



Trade-offs between extraterritorial prospecting and helping in a cooperative mammal

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Males commonly face a trade-off between investment in offspring care and time spent seeking additional breeding opportunities. Although this trade-off is central to our understanding of the evolution of male parental care, it has been largely ignored by studies of male alloparental care in cooperative societies, where male helpers could face a similar problem. We investigated whether male helpers in cooperative societies of meerkats *Suricata suricatta* trade off their cooperative contributions to pup feeding against extraterritorial prospecting for mating and dispersal opportunities. Not only did male helpers spend extended periods away from the group during pup care periods, but those that spent most time prospecting also contributed least to pup feeding when present in the group. Regular prospectors lost the most weight over the pup-feeding period and male testosterone levels increased in association with prospecting. As both reduced body condition and elevated testosterone have been shown to compromise the expression of offspring care, these findings provide likely explanations for the reduced pup-feeding rates of regular prospectors. Despite their lapses in contributions to cooperative activities, we found no evidence for punishment of prospectors by other group members, suggesting that helpers are able to adjust their contributions according to their own optima. These findings reveal that male helpers in cooperative species can face similar trade-offs to male parents in noncooperative species, between investment in offspring care and alternative fitness-maximizing tactics such as prospecting. We discuss the broader implications of this work for our understanding of both individual variation and sex differences in contributions to cooperative behaviour.

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Males commonly face a trade-off between investment in offspring care and time spent seeking additional breeding opportunities (Trivers 1972). This trade-off is central to our understanding of the evolution of male parental care (Trivers 1972; Clutton-Brock 1991; Manica & Johnstone 2005), yet it has been largely ignored by attempts to understand the evolution of male alloparental care in cooperative societies (in which individuals help to rear offspring that are not their own). If male helpers in cooperative species experience a similar trade-off to male parents in noncooperative species, this could have important ramifications for our understanding of both individual variation and sex differences in contributions to cooperative behaviours. In this study, we investigated whether male helpers in cooperative societies of meerkats,

Suricata suricatta, experience a trade-off between alloparental care and extraterritorial prospecting for mating and dispersal opportunities, the proximate factors that could mediate such a trade-off, and the extent to which it gives rise to conflict with other group members.

Helpers are known to conduct extraterritorial prospecting forays in many cooperative vertebrates (e.g. Koenig & Stacey 1990; Woolfenden & Fitzpatrick 1990; Walters et al. 1992; Doolan & Macdonald 1996; Sillero-Zubiri et al. 1996; Creel & Creel 2002). Prospecting may yield immediate fitness benefits by circumventing local constraints on subordinate reproduction (e.g. reproductive monopolies: Keller & Reeve 1994; or a lack of access to unrelated breeding partners: O'Riain et al. 2000), and longer-term fitness benefits by facilitating the assessment and seizure of dispersal opportunities (Waser 1996; Young 2003). To maximize their fitness over the long term, helpers may therefore invest in a combination of both alloparental care and extraterritorial prospecting.

Extraterritorial prospecting is likely to trade off against helping simply because prospectors are unable to care for

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offspring while on forays. In addition, effects of prospecting on an individual's body condition or physiology could affect the expression of offspring care even when it is available to help. Prospectors may return to their group in reduced condition, either as a result of the inefficiency of foraging alone (Creel & Creel 2002) or because they forego foraging in favour of seeking and competing for mating and dispersal opportunities (e.g. Koenig 1981; Griffin et al. 2003). As investment in cooperative care is typically both costly and condition dependent (e.g. Heinsohn & Cockburn 1994; Clutton-Brock et al. 2002; Russell et al. 2003), regular prospectors may reduce their helper contributions to recoup any condition lost during their forays. Prospectors may also return to their group in an altered endocrine state, having experienced intrasexual competition over mating and dispersal opportunities, which is known to stimulate the production of androgens in both sexes (Wingfield et al. 1990; Langmore et al. 2002). While elevated levels of testosterone typically interfere with parental care (Wingfield et al. 1990; Ketterson & Nolan 1994), elevated levels of the peptide hormone prolactin are thought to facilitate its expression (de Vlaming 1979; Buntin 1996). As recent studies suggest that similar endocrine processes mediate the expression of alloparental care in cooperative species (e.g. Schoech et al. 1996; Ziegler et al. 1996; Khan et al. 2001; Roberts et al. 2001), effects of prospecting on concentrations of either hormone could alter the expression of offspring care by regular prospectors.

