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'False feeding' and aggression in meerkat societies

T. H. CLUTTON-BROCK*†, A. F. RUSSELL*‡, L. L. SHARPE§ & N. R. JORDAN*§
*Department of Zoology, University of Cambridge
†Mammal Research Institute, University of Pretoria, South Africa
‡Department of Animal and Plant Sciences, University of Sheffield
§Department of Zoology, University of Stellenbosch

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In cooperative societies, group members are expected to be punished for being lazy and so behaviours that exaggerate an individual's contribution to cooperation may be favoured by selection. In cooperative meerkats, *Suricata suricatta*, helpers vary in their level of care and, within breeding attempts, helpers can be categorized as 'generous' or 'lazy'. Lazy helpers were more likely to carry food to pups and then eat it themselves and lazy males received more aggression, supporting the idea that 'false feeding' could be an adaptive tactic used to exaggerate individual contributions to care. However, our results are also consistent with the more parsimonious idea that 'false feeding' occurs when individuals decide not to deliver food items after assessing the needs of pups relative to their own. Group members were not obviously deceived by 'false feeders' nor was 'false feeding' associated with any obvious benefit. In general, the frequency of 'false feeding' increased when the net benefits of feeding pups were likely to be low. The frequency of 'false feeding' increased with rising food item value and with decreasing pup dependency on food provided by helpers. Female helpers (which feed pups more than male helpers and preferentially feed female pups) 'false fed' less than male helpers and 'false fed' male pups more than female pups. We suggest that there is little unequivocal evidence of deception by helpers over contributions to care in cooperative vertebrates and that 'false feeding' may occur where helpers adjust their decisions immediately before feeding young or where they are subject to conflicting motivations.

Cheating, behaviour that increases an individual's fitness through the deception of others (Semple & McComb 1996), is widely acknowledged as an important impediment to the evolution of cooperation in animal societies (Maynard Smith 1982). Despite widespread interest in cheating (Clutton-Brock & Parker 1995; Dugatkin 1997; Whiten & Byrne 1997; Putland 2001), firm evidence of deception is scarce. One well-documented example of a potentially deceptive tactic is the 'false feeding' of young by carers in cooperative birds, where group members visit nests containing dependent young but either take no food (Clarke 1984; Poiani 1993) or carry food to the nest but then eat it themselves (Boland et al. 1997a). For example, in white-winged choughs, *Corcorax melanorhamphos*, some helpers eat up to 30% of food items that they bring to nests (Boland et al. 1997a). In this case, the frequency of 'false feeding' increases when other group members are not watching and declines when food supplies are experimentally supplemented. It is commonly assumed that individuals that visit nests, but do not feed the young, are attempting to mislead other group members as to their level of investment. However, an alternative explanation of 'false feeding' is that individuals cannot assess the needs of nestlings until they have reached the nest and that 'false feeding' occurs where individuals decide not to provision after evaluating the needs of offspring relative to their own (Canestrari et al. 2004).

If 'false feeding' is a deceptive tactic, it is likely to occur where individuals are able to gain significant benefits by exaggerating their own level of contribution. Lazy helpers might benefit by 'false feeding' if they are more likely to be punished or evicted from the group than more generous helpers (Gaston 1978; Reeve 1992; Mulder & Langmore 1993; Boland et al. 1997a). Helpers that may breed with other group members in the future might benefit by 'false feeding' if mating preferences are affected by feeding rates

Correspondence: T. H. Clutton-Brock, Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K. A. F. Russell is at the Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, U.K. L. L. Sharpe and N. R. Jordan are at the Department of Zoology, University of Stellenbosch, Matieland 7602, South Africa.

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(Zahavi & Zahavi 1997). Finally, individuals might gain from 'false feeding' if feeding is costly and exaggeration of feeding rates encourages increases in the rate at which other group members feed the young. By contrast, if 'false feeding' simply arises as a consequence of an assessment of the relative needs of dependent young, 'false-feeding' rates might be expected to vary with the motivation of individuals to feed young and the relative requirements of those young. In this case, there should be little evidence that 'false feeders' deceive other group members or that they gain significant benefits from their actions.

To distinguish between these alternatives, we need to know considerably more about the distribution and potential benefits of 'false feeding'. We investigated the distribution and frequency of 'false feeding' and examined relations between 'false feeding' and aggression in groups of cooperative meerkats, *Suricata suricatta*. Meerkats live in groups of up to 50 that include a dominant male and female which are responsible for most breeding attempts within the group (Clutton-Brock et al. 2001a; Griffin et al. 2003; Russell et al. 2003a) and (largely) nonbreeding helpers that provide most of the pup care (Clutton-Brock et al. 2002, 2004). Individuals usually remain in their group of birth and help for 1–2 years. After this age, males typically disperse voluntarily to breed in other groups or to form new ones. Adolescent females are commonly driven out of the group by the dominant female, although if they inherit the dominant position (on the death of the dominant), they may remain and breed in their natal group throughout their lives (Clutton-Brock et al. 1998).

Individuals begin to contribute to cooperation from independence at 3 months, although contributions by those under 6 months are typically low (Clutton-Brock et al. 2002). Helpers of both sexes guard young at the burrow during their (the young's) first month of life. From around 1 month, pups begin to travel with the group on foraging trips, and for the next 2 months are provided with invertebrates and small vertebrates (Brotherton et al. 2001). All group members participate in feeding pups, but individual contributions vary considerably (Clutton-Brock et al. 2002, 2003, 2004). Significant fractions of this variation are explained by age (animals of 3–6 months and over 2 years feed less than those of 6–24 months) and sex (males contribute less than females; Clutton-Brock et al. 2002). In addition, among female helpers less than a year old, pup-feeding rates increase with body weight, whereas, among older females, pup-feeding rates are positively correlated with rates of daily weight gain (Clutton-Brock et al. 2002, 2003).

When dependent pups are foraging with the group, they run between group members begging for food (Manser & Avey 2000; Brotherton et al. 2001). After a carer locates a food item, it either eats it immediately or picks it up and runs, usually to the closest pup. Pups that are approached by helpers give an excited, bubbling call in anticipation of being fed. In around 9% of cases, pups do not immediately take the food item and helpers usually eat it themselves. In an additional 3% of cases, carers reach the pup but eat the food item in front of the pup, despite the pup's continued begging, which we define as 'false feeding' (Brotherton et al. 2001). In contrast to birds, where individuals may visit nests when no other group members are present, feeding meerkats are usually within sight of many or all other group members and it is not feasible to compare the distribution of 'false-feeding' behaviour of carers in the absence versus presence of other animals.

First, we examined the distribution of 'false feeding'. In particular, we investigated whether individuals vary in their propensity to 'false feed' according to their sex, age, dominance, nutritional and immigrant status, as well as their provisioning frequency. Second, we examined the relative frequency with which pups of different sex, age and nutritional status are 'false fed'. Third, we examined the distribution of aggression and the potential benefits that carers might gain by exaggerating their level of contribution. In particular, we investigated whether carers with low rates of pup feeding are likely to receive more aggression than more generous individuals. Finally, we examined the relation between 'false feeding' and aggression.

