Energetics of cooperative breeding in meerkats

*Suricata suricatta*

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\textbf{Abstract.} We investigate whether energetic constraints play a role in determining social structure in cooperatively breeding meerkats *Suricata suricatta*. Energetics may be important at various stages of the reproductive cycle. Peak lactation and peak pup feeding are potentially the most energetically stressful periods for lactating mothers and subordinate helpers, respectively. Here, we review current data on lactation and present additional information on helping behaviour. Daily energy expenditure (DEE) of dominant females, subordinate helpers and pups were not particularly high during peak lactation. However, metabolisable energy intakes of lactating mothers (calculated from isotope-based estimates of offspring milk energy intake) were not significantly different from maximal suggested limits (at around seven times resting metabolic rate). DEEs of lactating mothers also increased with litter size, but decreased with group size. By comparison, during peak pup feeding, DEE values of helpers were not greater than those measured prior to breeding. Nor was there any apparent difference in DEE between “keen” and “lazy” helpers, suggesting that helping may not be energetically costly. These results confirm hypotheses that, in cooperatively breeding societies, breeders have high energy costs, which can be reduced by helpers. However, they do not support the notion that helpers incur substantial energetic costs in raising young. © 2004 Elsevier B.V. All rights reserved.

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1. Introduction

Research into the evolution of cooperative breeding has focused on three main questions [1,2]: Why do helpers remain in their natal group after reaching sexual maturity? Why do they not breed? And why do they assist other individuals to rear their young? Usual answers include that dispersal and reproduction have high costs in young animals, and, that non-breeding individuals can gain increments to the indirect component of their inclusive fitness that are sufficient to offset the marginal fitness costs of helping. While previous studies have outlined the probable answers to these questions, we still lack the understanding required to explain the processes involved.

Energetic constraints have previously been suggested to play a key role in limiting the capacity of females to breed successfully without helpers [3–5]. They may limit offspring survival [6] as well as prevent or delay independent breeding of subordinates [7–9]. In some cooperative breeders, for example, the development of feeding skills appears to be unusually slow, providing a plausible explanation of why younger individuals do not attempt to disperse or breed until their feeding skills (and therefore energy intake) approach that of adults [10]. However, few studies have directly examined the importance of energy in cooperative breeding systems. Studies of birds have shown that helping may be energetically costly and incur a delayed mortality cost to the donor [11,12], but may also increase growth rates of offspring [13]. Other studies have shown that helpers may have positive effects on breeders by reducing their energy expenditure [3,5] or thermoregulatory costs [14,15]. Therefore, to understand the evolution of cooperative breeding in mammals, it is important to determine whether energetics may also have played a role.

In some cooperative societies, parents are capable of breeding without helpers, but in a few, breeding is typically unsuccessful in the absence of helpers. One suggestion is that high reproductive skew may evolve in tandem with high energetic costs of reproduction. Hence, one hypothesis for the occurrence of obligate cooperative breeding is that, following the evolution of cooperation, selection for female fecundity (and hence the energy required for reproduction) has increased such that breeders are unable to raise their young unassisted [4]. This hypothesis predicts that: (i) the daily energy expenditure (DEE) of breeding females is high, (ii) helpers invest substantial amounts of energy in raising young, and, (iii) the presence of multiple helpers reduces the energy costs to breeding females.

Meerkats are a classic example of an obligate cooperatively breeding mammal. They are small (<0.9 kg), diurnal carnivores that live in groups of 2–40, accompanied by dependent offspring. Groups typically include a single dominant pair and a variable number of helpers of both sexes. The dominant female may breed up to four times per year and is responsible for 80% of the litters born in her group. Subordinates of both sexes assist in raising young (0–4 weeks of age) by guarding pups at the natal burrow (“babysitting”), feeding them (1–3 months of age) after they start to move with the group (“pup-feeding”) and acting as sentinels while the group is foraging (“guarding”) [16,17]. Subordinate females breed occasionally, either in synchrony with the dominant female or at other times [18]. In addition, in up to 20% of litters, subordinate females may lactate to the dominant female’s pups, even if they have not bred themselves (“allo-lactators”). The
number of allo-lactators varies, usually between 0 and 2, and is correlated with the total number of female helpers in the group [19]. When mixed litters do occur, it is unclear whether subordinates lactate principally to their own offspring or indeed whether they produce milk that is of the same energy content as that of the dominant female.

In contrast to the observed helping behaviours and the mutualistic benefits individuals may derive from increasing by their presence the size of the group they live in [20], both dominant and subordinate females are commonly infanticidal (towards pups of their own group) [21]. This suggests that there may be possible bottlenecks on energy provisioning to offspring at some stage in reproduction. Therefore, it may be to a mother’s benefit to try to make sure that her own pups are the ones to pass through this bottleneck.

Energetics may be important at various stages of the reproductive cycle. In meerkats, two periods are likely to be of primary concern: peak lactation and peak pup feeding. Studies of female mammals show that food intake generally increases throughout gestation and lactation and reaches a maximum during peak lactation [22]; the female must provide sufficient milk for offspring that are large but still dependent on her for all their nutritional requirements. Therefore, peak lactation is likely to be a key period as it defines the time that is potentially the most energetically stressful for the mother. By comparison, during peak pup feeding, offspring are dependent on helpers who must forage to meet both their own increased energy demands and those of the growing offspring. Therefore, this period is potentially the most energetically stressful for helpers.