If helpers do trade off prospecting against their contributions to cooperative activities, conflict may arise with other group members. This is because reductions in one individual's contributions may adversely affect the fitness of other group members, either by reducing local productivity (e.g. Clutton-Brock et al. 2001b), or by increasing the costly workload required of others (e.g. Khan & Walters 2002). Few studies have investigated whether members of cooperative societies are in conflict over their relative work rates, with mixed results. Early studies of social insects suggested that queens may use aggression to motivate 'lazy' workers (Reeve & Gamboa 1983, 1987). Initial research yielded similar results in naked mole-rats, *Heterocephalus glaber* (Reeve 1992), but further work failed to reach the same conclusions (Jacobs & Jarvis 1996; Clarke & Faulkes 2001). Two studies used temporary helper removal experiments to simulate a cessation of helping and found that returning helpers were often attacked (Mulder & Langmore 1993; Balshine-Earn et al. 1998). However, it is difficult to rule out the possibility that this aggression resulted in part from the disruption of a dominance hierarchy. Further studies are clearly required to clarify the role of punishment in governing helper contributions, and species in which helpers face a trade-off between alloparental care and other activities may prove ideal subjects.

In meerkat societies, young of both sexes delay dispersal from their natal group and help to rear future generations of offspring born to dominants (Clutton-Brock et al. 2002). Male helpers also regularly conduct extraterritorial prospecting forays, ranging in length from an afternoon to a month at a time (Young 2003). During these forays,

they attempt both to mate with females in other groups and to seize dispersal opportunities, subject to aggressive encounters with foreign males (Doolan & Macdonald 1996; Griffin et al. 2003; Young 2003). Although variation in individual contributions to cooperation has received considerable attention in this species (e.g. Clutton-Brock et al. 2002), the extent to which males trade off their investment in prospecting against their investment in care has yet to be investigated. As helper contributions to pup feeding influence offspring growth and survival and thereby the fitness of all group members (Clutton-Brock et al. 2001b; Russell et al. 2002), any trade-off between prospecting and pup feeding might be expected to fuel within-group conflict over prospecting rates. Indeed, recent work suggests that male meerkats with lower pup-feeding rates may be subjected to higher rates of aggression (Clutton-Brock et al. 2005), although the role of prospecting in this association remains unexplored.

Using data from our long-term study of meerkat societies, we investigated three specific questions: (1) do male helpers trade off their investment in extraterritorial prospecting against their contributions to cooperative pup feeding; (2) could any such trade-off be mediated by effects of prospecting on a male's body condition and/or endocrine state; and (3) is there any evidence of within-group conflict over the prospecting rates of male helpers?

METHODS

Study Population and Data Collection

We conducted the study on ranchland in the South African Kalahari Desert (26°59'S, 21°50'E) between November 1998 and May 2002. Details of the study site, population and climate have been described in detail elsewhere (Russell et al. 2002). Our study population comprised 10 focal groups of meerkats that had been habituated to close observation, allowing us to collect detailed behavioural, weight and endocrine data. All individuals in each group were individually recognizable by unique 'hair cuts', which were easily maintained while the animals rested, without the need for capture. All research protocols were approved by the Research Ethics Committee at the University of Pretoria, and Northern Cape Conservation granted permission to conduct the research.

We visited study groups at least once every 3 days to assess group composition and collect behavioural data. Here, we refer to individuals under 90 days old as pups and individuals over 1 year old as adults. All pup-feeding events (the donation of a prey item to a pup) and aggressive interactions were recorded ad libitum. Individuals were classified as having had an aggressive interaction if (1) they were subjected to one of five aggressive behaviours: attacks (where one animal bit another); hip-slams (where one animal attempted to displace another with a sideways motion of the hips); chin-marks (where one animal rubbed its chin on another); charges (where one animal ran directly at another); and sits (where one

animal sat on another's head); or (2) they showed behavioural submission to another group member (a clear lowering of the head and shoulders, associated with a high-pitched peeping vocalization). Rates of pup feeding and aggressive interactions could then be calculated for each individual on a given day by accounting for observation time. Individuals were weighed on an electronic balance, both before ('morning weights') and at the end of ('midday weights') the morning foraging period. We used rates of morning weight gain as an indication of an individual's foraging success (g/h), calculated as (midday weight – morning weight)/number of hours between weighing sessions. We used these absolute rates of morning weight gain for paired comparisons between contexts for the same individual. When an analysis considered several individuals, we standardized this measure of weight gain by dividing again by the individual's morning weight, yielding a proportional rate of morning weight gain (% morning weight/h).