METHODS

Study Sites

We studied levels of 'false feeding' and aggression at two locations in the South African Kalahari: in the Kalahari Gemsbok National Park (25°17′S, 20°32′E) and on ranch-land, 200 km to the east near Vanzylsrus (26°58′S, 21°49′E). Data were collected during more than 7000 group-hours of observations during periods of pup feeding on four groups in the Park between January 1996 and May 1998 and 14 groups in the ranch-land between December 1996 and May 2002. Descriptions of habitat and climate are provided elsewhere (Clutton-Brock et al. 1999; Russell et al. 2002). All individuals in each group were individually recognizable by unique 'hair cuts' which were administered and maintained, without the need for capture, using scissors while animals were resting. Individuals were also habituated to close observation (from <1 m) and most could be weighed repeatedly each day by enticing them on to top-pan electronic balances (± 1 g) using crumbs of hard-boiled egg. The ages of over 90% of individuals were known precisely ($\pm$ 5 days), since their development had been monitored since birth. We define pups as animals of <3 months, juveniles as 3–6 months, subadults as 6–12 months, yearlings as 12–24 months and adults as >24 months.

Distribution of 'False Feeding'

The frequency of 'false feeding' was investigated as a proportion of total 'attempted' pup feeds (see below). Individual contributions to pup feeding and levels of 'false feeding' were obtained during observations of 3–4 h conducted every 1–5 days during the pup-provisioning period of each litter (i.e. from pup emergence to independence, ca. 50 days). During our observations, we attempted to record every pup feed and, where group sizes were large, more than one observer was involved with sampling.

During our 7000 group-hours of observations, we observed 67 297 'attempted' pup feeds by 502 individuals during 161 breeding attempts in the 18 groups. Attempted pup feeds include those in which carers successfully delivered prey items to pups and those in which they did not, either because the pup refused or lost the prey item or because the carer 'false fed' the pup. However, our final analysis excluded a total of 8141 'attempted' feeds. Since our primary aim was to investigate the factors that influence when a carer presents a prey item to a pup before consuming it itself, we excluded 9% of all ($N = 6057$) 'attempted' pup feeds when the carer consumed a prey item after the pup refused it, usually because the pup it approached was already consuming an item delivered by another carer. In addition, we further restricted our analysis to include only feeders for which at least five feeding 'attempts' were observed during the rearing of a single litter, to avoid including zero rates of 'false feeding' for helpers that were rarely observed to feed pups. Most of these involved litters that were observed infrequently. Thus, our analysis of 'false feeding' was conducted on 59 156 'attempted' pup feeds (of which 1903 (3%) were 'false') by 478 individuals during the rearing of 155 litters.

To analyse the relative frequency of 'false-feeding' events, we used a generalized linear mixed model in which the number of times individuals were observed to 'false feed' a litter was fitted to a binomial error structure (with logit link function) and the number of times individuals were observed to visit pups with food during the rearing of a litter was fitted as the binomial denominator. Individual, litter and group identities were fitted as random terms to control for repeated measures of each (1–97 measures/individual, 1–165 measures/litter, 13–1957 measures/group). Explanatory terms fitted were: observation time, number of 'attempted' pup feeds, carer number (individuals over 6 months), carer status (age, dominance status, sex, weight, rate of daily weight gain), prey size delivered (small, medium, large; Brotherton et al. 2001) and attributes of the pup (sex, age, weight).

We also tested the effects of manipulating the nutritional status of helpers on their proportion of 'false feeds'. We fed 25 helpers over 6 months old with 25 g of hard-boiled egg each day for an average of 52 days during pup development (i.e. during the periods of both babysitting and pup feeding). The proportion of attempted feeds that were 'false' by the 25 helpers were compared with those proportions by 66 unfed controls of similar age and sex that were helping to rear the same litters. Overall, we observed 8046 pup visits (of which 3% were false) by the 91 individuals, in 19 litters from six groups. We used Wilcoxon matched-pairs tests to test whether fed helpers 'false fed' pups a lower proportion of food items that they brought than unfed helpers, as shown by Boland et al. (1997a) in white-winged choughs.

Distribution of Aggression

Data on aggression were collected during the same 7000 group-hours of observation used to estimate rates of pup feeding and 'false feeding'. During this time, we attempted to document all interactions where one individual growled, hip-slammed, bit or chased another individual in the same group, and more than one observer was involved with sampling where group sizes were large. Such aggressive interactions mostly occurred during general periods of social interaction. In total, we observed 3196 interactions in which we identified the recipient of aggression and 2786 (87%) in which both the initiator and recipient were identified. We conducted two analyses, one to investigate which animals initiate aggressive interactions and one to investigate which receive aggression. Both analyses were conducted on numbers of observations of aggression during the pup-feeding period of a litter in a generalized linear mixed model with Poisson error structure. Individuals for which no aggression was observed during the rearing of a litter were omitted because of data distribution problems. Although our analyses of aggression initiated and received are based on (nonzero) frequencies, we also analysed the data in terms of the probabilities that individuals were observed to initiate or receive any aggression during pup-provisioning periods and found the results to be qualitatively similar.

Analysis of the initiation of aggression was conducted on the 2786 aggressive interactions observed in which both initiator ($N = 132$ individuals, 1–48 measures/individual) and receiver ($N = 218$ individuals, 1–20 measures/individual) were known. Bouts of aggression initiated were observed during the rearing of 56 litters (1–42 measures/litter) in 10 groups (13–207 measures/group). In this analysis, we fitted observation time, carer number, dominance status, sex and age of both initiators and receivers as fixed effects, while identities of the initiator, the litter and the group were fitted as random terms. Analysis of aggression received was conducted without consideration of the identity of the initiator of aggression and hence was conducted on all 3196 instances of aggression directed at 238 individuals (1–9 measures/individual). Bouts of aggression received were observed during the rearing of 56 litters (1–22 measures/litter) in 10 groups (7–134 measures/group). In our analysis of aggression received, we fitted observation time, carer number and the dominance status, sex and age of receivers, as well as the rate at which individuals were observed to feed litters (pup-feeds/3 h) as fixed effects. The receiver's identity and the identity of the litter and group were fitted as random terms.

False Feeding and Aggression Received

We investigated whether rates of aggression received were influenced by whether individuals were observed to 'false feed' during the rearing of a litter. To investigate whether this was the case, we simply reran the analysis on aggression received (outlined above) while fitting whether or not individuals were observed to 'false feed' during the rearing of a litter as an additional fixed effect.

Statistical Analysis

Generalized linear mixed models (GLMM) were conducted in GENSTAT 5, release 4.1 (GENSTAT, Rothamsted

Experimental Station, Harpenden, U.K.). GLMM are similar to generalized linear models except that they allow both fixed and random terms to be fitted, with random terms taking into consideration repeated measures within individuals, litters and/or groups (Schall 1991). The significance of explanatory terms in GLMM is assessed by their Wald statistics, which are distributed as χ^2 for each term fitted last in the model. For interactions containing factors, GENSTAT outputs show the level of significance for the first level of each interaction only. By changing the order in which levels of factors are entered into the models, the significance values of each level of a factor within an interaction can be obtained within the overall model.

