20-min focal watches on pups in which we recorded all aggressive interactions initiated by the focal pup, the time that the focal pup spent within 2 m of each helper and the time that the focal pup spent within 2 m of each littermate. Aggression was defined as all occasions where an aggressor snapped or actively fought and grappled with a littermate. Focal watches were conducted when pups were actively social foraging (i.e., begging for food while following older group members; Brotherton et al. 2001; Sharpe and Cherry 2003) and were paused if pups stopped social foraging for more than 30 s (i.e., if they began resting or playing). Data were recorded on handheld Psion LZ64 dataloggers (Psion Teklogix Ltd, Bourne End, United Kingdom) and times were accurate to 1 s. We only included data 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. All focal watches were conducted between March 2004 and May 2005.

Statistical analysis

Statistical analyses were conducted in Minitab 13 (Minitab Inc., State college, PA) unless multifactorial statistics were required, in which case these were performed in Genstat 8 (Lawes Agricultural Trust, Rothamsted, United Kingdom). As most multifactorial analyses involved repeated sampling of individuals, litters, groups, or days, we used Generalized Linear Mixed Models. These are similar to Generalized Linear Models but allow both fixed and random terms to be included. In all mixed models, 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 their level of nonsignificance and to check that significant terms had not been wrongly excluded. All 2-way interactions were tested, but results are only presented if found to explain significant variation. Post hoc comparisons were computed by dividing the differences between the parameter estimates by the standard error (SE) differences between pairs and interpreting the output as a *t*-test, with the degrees of freedom being equal to the residual of the model (McGowan et al. 2006). All statistical tests were 2-tailed.

Patterns of aggression

To investigate the influence of food availability and offspring characteristics on pup aggression, we fitted whether the focal pup was involved in an aggressive interaction during a focal watch (1 = Yes, 0 = No) as the binomial response term in a Generalized Linear Mixed Model. Two measures of food availability were included as covariates: rainfall in the previous 30 days (mm) and helper number (all group members > 6 months), both of which have been shown to influence the growth and survival of pups and to be closely correlated with the amount of food pups find for themselves or are fed by adults (Barnard 2000; Clutton-Brock, Russell, et al. 2001; Russell et al. 2002). We also included the following pup characteristics; age on the day of the focal watch (in days), sex, weight relative to the litter mean in the week prior to the focal watch (g), litter size on the day of the focal watch and litter sex ratio (Male biased $\geq 60\%$ male, Equal = 40–60% male, Female biased $\leq 40\%$ male). The date of the focal watch, pup identity, litter identity, and group identity were included as random terms. All focal watches were between 19.5 and 20.5 min long. This analysis

used a data set comprising 265 focal watches on 78 pups (mean = 3.4 focals per pup, range = 1–10) from 22 litters in 12 groups.

To experimentally investigate the influence of food availability on rates of aggression, we conducted a supplemental feeding experiment in which we fed one pup in a litter at the start of the morning foraging period, whereas a same-sex control received nothing. Litters were chosen for the experiment if they contained 2 pups of the same sex that were of similar weight, hind-foot length, and condition (Thornton 2008); pups within an experimental pair were therefore similar in every respect except experimental treatment. One pup in each pair was chosen at random and fed at the start of the morning foraging period with 12 g of hardboiled hen's egg. Pups were fed without the need for capture from a deep bowl that prevented other individuals stealing egg. Pups showed no fearful responses during feeding and did not avoid contact with others once they had been fed. Both the fed and control pup were then watched continuously for 3 h and all aggressive interactions initiated by the focal pup toward any other pup in the litter were recorded. Focal watches were conducted simultaneously by 2 observers who were randomly allocated to treatment. Focal watches on both pups were paused if the pup did anything other than begging or looking for food (e.g., playing, sleeping, and responding to predator alarms) for more than 30 s. The measures of pup competition reported therefore represent rates within available foraging time for both the fed and control pup. Feeding experiments were conducted on 12 pairs in 11 litters in 7 groups. All supplemental feeding experiments were conducted during the peak pup-feeding period (mean pup age = 55 days, range 46–63). The total number of aggressive interactions initiated by fed and control pups per hour were compared using a paired *t*-test.

Aggression between littermates

To investigate whether pups differed in the probability they were involved in aggressive interactions with particular littermates, we recorded whether the focal pup instigated aggression toward any pups that it encountered during a focal watch when a helper was within 2 m (as most aggression involves pups defending their current helper from approaches by littermates). Whether aggression toward an encountered littermate occurred (1 = Yes, 0 = No) was fitted as the binomial response term in a GLMM. The sex of the focal pup, the sex of the littermate, and the difference in weight between the focal pup and littermate on the morning of the focal watch (similar = within 10 g; focal pup heavier ≥ 10 g heavier; focal pup lighter ≥ 10 g lighter) were included as the main terms of interest. This analysis also controlled for helper number, rainfall in the previous 30 days (mm), pup age (days), litter size, litter sex ratio, and the amount of time spent with each littermate when a helper was present (mins). The identity of the focal pup, littermate, litter, group, and the date of the focal watch were included as random terms. Analysis was based on 330 dyads from 45 focal pups in 12 litters in 9 groups.