We considered males to have conducted a prospecting foray if they were observed as absent from their group or were sighted elsewhere. Each prospecting foray was assigned a leave date (the earliest day the male could have left the group) and a return date (the latest day the male could have returned). These dates were generally accurate to the day. Subordinate adult males that had yet to disperse from their natal groups spent considerably more time prospecting than either immigrant subordinate males or dominant males (Young 2003), so our analyses focus on these males only.

Blood Sampling and Endocrine Assays

Target animals were placed in a capture bag and immobilized with a single intramuscular injection of Anaket-V at 5 mg/kg (100 mg/ml Ketamine hydrochloride) and Dormitor at 0.03 mg/kg (1 mg/ml Medetomidine hydrochloride) as per O'Riain et al. (2000). Blood (1 ml) was drawn from the jugular vein within 4–6 min of capture to minimize the effect of capture stress on prolactin release (Carlson et al. 2003). All samples were collected between 1600 and 2000 hours to minimize diel variation. The effects of the sedative were reversed with a single intramuscular injection of Antisedan at 0.2 mg/kg (5 mg/ml Atipamezole). Recovering animals were monitored in a large ventilated container, and were returned to their groups once fully coordinated (60–90 min after capture), typically at the evening sleeping burrow. All animals reintegrated quickly into their groups and the capture procedure had no detectable effect on either their behaviour or habituation. Blood samples were immediately placed on ice and, on return to base camp, were centrifuged for 5 min at 500 g and the plasma drawn off. Plasma samples were kept frozen until assaying.

To assay samples for testosterone we used Coat-a-Count Testosterone kits (Diagnostic Products Corporation, Los Angeles, California, U.S.A.), which had been validated for use with meerkat plasma (Carlson et al. 2004). Assay sensitivity was 20 ng/dl. Intra- and interassay coefficients of variation were 4.1% and 6.2%, respectively. To assay

samples for prolactin we used a highly specific heterologous radioimmunoassay (using rabbit antiserum to human prolactin and canine [¹²⁵I] iodoprolactin), which had been validated for use with meerkat plasma (Carlson et al. 2003). Assay sensitivity was 0.05 ng/ml. Intra- and interassay coefficients of variation were 8.3% and 12.6%, respectively.

Statistical Analyses

For all statistical analyses we used GenStat (5th edn, release 4.2, Lawes Agricultural Trust, Rothamsted, Harpenden, U.K.). Most analyses required the use of multivariate statistics, for which General(ized) Linear Models (GLMs) were used. All terms were initially entered into the model and then sequentially dropped until only terms whose elimination would have significantly reduced the explanatory power of the model remained. All two-way interactions were tested, but only those that were significant are presented in the tables. The significance of a term was derived by dropping it from the final model (if it was part of the final model), or adding it to the final model and then dropping it (if it was not part of the final model). Three such analyses involved repeated measures of the same individual, breeding attempt or group, and in these cases General(ized) Linear Mixed Models (GLMMs) were used. These are similar to GLMs but allow both fixed terms and random terms to be defined. Random terms allow the analysis to take account of repeated measures, and were included only if the analysis indicated significant repeatability at that level (as per Pinheiro & Bates 2000). All statistical tests were two tailed.