Potential explanatory variables were averaged for each individual during the period of provisioning for each litter, except for measures of weight and weight gain. The weight of individuals was calculated as their mean morning, preforaging weights over the 3 months prior to the provisioning period of the current litter, while rates of daily weight gain were calculated as the mean change in weight (g/h) between morning and lunch weighing sessions (3–4 h later) over the same period (Clutton-Brock et al. 2002).

RESULTS

Distribution of 'False Feeding'

In around 12% of all cases where group members found a food item and carried it to a pup, they ate it themselves. However, in approximately 75% of these cases (9% of all pup feeds) the pup they approached was already eating, showed little interest or failed to see the item that was offered. In only 3% of all pup feeds did carers bring a food item to a pup and eat it themselves when pups knew where the item was and continued begging. The probability that group members would 'false feed' was higher when a large food item was brought to a pup than when a small item was brought ($\chi^2_2 = 84.87$, $P < 0.001$; Fig. 1a) and was greater in small groups ($\chi^2_1 = 6.07$, $P = 0.014$; Fig. 1b), where helpers give away a larger proportion of the food items they find to pups (Clutton-Brock et al. 2001b).

'False-feeding' rates varied significantly with the sex and age/status of carers (Fig. 2a, b). Males 'false fed' pups more than females ($\chi^2_1 = 6.40$, $P = 0.010$). 'False feeding' was most common among juvenile helpers (3–6 months), least common in subadults (6–12 months) and yearlings (12–24 months) and intermediate in subordinate and dominant adults (>24 months; $\chi^2_4 = 15.66$, $P = 0.004$). No interaction was found between sex and age/status on rates of 'false feeding' ($\chi^2_4 = 2.31$, $P = 0.68$).

Across individuals, the frequency of 'false feeding' was negatively correlated with the rate at which individuals fed pups, although the significance of this correlation varied between age/sex status, generating a significant interaction between age/sex status and the frequency of pup feeding on the frequency of 'false feeding' ($\chi^2_4 = 16.99$, $P = 0.002$; Fig. 3a–d). Among males, significant negative relations between pup-feeding rates and 'false-feeding' rates were common to all age/status categories except subordinate adults (juveniles: $\chi^2_1 = 19.33$, $P < 0.001$; subadults: $\chi^2_1 = 7.06$, $P = 0.008$; yearlings: $\chi^2_1 = 3.87$, $P = 0.049$; subordinate adults: $\chi^2_1 = 0.22$, $P = 0.64$; dominants: $\chi^2_1 = 3.71$, $P = 0.054$). Among females, significant negative relations between pup-feeding rates and 'false-feeding' rates were restricted to adults (subordinates: $\chi^2_1 = 5.21$, $P = 0.022$; dominants: $\chi^2_1 = 23.94$, $P < 0.001$; range of other P values: $\chi^2_1 = 1.65 - 0.02$, $P = 0.20–0.88$).

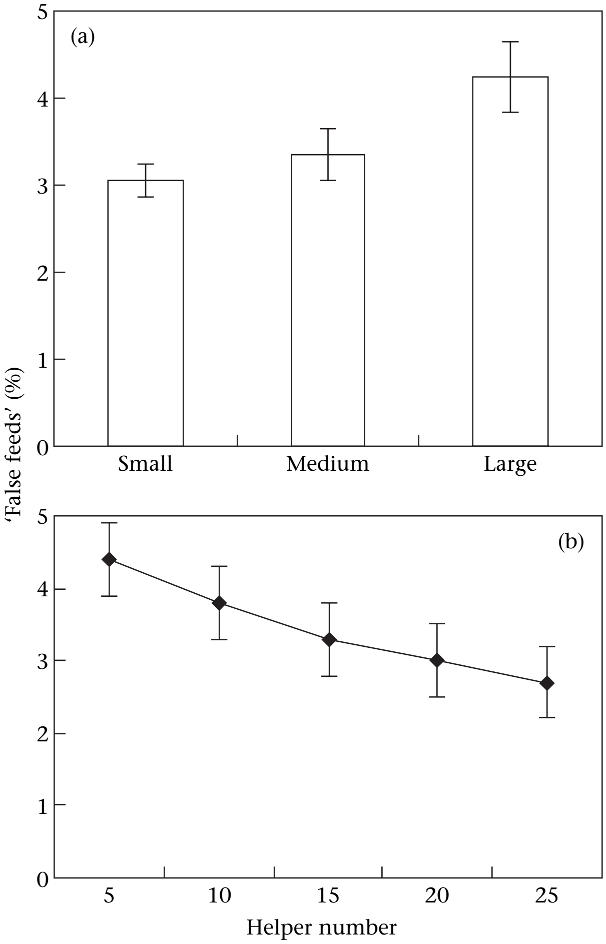

Figure 1. (a) Percentage of pup-feeding attempts involving prey of different size categories that were classified as 'false feeds'; (b) percentage of pup-feeding attempts classified as 'false feeds' in groups of different size. Both (a) and (b) show sexes combined because sex differences were not significant, and (b) shows the predicted mean relationship from the model. Means are shown ± 1 SE.

Among male helpers, rates of 'false feeding' were correlated with relative weight: male helpers that were heavy for their age 'false fed' more than those that were light for their age (Fig. 4a). No similar effect was found among females, generating a significant interaction between body weight and sex on rates of 'false feeding' ($\chi^2_1 = 4.33$, $P = 0.033$). In addition, helpers whose food intake had been experimentally supplemented reduced 'false-feeding' rates by around 35% (from 3.5 to 2%), but this decrease failed

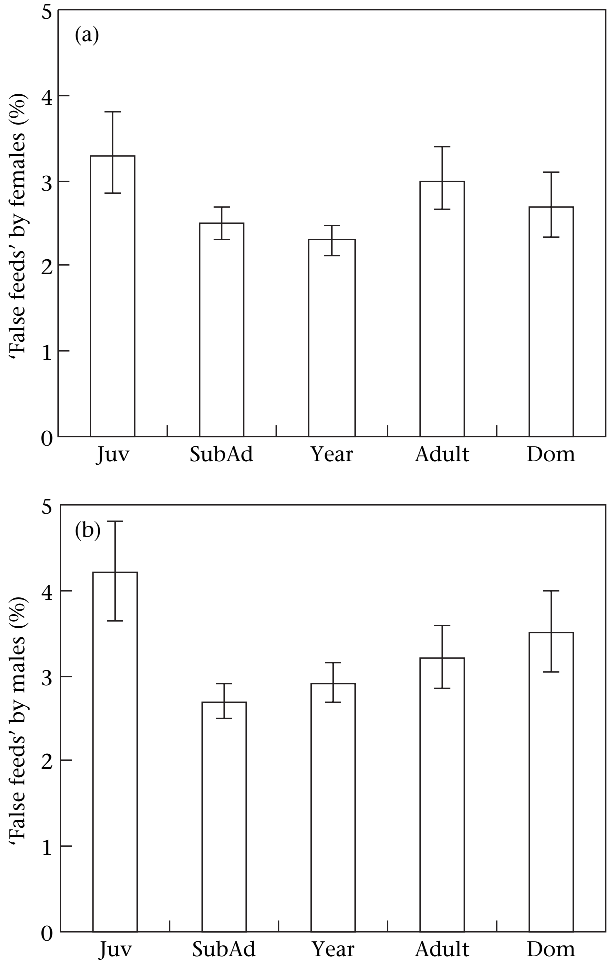

Figure 2. (a) Percentage of pup feeds by (a) females and (b) males of different age and status that were classified as 'false feeds'. Juv: juvenile; SubAd: subadult; Year: yearling; Adult: subordinate adult; Dom: dominant adult. Means are shown ± 1 SE.