RESULTS

Patterns of aggression

The number of aggressive interactions observed between foraging pups was highly variable, ranging from 0 to 31 interactions per individual per h (mean \pm standard deviation = 3.03 ± 4.09). The probability that a pup was involved in an aggressive interaction during a 20-min focal watch was highest when pups were between 30 and 55 days of age, and decreased significantly in pups older than 55 days (Table 1, Figure 1a).

Table 1
Factors affecting the probability of aggression (GLMM)

Explanatory terms	Probability of aggression per 20 min focal watch (g)		
	Estimate \pm SE	Wald statistic (χ^2)	<i>P</i>
Pup age (days)	-0.054 \pm 0.011	24.43	<0.001
Rainfall 30 days pre focal*helper number	See Figure 1b	5.80	0.016
Rainfall 30 days prefocal (mm)	See Figure 1b	3.91	0.048
Helper number	See Figure 1b	0.67	0.41
Litter sex ratio			
Equal	0.00 \pm 0.00	0.71	0.49
Female bias	0.47 \pm 0.45		
Male bias	0.48 \pm 0.57		
Litter size	0.082 \pm 0.17	0.24	0.63
Relative pup weight	-0.015 \pm 0.044	0.12	0.73
Pup sex			
Female	0.00 \pm 0.00	0.00	0.95
Male	0.019 \pm 0.29		
Constant	-0.090 \pm 0.24		

Significant terms are highlighted in bold. Group identity (component \pm error = 0.40 ± 0.29), litter identity (0.017 ± 0.21), focal pup identity (0.00 ± 0.00), and date (0.00 ± 0.00) were included as random terms.

There was also a significant interaction between rainfall in the previous 30 days and helper number. When rainfall was high the probability of aggression declined as the number of helpers increased, but when rainfall was low the probability of aggression remained high, even in groups with many helpers (Table 1; Figure 1b). Post hoc comparisons revealed a significantly lower probability of aggression during periods of high rainfall when compared to periods of lower rainfall in groups with many helpers: $t = 3.099$, $P < 0.005$, but no significant drop in aggression during periods of high rainfall in groups with few or intermediate numbers of helpers (GLMM post hoc comparison: 10–14 helpers $t = 0.84$, $P > 0.1$; <10 helpers $t = 0.80$, $P > 0.1$). Males and females did not differ in the probability they were involved in an aggressive interaction (Table 1). There was also no influence of the relative weight of the focal pup in comparison to its littermates, the sex ratio of the litter or litter size (Table 1).

Experimentally increasing pup food intake prior to a foraging session (and hence experimentally reducing pup hunger levels) significantly reduced rates of aggression in fed pups in comparison to unfed controls (Paired *t*-test: $t = 4.02$, $n = 12$, $P = 0.002$; Figure 2). There was no evidence that experimentally fed pups recovered aggressiveness across the 3-h focal period as rates of aggression in fed pups did not differ significantly between the end of the focal period (2–3 h post-feeding, median \pm interquartile range = $0.5 \pm 0.0, 1.0$) and the beginning (0–1 h post feeding, $0.0 \pm 0.0, 1.0$; Wilcoxon signed ranks test: $W = 7.5$, $P = 1.00$).

Aggression between littermates

After controlling for a significant negative influence of pup age, rainfall in the previous 30 days and litter size, there was no evidence that the sex of the littermate or the focal pup influenced the probability of aggression (Table 2), and there was no significant interaction (GLMM: Littermate sex*focal pup sex: $\chi^2 = 0.21$, $P = 0.65$). There was also no evidence that the weight difference between the 2 pups had any influence on the likelihood of aggression (Table 2).