Trade-off between prospecting and pup feeding

We used a GLMM to investigate the influence of the number of days a male spent prospecting during the peak pup-feeding period of a given breeding attempt (when the pups are 30–75 days old) on his mean pup-feeding rate on the days that he was present in the group during that period. Each male's mean pup-feeding rate for each peak pup-feeding period was calculated as the total number of pup feeds he was observed donating, divided by the number of hours an observer was present at the group when the male was also present. Males were included in the analysis only if they had been sampled for at least 10 h of ad libitum data collection during the relevant pup-feeding period. Pup-feeding rates were normalized for analysis with a square-root transformation. In addition to the number of days spent prospecting, several terms were fitted to the model: male age; group size (excluding pups); litter size; maximum temperature; rainfall; male morning weight (when in the group); male proportional morning weight gain/h (when in the group); and helper-pup relatedness. All terms were average values calculated from all measures available over the relevant peak pup-feeding period. Relatedness was calculated with genetically assigned paternities and maternities (Griffin et al. 2003) and was considered as a three-level factor: High if the helper and the litter shared both parents; Medium if they

shared one parent; and Low if they shared no parents. Table 1 gives the sample size and the significance of the random terms.

Prospecting and body weight

To assess the effect of individual prospecting forays on a male's weight, we compared males' morning weights on the day of departure to those on the morning after their return from the same foray ($N = 103$ males). To establish whether males attempted to compensate for any weight change while prospecting, we compared prospectors' rates of weight gain on the morning of the day before departure with those on the morning of the day after their return ($N = 50$ males). For both analyses, data for multiple forays by the same male were averaged to eliminate pseudoreplication.

To investigate the longer-term effect of regular prospecting on a male's weight, we used a GLMM to assess the effect of the number of days a male spent prospecting during the peak pup-feeding period on his proportional weight change across that period. For each male, we

Table 1. General Linear Mixed Model investigating the effect of time spent prospecting during peak pup-feeding periods on a male's pup-feeding rate when present in the group

	Wald statistic (χ^2)	df	P
Full model			
Group size (excluding pups)	46.65	1	<0.001
Total time spent prospecting (days)	19.62	1	<0.001
Litter size	11.00	1	<0.001
Male age (days)	9.60	1	0.002
Total rainfall	6.41	1	0.011
Relatedness to litter (High, Medium, Low)	4.06	2	0.13
Average maximum temperature	1.38	1	0.24
Average morning weight (g)*	0.19	1	0.67
Average rate of morning weight gain (g/h)	0.10	1	0.76
Final model	Average effect	SE	
Constant	0.62	0.024	
Group size (excluding pups)	-0.025	0.0037	
Time spent prospecting (days)	-0.012	0.0024	
Litter size	0.062	0.019	
Male age (days)	-0.00022	0.000071	
Total rainfall	0.0012	0.00047	

This analysis was based on a sample of 269 pup-feeding rates from 105 males during the peak pup-feeding periods of 53 breeding attempts in nine groups. There was significant repeatability of pup-feeding rates by both breeding attempt and male identity ($P < 0.05$), so both were included as random factors in the GLMM. There was no significant repeatability of group identity ($P > 0.1$). 'Average effect' refers to the model coefficient for a given independent variable.

*Residuals taken against male age.

calculated a mean start weight by averaging all his morning weights within 2 days of the pups becoming 30 days old. A mean end weight was calculated in the same way, around the day the pups were 75 days old. A male's proportional weight change was then calculated, for each pup-feeding period, as the weight change across the pup-feeding period (mean end weight minus mean start weight) divided by the mean start weight. In addition to the number of days spent prospecting, several terms were fitted to the model: male age; the male's average pup-feeding rate when present in the group; group size (excluding pups); litter size; maximum daily temperature and rainfall. All terms were average values calculated from all measures available over the relevant peak pup-feeding period. Table 2 gives the sample size and the significance of the random terms.

Prospecting and endocrine state

To assess the effects of prospecting on hormone levels, we collected blood samples from males in three contexts: baseline: not within 4 days of a prospecting foray, but not during nonprospecting periods (March and April, Young 2003); prospecting day: while away from the group; return: within 3 days of return from prospecting. Within each context, each blood sample was collected from a different male, to avoid pseudoreplication. We used

Table 2. General Linear Mixed Model investigating the effect of time spent prospecting on a male's proportional weight change across the peak pup-feeding period