to reach statistical significance (Wilcoxon matched-pair (two-tailed) test: $Z = 164$, $N = 23$, $P = 0.096$; Fig. 4b). In contrast, neither in males nor in females were 'false-feeding' rates significantly correlated with foraging success as measured by rates of daily weight gain (sexes combined: $\chi^2_1 = 1.02$, $P = 0.31$).

We found little evidence to suggest that relatedness influenced 'false-feeding' rates. When we controlled for differences in age, the relative frequency of 'false feeding' did not differ between adult helpers and breeding dominants ($\chi^2_1 = 0.01$, $P = 0.93$). Nor did subordinate immigrant males or subordinate founding males (which sometimes bred in the group; Griffin et al. 2003) 'false feed' more than natal males (which rarely bred there; $\chi^2_1 = 2.77$, $P = 0.096$), although there was a nonsignificant trend in this direction.

'False Feeding' and Pup Characteristics

The relative frequency of 'false feeding' varied with the characteristics of the pup being fed. Young pups (less than 35 days old which are still largely dependent upon milk) and older pups (more than 75 days old which are largely independent) were more likely to be 'false fed' than pups of between 35 and 75 days ($\chi^2_1 = 46.18$, $P < 0.0001$; Fig. 5a). In addition, male pups were more likely to be 'false fed' than female pups ($\chi^2_1 = 15.26$, $P < 0.001$; Fig. 5b). This result was likely to have arisen, in part, because female helpers were significantly more likely to 'false feed' male pups than female pups ($\chi^2_1 = 5.92$, $P = 0.015$), although the nonsignificant trend in males was in the same direction ($\chi^2_1 = 1.71$, $P = 0.20$). In contrast, there were no significant effects on the probability that pups would be 'false fed' of either their daily weight gain ($\chi^2_1 = 0.58$, $P = 0.45$) or their age-related weight ($\chi^2_1 = 0.42$, $P = 0.52$).

Distribution of Aggression

Aggression was observed during the pup-feeding periods of only one-third of all litters, and aggression by an individual was observed only once in 35 individual-hours of observation, on average. Nevertheless, categories of individuals varied markedly in the rate at which they initiated bouts of aggression (Fig. 6a–c). Females were more aggressive than males ($\chi^2_1 = 20.41$, $P < 0.001$; Fig. 6a), and within each sex, aggression was initiated least commonly by subordinate juveniles and most commonly by dominant adults (females across all age/status classes: $\chi^2_4 = 98.58$, $P < 0.0001$; males across all age/status classes: $\chi^2_4 = 89.01$, $P < 0.0001$; Fig. 6a). In addition, dominant females were more aggressive towards subordinate females than towards subordinate males, whereas subordinate females were equally likely to direct aggression at males as females (status∗sex interaction; $\chi^2_1 = 20.41$, $P < 0.001$; Fig. 6b). Similarly, dominant males were more aggressive towards subordinate males than towards subordinate females, while subordinate males did not differentiate (status∗sex interaction; $\chi^2_1 = 23.28$, $P < 0.001$; Fig. 6c).

Rates of aggression received also varied widely between different classes of animal (Fig. 6d). Females generally received more aggression than males ($\chi^2_1 = 61.41$, $P < 0.001$), presumably because dominant females tended to be more aggressive than dominant males (Fig. 6a) and directed more aggression towards subordinate females than subordinate males (Fig. 6b). However, patterns of aggression received differed according to sex and age/status, generating a significant interaction between each on aggression received (interaction: $\chi^2_4 = 21.22$, $P < 0.001$). Within females, levels of aggression received increased linearly with age before declining if individuals became dominant (significance across all age/status classes: $\chi^2_4 = 112.66$, $P < 0.0001$). Within males, rates of aggression received remained low until they became adult, and dropped to a similar level as those of the dominant female if they became dominant (significance across all age/status classes: $\chi^2_4 = 121.43$, $P < 0.0001$).

Male helpers with low pup-feeding rates received more aggression than those with high pup-feeding rates ($\chi^2_1 = 4.65$, $P = 0.031$; Fig. 7a), but this was not the case