2. Discussion

2.1. Energy costs of reproduction: peak lactation

DEE of dominant lactating females, dominant males, subordinate females, subordinate males, allo-lactating subordinate females and pups were measured using the doubly labelled water technique [19,23,24]. We calculated metabolisable energy intake (MEI) of lactating females from isotope-based estimates of milk energy intake of offspring [25]. DEE of dominant lactating females was higher than other categories of animals but was not significantly high compared with allometric predictions of same-size free-ranging eutherians [26]. However, MEI was not significantly different from allometric values for maximal energy intake of 1601 kJ day$^{-1}$ [27], equating to a sustained energy intake of about seven times resting metabolic rate (RMR) (using a mean value of 241 kJ day$^{-1}$ for RMR, Scantlebury et al., unpublished data). This indicates that mothers were indeed energetically stressed in an attempt to produce enough milk for their growing offspring.

By comparison, the DEE and MEI values of non-lactating helpers were not high compared with allometric predictions (Fig. 1). For example, the predicted values of maximal MEI for subordinate males and females were 1390 and 1318 kJ day$^{-1}$; measured values were about half this prediction. Hence, helpers were not energetically stressed during peak lactation. Allo-lactating subordinate females were the only category of animals that lost weight during the measurement period. This mass loss was likely to have supported the energy costs of their lactation [19].

We also found that the presence of helpers affected the DEE of dominant lactating females: DEE was positively correlated with litter size and negatively correlated with the number of helpers (Fig. 2). In contrast, there was no relationship between litter size and the
number of helpers with the DEE of helpers. This indicates that non-lactating helpers serve to reduce the DEE of the lactating mother. This suggestion is supported by the fact that increased numbers of helpers do not significantly affect pup mass around the time of weaning, but do influence maternal mass around the time of the mothers’ subsequent conception [28]. Non-lactating helpers, therefore, allow dominant females to channel more of their resources into milk. This may have been achieved by relieving dominant females from babysitting duties [29], by improving their foraging efficiency [30] or perhaps by reducing thermoregulatory costs at night [31].

Using a larger data set collected from the same site and on the same groups but over a greater time period (1996–2001 inclusive), we found that the body mass of helpers generally decreased during the babysitting period as a whole (pups aged 0–24 days) with the magnitude of the mass loss positively related to the amount of time spent babysitting [29,32]. However, there were no significant differences between the DEE of helpers during lactation and non-breeding times, or between the DEE of males and females (Fig. 3). Data were collected from ~300 individual meerkats from 14 different groups and analysed for 22,082 morning, pre-foraging weights during non-breeding periods, 14,128 during babysitting periods and 24,060 during pup feeding [32].
2.2. Energy costs of reproduction: peak pup feeding

During pup feeding, offspring are wholly dependent on helpers to provision them with food (dominant individuals hardly ever feed young). Therefore, the period when the pups demand the maximum rate of feeding (when they are approximately 50–60 days old) is potentially energetically stressful for helpers. There is a strong evidence to suggest that helpers do indeed invest substantial amounts of resources in raising young. For example, increases in litter size are positively associated with increases in the proportion of food items that helpers give away. Furthermore, when groups are manipulated to decrease the ratio of helpers to pups (either by cross-fostering pups or by temporarily removing helpers), helpers have reduced rates of daily weight gain [32]. However, we do not know whether these apparent costs translate into actual differences in the energy costs of the various activities, and whether any particular activity (such as pup feeding) is limited, for example, by the rate of energy expenditure or the rate of energy collection, that an individual helper can sustain [33], as has suggested to be important in birds [8,34]. Presumably, it may be worthwhile foraging to feed pups at a high rate, as a small drop in foraging effort might produce a significant increase in mortality risk of offspring [30].

In an initial investigation, we measured the DEE values of subordinate males during peak pup feeding and compared these values with those obtained during peak lactation and non-breeding periods. Subordinate males were measured because subordinate females have a high likelihood of becoming evicted at breeding times [21]. Male helpers varied in the total amount of food items that they provisioned to pups. In some individuals, more than 30% of prey items found were offered to pups, whereas in others, less than 5% of items were given away (Scantlebury et al., unpublished data). There was no overall significant difference in the DEE of “keen” and “lazy” helpers at peak pup feeding or between these values and those measured previously prior to breeding ($F=3.51$, $P=0.053$) (Fig. 4). Therefore, it is not the case that DEE of helpers is particularly high during peak pup feeding, or that they forage particularly hard to meet energy demands. The fact that no significant differences in the DEE of keen and
lazy helpers were observed could be a result of the few numbers of individuals that have been measured to date, but, importantly these data suggest that the costs of helping per se may not be as high as previously thought. However, these results must also be interpreted with some caution as our impressions of animals’ helping activity may be based on a small sample of the total duration over which the DEE measurement is integrated, and therefore observations may not be truly representative of differences in helping behaviour. Alternatively, keen helpers may not increase their foraging efforts during pup feeding, but they may bear the costs of helping by drawing on their own body reserves, which they may then recuperate during subsequent non-breeding periods [32].

In summary, reproduction is energetically costly for dominant lactating females, who are energetically stressed in an attempt to eat enough to provide enough milk for their growing offspring. The concurrent energy throughput of helpers is significantly lower. Non-breeding helpers do, however, allow mothers to reduce their DEE during lactation, either by increasing their foraging efficiency or perhaps by increasing their thermoregulatory costs at night. In contrast to predictions from behavioural observations [32], during peak pup feeding, we did not find that subordinate helpers significantly increased their DEE, or that there was any difference in the DEE between keen and lazy helpers.

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References