	Wald statistic (χ^2)	df	P
Full model			
Average maximum temperature	11.09	1	<0.001
Group size (excluding pups)	6.91	1	0.009
Time spent prospecting (days)	6.25	1	0.012
Total rainfall	1.25	1	0.26
Pup-feeding rate (feeds/h)	0.23	1	0.63
Litter size	0.16	1	0.69
Male age (days)	0.01	1	0.93
Final model	Average effect	SE	
Constant	0.029	0.0080	
Average maximum temperature	-0.0049	0.0015	
Group size (excluding pups)	0.0035	0.0013	
Time spent prospecting (days)	-0.0015	0.00059	

This analysis was based on a sample of 225 proportional weight changes over the pup-feeding period, from 87 males during 52 breeding attempts in nine groups. There was significant repeatability of proportional weight changes by breeding attempt ($P < 0.05$), so it was included as a random factor in the GLMM. There was no significant repeatability of either male or group identity ($P > 0.1$). 'Average effect' refers to the model coefficient for a given independent variable.

separate GLMs to examine the effect of prospecting context on plasma levels of testosterone and prolactin (which were both normally distributed), while simultaneously controlling for variation in male age. The testosterone analysis used a data set of 44 samples (21 baseline, 10 prospecting, 13 return). The prolactin analysis used a data set of 47 samples (25 baseline, 11 prospecting, 11 return). Males were sampled from a total of eight breeding groups for both analyses.

Prospecting and conflict with other group members

We conducted three analyses to investigate whether prospecting activities gave rise to overt conflict with other group members. First, a male's rate of receipt of aggressive interactions on his day of return from a foray was compared to his average rate for the week prior to departure ($N = 40$ males). Where rates were available for multiple forays by the same male, average values were calculated. Forays were considered in this analysis only if the male had not left the group during the week prior to departure.

Second, a male's rate of receipt of aggressive interactions on the day of return from a foray was compared for pup-feeding periods and periods when there were no pups in the group ($N = 38$ males). Where rates were available for multiple forays by the same male in a given context, average values were calculated.

Third, we used a GLMM to investigate the effect of the number of days a male spent prospecting during the peak pup-feeding period, and his mean pup-feeding rate during the same period, on the probability that he received one or more aggressive interactions during that period. Because aggressive interactions were so infrequent, it was not possible to analyse the rate of receipt of aggressive interactions as a continuous variable. Instead, each male was classified as having received either some (one or more) or no aggressive interactions during each peak pup-feeding period, and this binary term was set as the binomial response in the GLMM. Total observation time was included as a fixed effect in the model, in addition to male age, group size (excluding pups), rainfall, maximum temperature and the ratio of helpers (nonpups) to pups. The analysis was based on a sample of 267 binary aggressive interaction 'rates' for 106 subordinate males, during 53 breeding attempts by dominant females in nine groups. There was significant repeatability of aggressive interaction 'rates' by breeding attempt ($P < 0.05$), so it was included as a random factor in the GLMM, but there was no significant repeatability of either male or group identity (both $P > 0.1$).

RESULTS

Trade-off Between Prospecting and Pup Feeding

During the 45-day peak pup-feeding period, subordinate adult males in their natal groups spent an average \pm SE of 3.72 ± 0.34 days prospecting (range 0–35 days, $N = 322$

pup-feeding periods for 116 males). Among males, 44% spent no days prospecting, 39% spent 1–7 days prospecting, 10% spent 8–14 days prospecting and 7% spent more than 14 days prospecting. Not only were prospectors unavailable for pup feeding while absent from the group, but when they were actually present, those males that spent more time prospecting during peak pup-feeding periods also fed the pups at lower rates than other males (Fig. 1, Table 1).

Prospecting and Body Weight

Male body weights fell significantly during prospecting forays (paired t test: $t_{102} = 8.97$, $P < 0.001$; Fig. 2a). Males then gained weight significantly faster on the day after their return from prospecting, relative to the day before their departure ($t_{49} = 2.01$, $P = 0.05$; Fig. 2b). However, the most frequent prospectors did not completely offset their prospecting weight losses, as the number of days a male spent prospecting during the peak pup-feeding period had a significant negative effect on his proportional weight change across that period (Table 2).