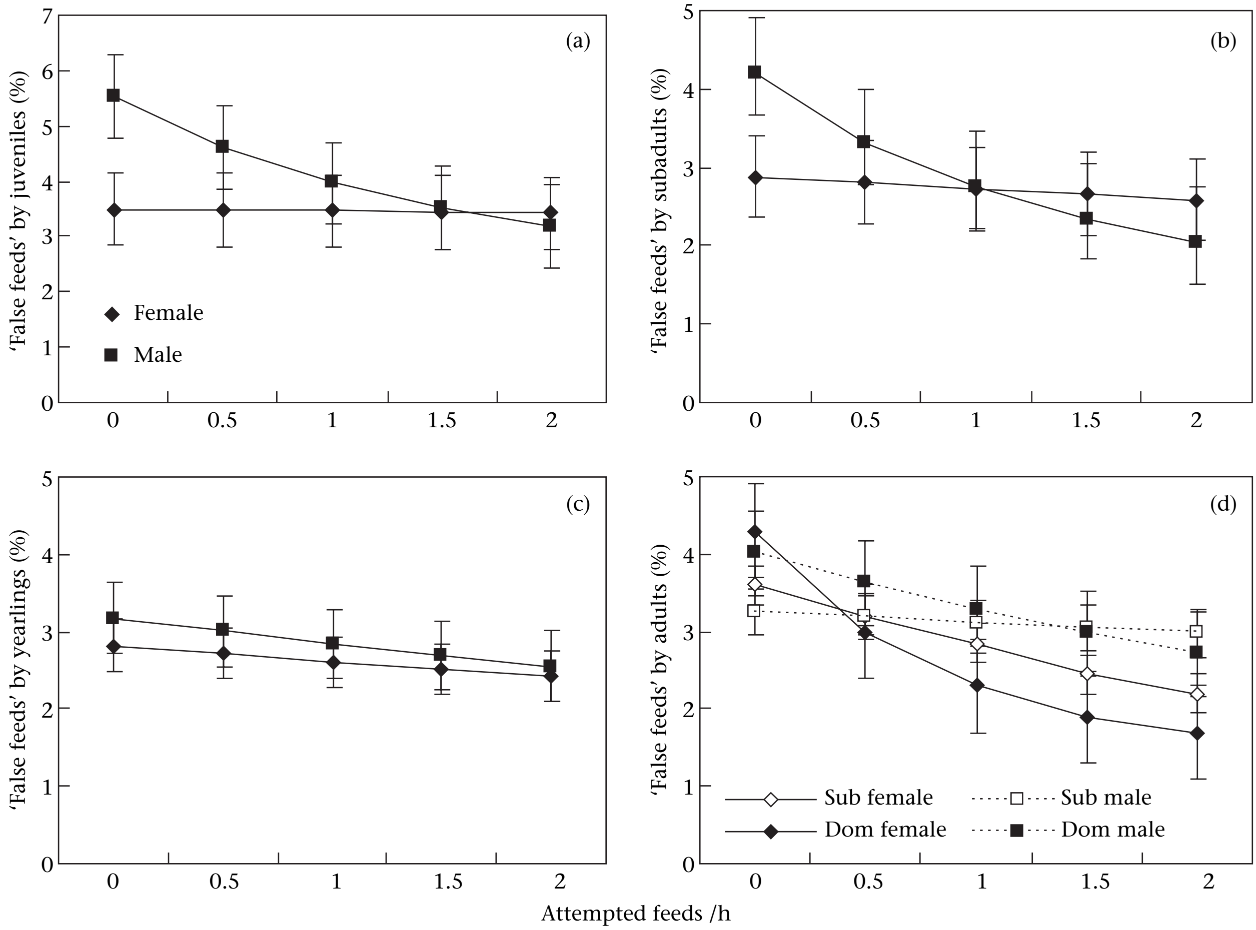

Figure 3. Relations between contribution to pup feeding and percentage of those contributions that were false among: (a) juveniles; (b) subadults; (c) yearlings; and (d) subordinate (Sub) and dominant (Dom) adults. Predicted relations from the model are shown. Means are shown ± 1 SE.

among females (see below). The frequency with which male helpers were the target of aggression was greater in small groups (where helper:pup ratios were relatively low) than in large groups (where helper:pup ratios were relatively high; $\chi^2_1 = 13.13$, $P < 0.001$; Fig. 7b), whereas group size had a lower influence on aggression received by females (see below). These results were not influenced by whether the male was an immigrant or natal individual (immigrant/natal∗feeding rate: $\chi^2_1 = 0.62$, $P = 0.43$). In addition, our results are unlikely to be confounded by any correlation between the incidence of immigration events, general levels of aggression and levels of pup feeding (Young 2003), because males with low pup-feeding rates still received more aggression when all instances of aggression within 3 months of immigration events were omitted ($\chi^2_1 = 5.50$, $P = 0.019$). Nor are they likely to be confounded by any correlation between male roving, levels of aggression received and contributions to pup care (Young 2003), because correlations between pup-feeding rates and aggression remained significant when we restricted our analysis to include only those males under a year old ($\chi^2_1 = 4.33$, $P = 0.038$), which rarely rove (Clutton-Brock et al. 2002).

Although the overall rate of aggression received by female helpers was higher, there was no significant relation between the provisioning rate and frequency of aggression received by females ($\chi^2_1 = 0.79$, $P = 0.38$; Fig 7a). In addition, the frequency with which female helpers received aggression varied significantly less with group size than it did for males, generating a significant interaction between sex and group size on aggression received (interaction: $\chi^2_1 = 7.86$, $P = 0.005$; Fig. 7b). Finally, females that provisioned a previous litter at a high rate were no more likely to be evicted from a group than those that provisioned a previous litter at a low rate (Young 2003).

'False Feeding' and Aggression

Individuals that 'false fed' pups were seldom threatened or attacked by other group members immediately after failing to feed the pup. However, males that 'false fed' a litter were the targets of more frequent aggression than those that were not observed to 'false feed' a litter ($\chi^2_1 = 5.01$, $P = 0.025$), whereas no similar effect was

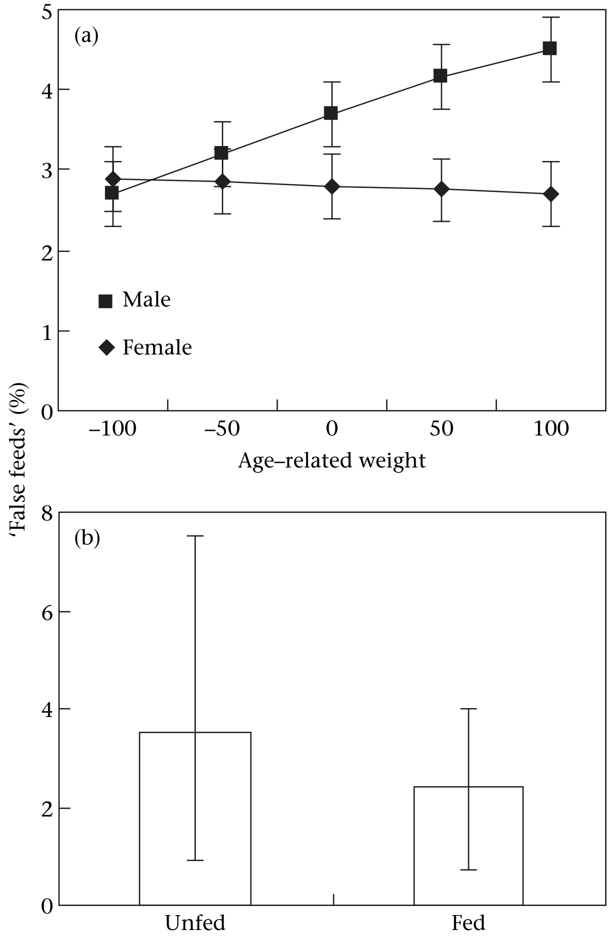

Figure 4. (a) Percentage of pup feeds by male and female carers (>6 months old) of different relative weights that were classified as 'false feeds'. An individual's age-related weight is a measure of its deviation from the expected weight for its age. (b) Percentage of pup feeds classified as 'false' by helpers (6–18 months) that had their daily food intake experimentally increased ('fed') versus unfed controls. The predicted relation from the model is shown in (a). Means are shown ± 1 SE.