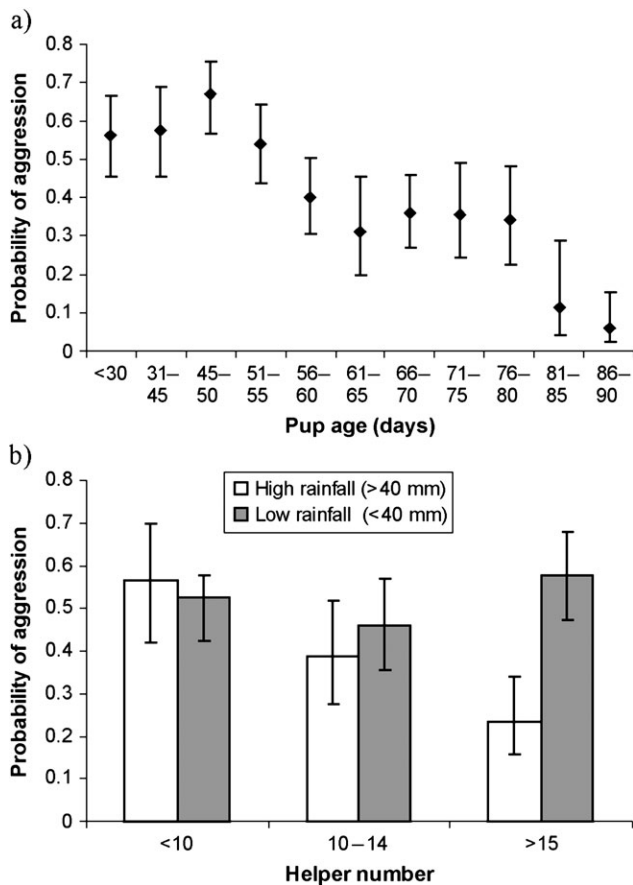


Figure 1
The influence of (a) pup age and (b) helper number during periods of high and low rainfall on the probability that a pup was involved in aggression during a 20-min focal watch. Graphs show predicted means from a GLMM controlling for the significant terms in Table 1. Data were from 265 focal watches on 78 pups in 22 litters.

DISCUSSION

Our results indicate that food availability plays an important role in regulating the frequency of aggression between meerkat pups. The probability that offspring were involved in aggression during a focal watch was significantly higher when rainfall in the previous 30 days was low, particularly in groups with few helpers, and both helper number and rainfall have been shown to be good indicators of the amount of food available to meerkat pups (Barnard 2000; Clutton-Brock, Russell, et al. 2001). Provisioning experiments confirmed the causality of these findings and demonstrated that short-term increases in pup food intake reduced rates of aggression by more than 60%. Although several studies have demonstrated a link between food availability and aggression in facultatively siblicidal species (for a review see Drummond 2001b), our results provide the first evidence that food amount can influence rates of aggressive competition in species where aggressive attacks are common, but not lethal.

Experimental manipulations of offspring food availability are often difficult to interpret, as if offspring are prevented from receiving parentally provided food, it is not always clear whether changes in aggression arise through increases in offspring hunger, or simply because offspring are frustrated at not being able to ingest visible food items (Drummond 2001b). By experimentally increasing food intake, rather than depriving offspring of food, our results demonstrate that in meerkat

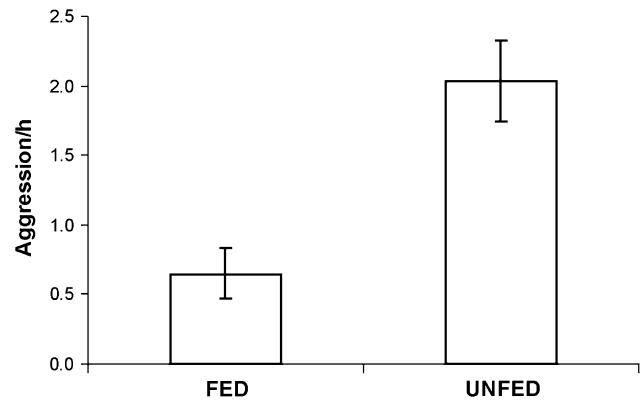


Figure 2
The influence of supplemental feeding on rates of aggression ($n = 12$ pup pairs from 7 groups).

pups, hunger, rather than frustration, is the major cause of increased aggression. This influence of hunger on meerkat pup aggression could arise because hunger increases pup aggression per se, or because hunger influences other aspects of pup behavior. For example, previous work has shown that meerkat pups spend more time attempting to find food for themselves, and less time begging from older group members, when they are in good condition (Thornton 2008). As a consequence, hunger may influence the amount of time that meerkat pups forage with older group members and hence the extent to which they benefit from aggressively defending helpers.

Table 2
Factors affecting which littermate pups direct aggression toward when a helper is within 2 m (GLMM)

Explanatory terms	Probability of aggression (g)		
	Estimate \pm SE	Wald statistic (χ^2)	<i>P</i>
Pup age (days)	-0.044 \pm 0.011	15.85	<0.001
Rainfall 30 days prefocal (mm)	-0.014 \pm 0.0060	40.7	0.026
Litter size	-0.28 \pm 0.14	4.20	0.047
Helper number	-0.037 \pm 0.040	0.82	0.37
Focal pup sex			
Female	0.00 \pm 0.00	0.69	0.41
Male	-0.23 \pm 0.29		
Littermate sex			
Female	0.00 \pm 0.00	0.66	0.42
Male	0.23 \pm 0.29		
Time spent with littermate (min)	0.029 \pm 0.081	0.13	0.72
Litter sex ratio			
Female bias	0.00 \pm 0.00	0.25	0.88
Equal	-0.97		
Male bias	-0.24		
Relative weight of littermate			
Heavier (>10 g heavier)	0.00 \pm 0.00	0.11	0.95
Similar (within 10g)	0.95		
Lighter (>10g lighter)	-0.059		
Constant	-1.071 \pm 0.16		

Significant terms are highlighted in bold. Group identity (component \pm error = 0.00 \pm 0.00), litter identity (0.00 \pm 0.00), focal pup identity (0.01 \pm 0.16), littermate identity (0.00 \pm 0.00), and date (0.23 \pm 0.24) were included as random terms.