Prospecting and Endocrine State

Testosterone levels were significantly affected by prospecting forays (GLM: $F_{2,43} = 6.53$, $P = 0.003$; Fig. 3), being higher while prospecting than on baseline days spent within the group, and tending to remain elevated within 3 days of return from prospecting (Fig. 3). There was no significant effect of male age on testosterone levels (GLM: $F_{1,41} = 0.22$, $P = 0.64$). Prolactin levels were not significantly affected by either prospecting forays (GLM: $F_{2,46} = 2.03$, $P = 0.14$) or male age (GLM: $F_{1,46} = 0.55$, $P = 0.46$).

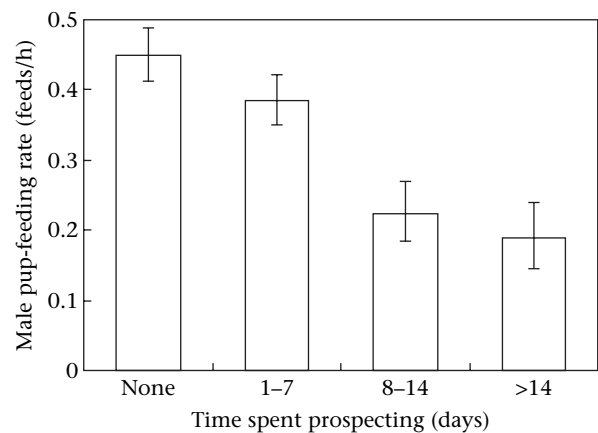


Figure 1. Pup-feeding rates of males, when present in the group, in relation to the total time spent prospecting during the 45-day peak pup-feeding period (Table 1). Means \pm SEs are predictions from the GLMM presented in Table 1, after we controlled for the effects of the other significant terms.

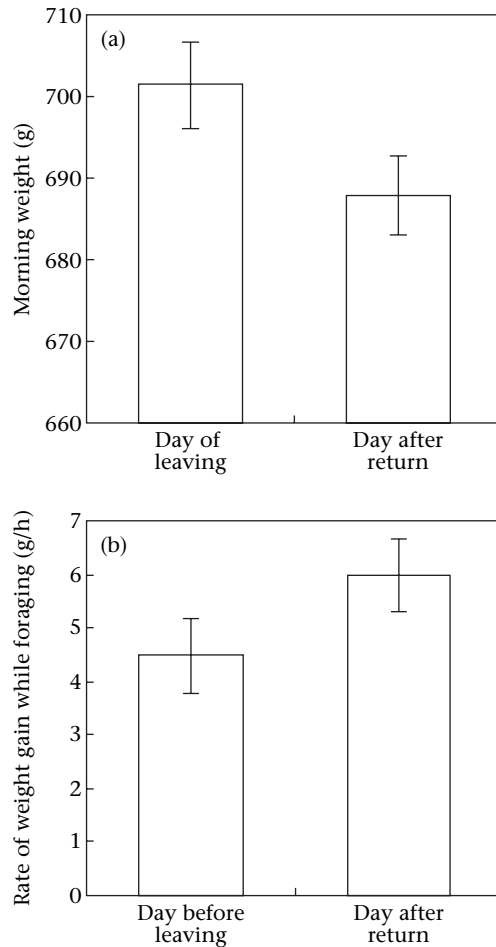


Figure 2. (a) Mean weights of 103 males \pm SE before and after their prospecting forays. (b) Mean rates of weight gain while foraging of 50 males \pm SE before and after their prospecting forays.

Prospecting and Conflict with Other Group Members

Aggressive interactions involving subordinate adult natal males were rare (on average only 0.023 interactions/male-hour; $N = 1297$ in 56 600 male-hours of ad libitum observation, of which only nine were actual attacks) and there was no evidence to suggest that they were associated with investment in prospecting forays. The rates of aggressive interactions received by males on the day of their return from a prospecting foray were not significantly different from those experienced by the same male on average during the week prior to departure (Wilcoxon matched-pairs test: $W = -11.00$, $N = 40$ males, $P = 0.57$). Returning prospectors did not experience higher rates of aggressive interactions during pup-feeding periods than during periods when the group was not caring for pups ($W = 35.00$, $N = 38$ males, $P = 0.30$). Finally, the probability of a male experiencing one or more aggressive interactions during the peak pup-feeding period was not significantly influenced by either the time the male spent prospecting during that period (GLMM: $\chi^2_1 = 0.1$, $P = 0.75$) or his average pup-feeding rate on the