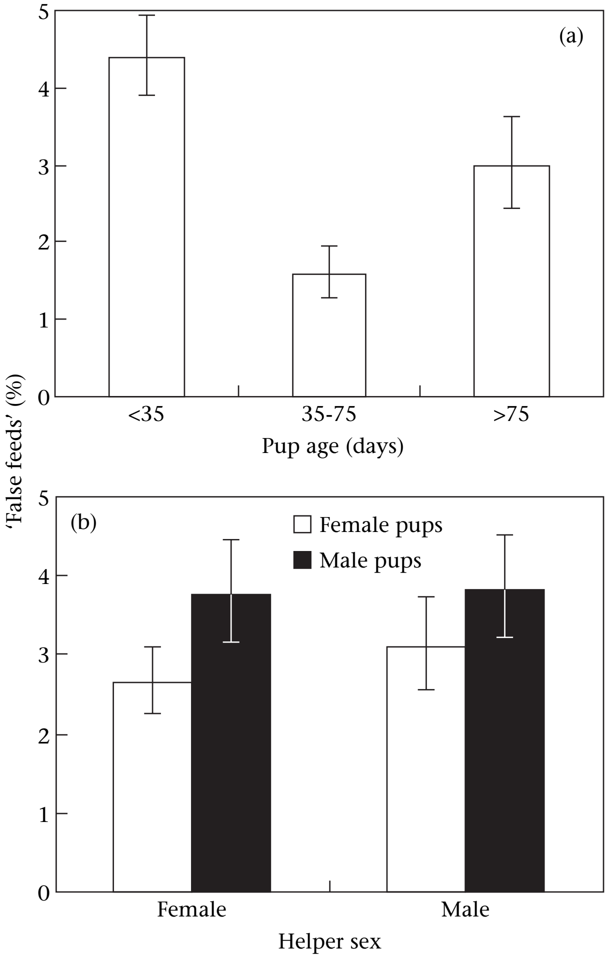

Figure 5. The effects of pup characteristics on the incidence of 'false feeding': (a) percentage of feeds to pups of three age classes that were classified as 'false feeds'; and (b) percentage of feeds to male and female pups by female and male helpers that were classified as 'false feeds'. Sexes are combined in (a) because no significant sex differences were found. Means are shown ± 1 SE.

observed among females ($\chi^2_1 = 0.09$, $P = 0.76$), generating a significant interaction between sex and 'false feeding' on aggression ($\chi^2_1 = 7.45$, $P = 0.006$; Fig. 8a). The increases in aggression directed at males seen to 'false feed' pups presumably occurred because dominant males (who principally target subordinate males, see Fig. 6c) were more aggressive towards 'false feeders' ($\chi^2_1 = 5.08$, $P = 0.024$; Fig. 8b), whereas dominant females (which principally target subordinate females, see Fig. 6b) appeared to treat 'false feeders' and non 'false feeders' more similarly ($\chi^2_1 = 1.42$, $P = 0.23$; Fig. 8b). This interpretation is supported by the finding that neither subordinate males ($\chi^2_1 = 0.93$, $P = 0.33$) nor subordinate females ($\chi^2_1 = 0.31$, $P = 0.58$) were more likely to be aggressive to individuals that false feed pups (Fig. 8c).

Again, instances of aggression received by males were not influenced by whether the male was an immigrant or natal (immigration status∗'false fed' or not: $\chi^2_1 = 0.57$, $P = 0.45$). In addition, our results are unlikely to be confounded by any correlation between immigration events, general levels of aggression and levels of 'false feeding', because the significance remained when all aggressive interactions within 3 months of immigration events were omitted ($\chi^2_1 = 6.16$, $P = 0.013$). Nor are our results likely to be confounded by a correlation between male roving, levels of aggression received and rates of 'false feeding', since correlations between 'false feeding' and aggression remained significant when we restricted our analysis to include only those males under a year old ($\chi^2_1 = 4.00$, $P = 0.045$), which rarely rove (Clutton-Brock et al. 2002).

DISCUSSION

Cheating is commonly expected to be widespread in cooperative societies, but evidence of deceptive tactics is scarce. One of the most obvious behaviours that may involve deception is 'false feeding' (Boland et al. 1997a),

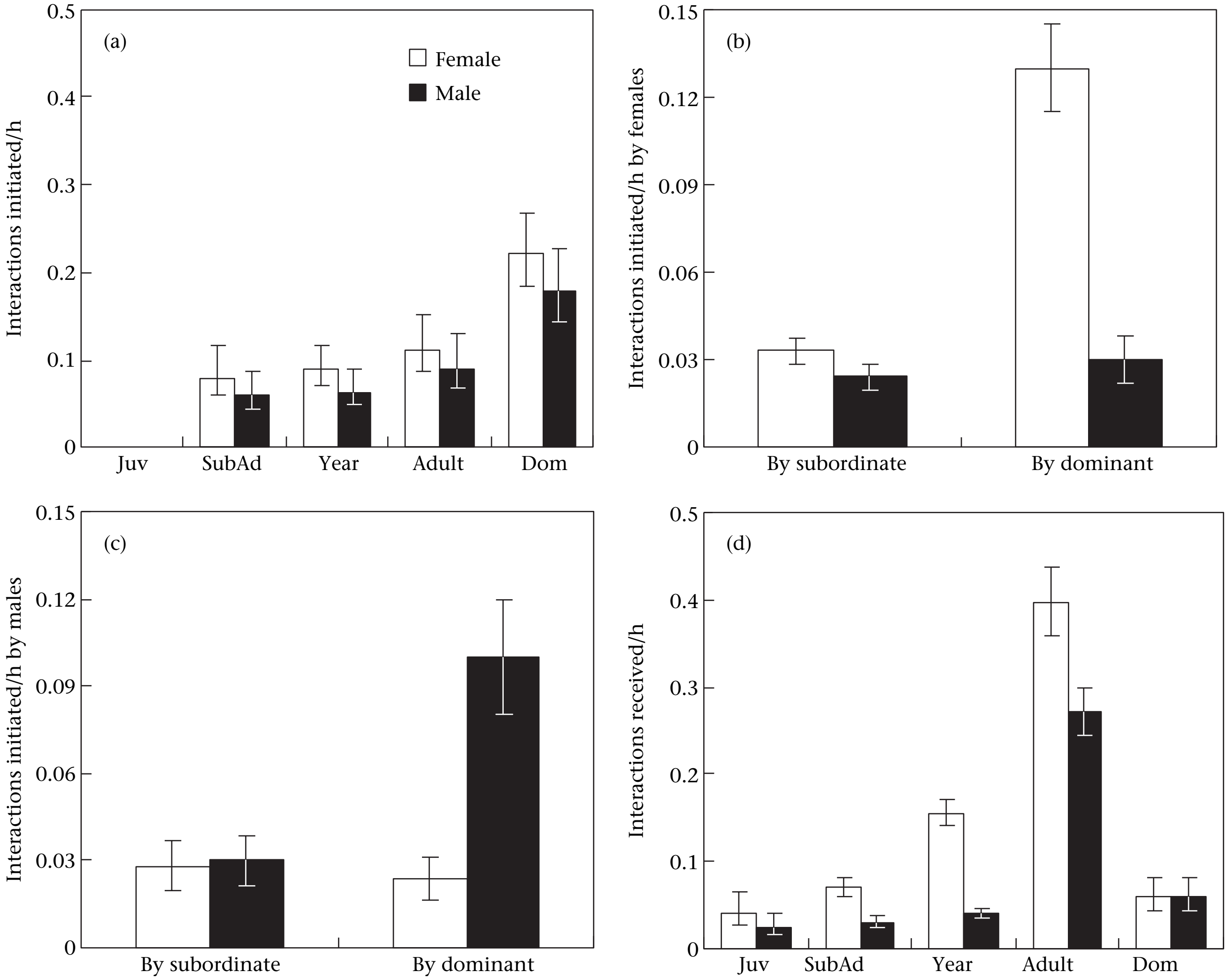

Figure 6. The distribution of aggression in meerkat groups: (a) the rate of aggressive interactions initiated by males and females of different age/status; (b) the rate of aggressive interactions initiated by subordinate and dominant females that were directed at females versus males; (c) the rate of aggressive interactions initiated by subordinate and dominant males that were directed at females versus males; and (d) the rate of aggressive interactions received by female and male group members of different age/status. Juv: juvenile; SubAd: subadult; Year: yearling; Adult: subordinate adult; Dom: dominant adult. Rates of aggression are inflated since only those individuals observed to initiate or receive any aggression are included. Means are shown ± 1 SE.