Rates of offspring aggression have also been shown to vary within litters or broods according to individual offspring characteristics, such as their relative age or weight (Drummond 2001a). In some facultatively siblicidal avian species, for example, the order in which offspring hatch influences both the amount of aggression they instigate and which broodmates they direct aggression toward, resulting in a dominance hierarchy which can persist throughout the nesting period (Valderrabano-Ibarra et al. 2007). Differences in aggressiveness between broodmates may not only allow more aggressive "dominant" chicks to secure a greater share of food, but could also be beneficial in later life if early dominance relationships persist into adulthood (Gonzalez-Voyer et al. 2007). If establishing future dominance relationships is important, this could have important consequences for patterns of aggression, as offspring may be expected to target aggression toward offspring with whom they are likely to compete in the future. In spotted hyenas (*Crocuta crocuta*), for example, within-sex adult social rank is correlated with reproductive success (Frank et al. 1991), and competition is highest in litters containing multiple offspring of the same sex (Frank et al. 1991; Golla et al. 1999 but see Wahaj and Holekamp 2006).

Establishing future dominance hierarchies could be particularly important in meerkat societies, as offspring remain in close contact for several years and are likely to compete with same-sex littermates for future breeding opportunities (Clutton-Brock et al. 2006; Hodge et al. 2008; Spong et al. 2008). However, our findings provide little support for the idea that establishment of dominance is the main function of aggression between meerkat pups. There is no evidence that pups are more aggressive to littermates of the same sex, who are likely to be the biggest future competitors. Pups also rarely behave submissively to one another, and, within dyads, there is no evidence that certain pups consistently win aggressive encounters (Hodge et al. 2007). In addition, meerkat pups are only aggressive when an immediate benefit is being contested; offspring are never aggressive when resting at the burrow, and rates of aggression decline when pups are able to find food independently. Dominance interactions are often subtle and infrequent however, and it is possible that hierarchies do exist that were not detected by this study but our results suggest establishing dominance hierarchies is unlikely to be the primary function of aggression among meerkat pups.

Most work on offspring aggression has been conducted in siblicidal avian systems (Mock and Parker 1997; Drummond 2001a) and the few mammalian species in which offspring aggression has been studied are also species in which aggression commonly results in the death of a sibling (e.g., hyenas, Frank et al. 1991; Golla et al. 1999; domestic pigs, *Sus scrofa*, Drake et al. 2008). There has been much debate over why aggression between siblings is not more widespread in non-siblicidal species (Mock 1985; Mock and Parker 1997; Drummond 2002). In meerkats, losing offspring move away from the winner and aggression therefore functions to remove littermates from the resource being contested, somewhat akin to territory defense. In most nestling birds however, aggression is unlikely to result in the removal of a competitor, as offspring are confined to the nest and are relatively immobile (unless of course aggression causes the death of a sibling and hence its removal from the nest). Offspring aggression of this kind, where the loser moves away rather than submitting to the aggressor, may be more widespread where offspring are able to move freely (such as when chicks have fledged) than when they are confined in space (Drummond 2006). This type of aggression is also likely to be most profitable where food comes from multiple sources (e.g., from multiple helpers, teats or food patches), as displaced offspring will be more likely to move to an alternative food source following an ag-

gressive interaction. Few studies have been able to investigate aggression among mammalian young once they have fledged or left the den, but there is some evidence that rates of aggression are higher between free-swimming red-necked grebe (*Podiceps grisegena*) chicks, than between chicks confined to the back of an adult (Kloskowski 2003). In addition, aggression among pied babbler chicks is common between fledglings but rarely occurs in the nest (Raihani N, personal communication).

In conclusion, our findings indicate that food availability has important implications for the frequency of offspring aggression in meerkat societies. Although the proximate causes of aggression in siblicidal species are well understood, this provides one of the first detailed investigations of offspring aggression in a species where offspring aggression does not commonly result in the death of a sibling as well as one of the first experimental tests of the influence of food availability on offspring aggression in a nonavian species. We suggest that nonviolent physical aggression may be more common in mobile feeding systems, where losers are able to move away from the aggressor and suggest that further investigation of patterns of aggression among fledglings or mobile offspring would be fruitful.

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