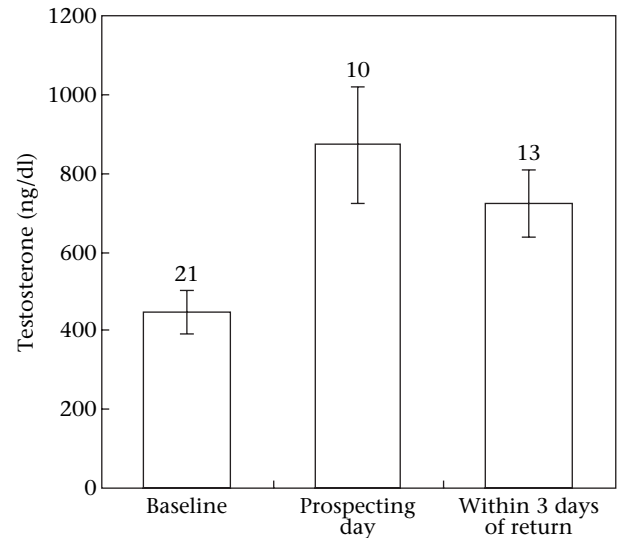


Figure 3. Plasma testosterone levels of males on 'baseline' days spent in their group (not within 4 days of a prospecting foray), on the prospecting day, and within 3 days of return from a prospecting foray. Tukey tests: baseline versus prospecting: $P = 0.005$; prospecting versus return: $P = 0.53$; return versus baseline: $P = 0.054$. Bars show means \pm SE with sample sizes above.

days he was present in the group (GLMM: $\chi^2_1 = 0.04$, $P = 0.85$), while we controlled for a significant positive effect of observation time (GLMM: $\chi^2_1 = 12.14$, $P < 0.001$). There was a nonsignificant trend for higher rates of aggressive interactions when rainfall was low (GLMM: $\chi^2_1 = 3.74$, $P = 0.053$), but no other fixed effects approached significance (all $P > 0.2$).

DISCUSSION

These findings strongly suggest that subordinate male meerkats trade off their investment in extraterritorial prospecting forays against their contributions to cooperative pup feeding. Not only were males unavailable to feed the pups while prospecting, but when males were present in the group, those that spent more time prospecting contributed less to cooperative pup feeding. Males experienced nutritional and physiological changes in association with prospecting (weight loss and elevated testosterone), which provide possible explanations for the reduced pup-feeding rates of regular prospectors, as both effects are known to compromise the expression of offspring care (Wingfield et al. 1990; Ketterson & Nolan 1994; Clutton-Brock et al. 2002). Despite the apparent trade-off between prospecting and pup feeding, prospecting did not elicit aggression from other group members, suggesting that prospectors are not punished for their absences. After considering these results in more detail, we discuss possible explanations for the lack of conflict over commitment to prospecting and the broader implications of this work for our understanding of cooperative animal societies.

Animals in poorer body condition commonly contribute less to offspring care, either as parents (e.g. Chastel

et al. 1995; Erikstad et al. 1997) or as helpers in cooperative societies (e.g. Clutton-Brock 2002; Hodge 2003). The weight loss associated with prospecting forays could therefore explain the reduced pup-feeding rates of regular prospectors. If males are able to recover this lost weight quickly though, the impact of weight loss on pup-feeding rates could be minimal. However, while males did increase their rates of food intake on return from a foray, the most frequent prospectors did not offset their prospecting losses completely, ultimately suffering the greatest weight loss over the entire pup-feeding period. If body condition does play a role in the trade-off between prospecting and helping, the fact that males do not appear to adjust their commitment to prospecting according to their body condition (A. Young, unpublished data) may exacerbate this trade-off in the long term. Rather than suspending their prospecting as their condition declines, regular prospectors may first reduce their contributions to pup feeding, only recovering any aggregate loss of condition in the nonbreeding season, when commitment to both activities ceases (Clutton-Brock et al. 2002; Young 2003).