and some aspects of the distribution of 'false feeding' in meerkats are consistent with the suggestion that it is a cheating tactic used to exaggerate the proportion of food that helpers give to pups. For example, male helpers were more likely to become the target of aggression if they had low provisioning rates (Fig. 7a) and males with low provisioning rates 'false fed' pups more frequently than those with higher provisioning rates (Fig. 3). In addition, males that are heavy for their age provision offspring at a lower level than those that are light for their age (Clutton-Brock et al. 2002). Consequently, heavy males may 'false feed' more than light males (Fig. 4a) to disguise the fact that they were not contributing as much to rearing young as their nutritional status would allow (Clutton-Brock et al. 2002).

On the other hand, the evidence that 'false feeding' is a cheating tactic in meerkats is equivocal. We found little evidence to suggest that 'false feeding' involves deception. Helpers that 'false fed' pups made no obvious attempt to disguise their actions and usually 'false fed' in the presence of other group members. In neither sex was there a close match between the age-related distribution of 'false feeding' (Fig. 2) and the age-related distribution of aggression received (Fig. 6d). Among females, pup-provisioning rates were associated with neither the amount of aggression received (Fig. 7a) nor the probability that they would be evicted from the group (Young 2003), and females received more aggression than males (Fig. 6d), despite contributing significantly more to pup feeding (Clutton-Brock et al. 2002). The increased frequency of aggression received by males that 'false fed' pups (Fig. 8a) relative to those that fed at a low level (Fig. 7a) suggests that 'false feeding' would be unsuccessful in deceiving other group members. Furthermore, the level of 'false feeding' does not appear to follow closely the benefits that individuals might derive from deceiving other group

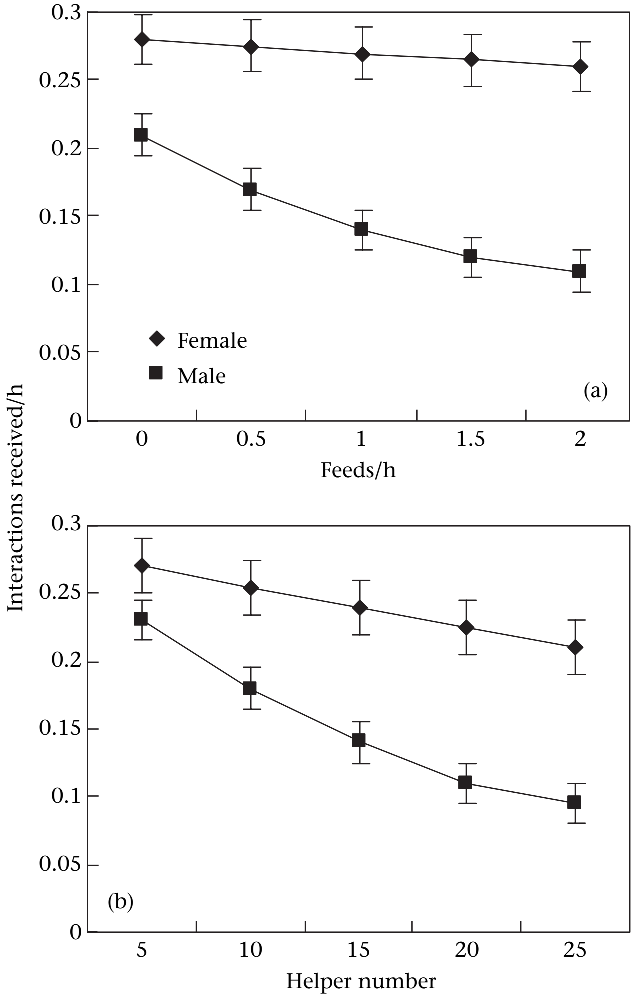

Figure 7. Factors affecting rates of aggression received: (a) rate of aggressive interactions received by subordinate males and females that fed pups at different rates; (b) rate of aggressive interactions received by subordinate males and females in groups of different size. Predicted relations from the model are shown and rates of aggression are inflated since only those individuals observed to initiate or receive any aggression are included. Means are shown ± 1 SE.

members. For example, that all group members varied their 'false-feeding' rate to the same extent with prey size (Fig. 1a), helper number (Fig. 1b) and pup age (Fig. 5a) suggests that any deception is likely to be of little benefit. In addition, immigrant, subordinate males (who may breed with the dominant female) did not show significantly higher rates of 'false feeding' than natal males (which are unlikely to breed in the group).

Studies of 'false feeding' in cooperative birds have also failed to find a close match between the distribution of 'false feeding' and the likely benefits that group members might derive from deceptive tactics. There is as yet no direct evidence that 'false feeding' successfully deceives other group members and causes them to modify their behaviour to the 'false feeder's' benefit (e.g. Putland 2001). In cooperatively breeding carrion crows, *Corvus corone*, resident breeding females 'false feed' more frequently than other individuals, but 'false feeding' is not more common in cooperative groups than in pairs nor when individuals are alone at the nest compared to times when group members are present (Canestrari et al. 2004). Furthermore, in other cases, evidence that 'false feeding' represents a deceptive tactic is also equivocal. For example, in white-winged choughs, Boland et al. (1997a) argued that 'false feeding' is a deceptive tactic on the grounds that (1) 'false feeds' usually occur when no other group members are watching; (2) 'false feeders' are sometimes punished by other group members; and (3) rates of 'false feeding' fall when group members are provided with supplementary food. However, an alternative, and simpler, possibility is that no deception is involved and that helpers that wait until they are alone at the nest before 'false feeding' gain immediate benefits by avoiding the risk of punishment. In this case, the situation is analogous to the behaviour of subordinate male primates, which commonly wait until the attention of the dominant male is distracted before attempting to mate with the female, thereby avoiding the risk of dangerous punishment (Dunbar 1984). In addition, reductions in 'false feeding' when supplementary food is available may arise simply because helpers are less hungry (Boland et al. 1997b), while 'false feeders' may be punished by other group members for laziness rather than deception.