Male testosterone levels increased in association with prospecting forays, probably because prospectors experience high rates of aggressive interactions as they approach foreign groups (Young 2003), which are known to stimulate testosterone surges in a variety of taxa (Wingfield et al. 1990). As prospector testosterone levels remained elevated after their return to the group and elevated testosterone levels are known to compromise the expression of offspring care in a number of species (Wingfield et al. 1990; Ketterson & Nolan 1994), this too provides a likely explanation for the lower pup-feeding rates of regular prospectors. Male prolactin levels appear to be unaffected by prospecting, which does not reduce the likely importance of the simultaneous changes in testosterone levels, as recent studies suggest that the inhibitory effects of testosterone on offspring care are mediated by a prolactin-independent mechanism, at least in birds (e.g. Schoech et al. 1998).

There are two alternative explanations for the apparent trade-off between prospecting and pup-feeding rates. First, as male meerkats reduce their contributions to pup feeding in the breeding attempt prior to dispersal (Clutton-Brock et al. 2002), the trade-off may arise because regular prospecting covaries with imminent dispersal (and thus reduced rates of pup feeding). However, such an association alone cannot explain the trade-off presented here, as neither the statistical significance nor the effect size of the negative association between prospecting and pup feeding (Table 1) are affected if all males within 6 months of dispersal are excluded from the analysis. Instead, the apparent trade-off between prospecting and helping provides a likely explanation for the reductions in pup care shown by males approaching dispersal (because these males are likely to be prospecting at high rates). Second, if males adjusted both their prospecting and pup-feeding rates in accordance with either their relatedness to the pups or their own age, this might explain the observed trade-off. However, variance in both helper-pup relatedness and helper age were controlled in our analysis of pup-feeding rates. Furthermore, previous analyses suggest that

meerkats feed their pups without regard to relatedness (Clutton-Brock et al. 2001a).

Although regular prospectors fed pups at reduced rates, we found no evidence that males were punished for their absences. This result is perhaps surprising, as cooperative pup feeding is known to influence pup growth and survival and thereby the fitness of all group members (Clutton-Brock et al. 2001b; Russell et al. 2002). There is also some evidence to suggest that 'lazy' males may be encouraged to feed pups by other group members (Clutton-Brock et al. 2005). One possible explanation for the lack of punishment of regular prospectors is that the associated costs to other group members are not sufficiently high for punishment to be adaptive (Clutton-Brock & Parker 1995). This might be expected if (1) prospecting forays are conducted sufficiently infrequently by a small enough proportion of helpers, that the resulting fitness cost to pups is low, and/or (2) other helpers minimize the cost to the pups by partially compensating for the absence of prospectors (for a parental care example, see Wright & Cuthill 1989). Indeed, previous results suggest that compensation of this kind is likely, as meerkat helpers contribute more to pup care when helper numbers are limited (Clutton-Brock et al. 2001a). Alternatively, meerkats may simply be unable to assess each other's contributions to pup feeding (but see Clutton-Brock et al. 2005). Perhaps the most likely explanation for a lack of punishment is that any small cost incurred by other group members is offset by the inclusive fitness benefits they accrue from the extraterritorial activities of prospectors. Prospecting males are typically closely related to other group members, who therefore stand to benefit if prospectors sire offspring in other groups or successfully disperse (Griffin et al. 2003).

Our findings provide evidence that male helpers in cooperative societies can face similar trade-offs to male parents in noncooperative species, between investment in offspring care and alternative fitness-maximizing tactics, such as prospecting. While a number of recent studies have attempted to explain individual variation in contributions to cooperation (e.g. Legge 2000; Clutton-Brock et al. 2001a), trade-offs of this kind are rarely considered in addition to more obvious explanatory variables such as helper age, sex, condition and relatedness (but see Cant & Field 2001). Indeed, our analyses indicate that commitment to prospecting is among the most important factors associated with the pup-feeding rates of adult male meerkats, suggesting that a lack of attention to possible trade-offs could mask the significance of other factors influencing helper motivation. Furthermore, helpers in many species show marked sex differences in their commitment to cooperative activities, which could be attributed to sex differences in the benefits of helping (Clutton-Brock et al. 2002). Our findings suggest that sex differences in cooperative tendencies may also arise if the sexes experience different trade-offs between helping and alternative tactics, such as prospecting. For example, only male meerkats conduct extraterritorial prospecting forays, which may explain in part why male meerkats feed pups at lower rates than females (Clutton-Brock et al. 2002).

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