Our data are consistent with the more parsimonious suggestions that helpers simply decide whether to feed or 'false feed' after assessing the needs of offspring relative to their own (Canestrari et al. 2004) or where conflicting motivational tendencies (in this case hunger and alloparental motivation) are finely balanced, with the result that helpers vacillate between alternative options. First, 'false feeding' in meerkat groups occurred when the motivation of helpers to feed pups was relatively weak (Clutton-Brock et al. 2002). Relative rates of 'false feeding' were high in helpers less than 6 months old (which were still growing rapidly) as well as in adult helpers (which were more likely to leave the group or to breed themselves) (Fig. 2). Males fed pups less than females and generally 'false fed' pups more than females, and males that were heavy for their age (which were likely to disperse sooner) 'false fed' pups more than lighter ones (Fig. 4a). Young males that provisioned at low rates were usually more likely to 'false feed' than those that provisioned at higher levels, whereas in females such significant relations were evident only among older individuals that were more likely to breed (Fig. 3). Among helpers of both sexes, rates of 'false feeding' appeared to be related to hunger: helpers were more likely to 'false feed' larger food items of higher nutritional value than smaller ones (Fig. 1a); 'false-feeding' rates increased in small groups (Fig. 1b), where demands on helpers are relatively high and individuals give pups a relatively larger proportion of the food items they find (Clutton-Brock et al. 2001b); and 'false-feeding' rates tended to be reduced by the provisioning of supplementary food (Fig. 4b; see also Boland et al. 1997a). In addition, female helpers are less motivated to feed male pups (Brotherton et al. 2001; Clutton-Brock et al. 2002) and, accordingly, females 'false fed' male pups more often than they 'false fed' female pups (Fig. 5b).

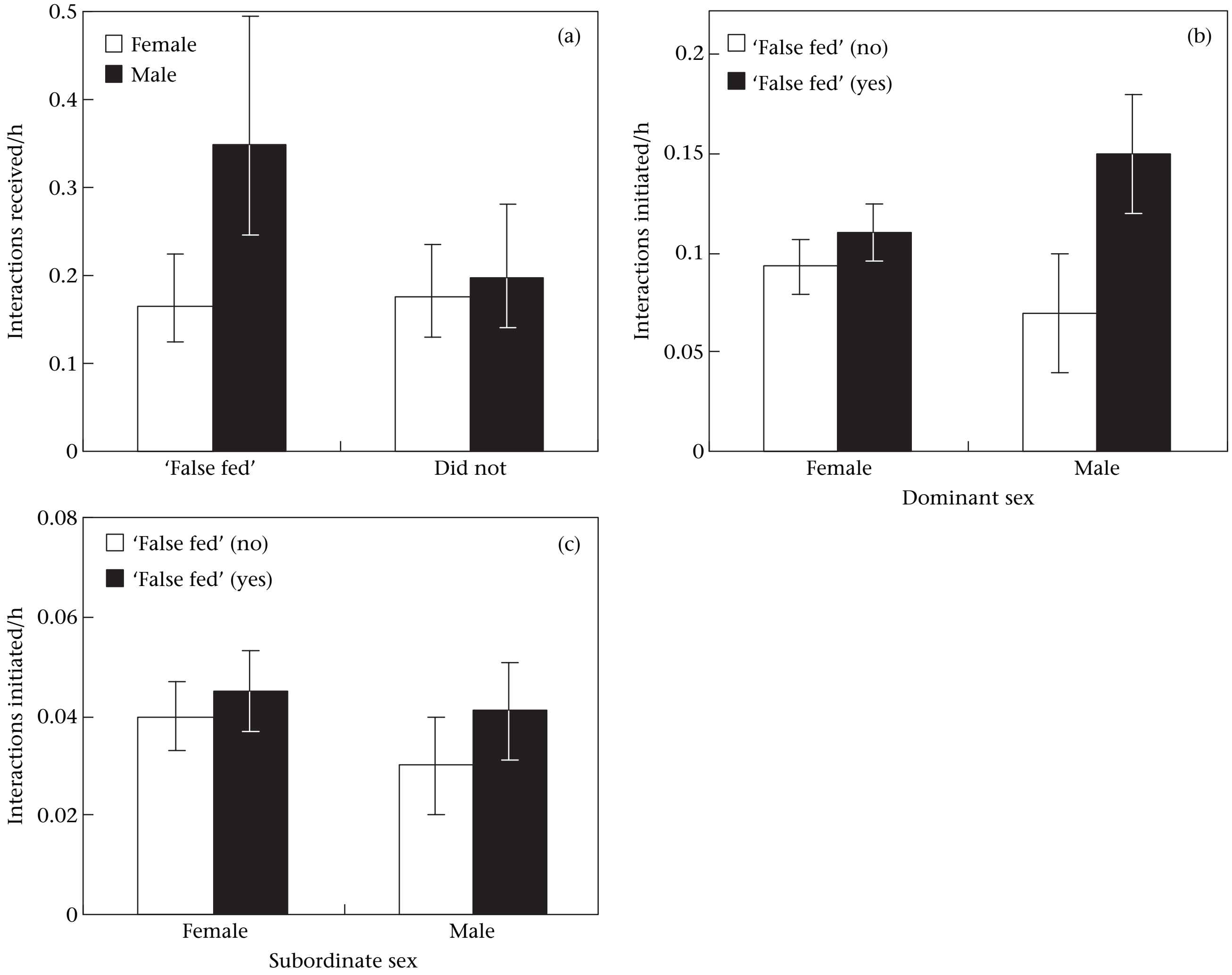

Figure 8. (a) Rate of aggressive interactions received by male and female carers that were or were not observed to 'false feed' litters; (b) rate of aggressive interactions initiated by the dominant female and male towards those that were and were not observed to 'false feed' pups; and (c) rate of aggressive interactions initiated by subordinate female and male group members towards those that were and were not observed to 'false feed' pups. Rates of aggression are inflated since only those individuals observed to initiate or receive any aggression are included. Means are shown ± 1 SE.

Second, 'false feeding' was more common where the relative needs of offspring were low (also see above). Individuals that brought food to pups that were already eating or that showed little interest in taking the food generally ate the item themselves. Pups that have begun to forage with the group only recently and are still largely dependent on milk, and those that are over 10 weeks of age, and are largely independent, do not beg as persistently as pups that are primarily dependent upon food provided by carers (Manser & Avey 2000) and were 'false fed' more (Fig. 5a). The relatively high rates at which male pups were 'false fed' could also occur because female helpers (which tend to discriminate against male pups; Brotherton et al. 2001; Clutton-Brock et al. 2002) determined the sex of pups only after reaching them.

In conclusion, despite the common expectation that cheating may be widespread in cooperative societies, firm evidence of deceptive tactics is rare. This may partly be a result of the problems associated with demonstrating that animals are using tactics that are designed to deceive (Semple & McComb 1996). However, an alternative possibility is that 'cheating' tactics are not as likely to be favoured in cooperative societies as is commonly supposed. In many specialized cooperative societies, the benefits to all group members increase with the size of the group and the direct benefits of contributing to the rearing of young may be large (Clutton-Brock et al. 2001c, 2002). In addition, the fitness costs of cooperative behaviour may be relatively low, since contributions to most cooperative activities are commonly conditional on the helper's nutritional status and previous contribution to cooperation (Russell et al. 2003b). Recent models of the evolution of cooperative societies show that, even where group members are unrelated to each other, the benefits of cooperation can prevent its erosion by cheating strategies and these effects are likely to be reinforced where most group members are related, as in meerkats and most other cooperative vertebrates (Kokko et al. 2001; Avilés et al. 2002).

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