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# Early body condition, time budgets and the acquisition of foraging skills in meerkats

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Early body condition commonly has important downstream effects on fitness. One, as yet unexplored, mechanism behind these effects may be that condition in early life affects time budgets and hence opportunities to learn critical skills. Meerkat, *Suricata suricatta*, pups must choose between begging for food from helpers and foraging for themselves. I found that pups in good condition early in life invested more time in foraging than individuals in poor condition and subsequently developed greater foraging efficiency, which was maintained in later life. Young pups spent an average of 18% of their time foraging, even though all pups were initially incompetent foragers and gained few direct benefits from their attempts. Pups whose hunger was reduced through experimental provisioning increased their investment in foraging. This suggests that investment in foraging is mediated by available energy reserves and raises the possibility that, although foraging is energetically costly, pups may gain long-term benefits by practising. Surprisingly, manipulating body weight through long-term experimental provisioning did not result in increased investment in foraging or improved foraging efficiency. Possible explanations for this result are considered. The findings presented here provide some support for the hypothesis that high body condition allows individuals to invest time in costly foraging practice, leading to the development of skills. These effects, acting in tandem with other processes such as differential neural development, may help to explain common links between early condition and future fitness.



*Keywords*: downstream effects; early condition; foraging skills; learning; meerkat; *Suricata suricatta*

Body condition in early life has important downstream effects on factors including metabolic rate (Verhulst et al. 2006), disease resistance (Lummaa 2003; Worthman & Kuzara 2005), growth (Johnsson & Bohlin 2006), sexual attractiveness (Gustafsson et al. 1995; Nowicki et al. 1998) and survival and reproductive success (Lindström 1999). These effects may be mediated through a variety of mechanisms including reduced investment in tissue development by individuals of low birth weight (Metcalfe & Monaghan 2001), physiological costs of compensatory growth (Metcalfe & Monaghan 2001; Johnsson & Bohlin 2006) and increased competitive abilities of larger individuals (Kruuk et al. 1999).

In some cases, the downstream effects of early body condition may be mediated through learning of information or skills of critical fitness value. For example, Nowicki et al. (1998) suggested that song learning in passerines may be influenced by the effects of nutritional stress in early life on neural development. However, the development of critical skills may not always be determined directly by energetic constraints on neural development during the period of growth. It is increasingly clear that adult phenotypes can also be affected by what individuals do during the juvenile period. For example, fish that eat hard items as juveniles develop larger jaw muscles than peers that feed only on soft items (Mittelbach et al. 1999). In some situations, juveniles may engage in behaviour which, while it has no obvious current benefit, may serve to accelerate physical or behavioural development which will be beneficial in the future. Infant spotted hyenas, *Crocuta crocuta*, for example, spend a great deal of time chewing on bones and other objects. Although it provides no nutritional rewards, this jaw exercise promotes the development of jaw muscles and skull bones which will later be necessary for the consumption of antelope carcasses (Holekamp & Smale 1998; West-Eberhard 2003).

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Although both early body condition and actions performed in early life can have important downstream effects, whether the two factors interact has yet to be investigated. Animals modify their time budgets according to their energetic state or body condition (Cuthill & Houston 1997), and experience often plays an important role in skill acquisition (e.g. prey handling: Caro 1980; Thornton & McAuliffe 2006). Early condition might therefore influence skill acquisition by affecting time budgets and hence opportunities for learning. For example, if individuals in better condition can afford to invest more time practising critical skills, they may develop greater performance than those in poorer condition.

The development of foraging behaviour may be a particularly useful context in which to examine this possibility because foraging skills commonly improve with experience (Lack 1954; Brown 1987; Rovero et al. 1999) and the development of competent foraging abilities is critical for survival and fitness. I investigated whether early body condition affects the time that meerkat, *Suricata suricatta*, pups invest in foraging and their foraging skill development. Meerkats are cooperatively breeding mongooses living in groups of 2–50 individuals in semiarid regions of southern Africa. Groups comprise a dominant male and female, who are the parents of over 80% of the pups born in the group (Clutton-Brock et al. 2001a), and a variable number of helpers of both sexes that assist in feeding pups (Brotherton et al. 2001). When pups begin to accompany the foraging group at around 30 days of age, they have poor foraging skills and are dependent almost entirely on food provisioned by adults in response to begging calls (Manser & Avey 2000; Brotherton et al. 2001). Until approximately 35 days of age, pups may receive milk from mothers and allolactating helpers in addition to solid food (Russell et al. 2002). Pup foraging and prey handling skills improve with age (Thornton & McAuliffe 2006; Thornton 2007) and pups reach nutritional independence at around 90 days. Until they are able to find all their food independently, pups must choose between begging for food from adults and investing time in foraging for themselves. Initially, foraging behaviour may result in net energetic costs because young pups show very low success, but investment in foraging may provide pups with valuable experience. Pups in better condition may therefore be expected to invest a greater proportion of time in foraging and to subsequently develop greater foraging skills. Of course, foraging skills incorporate many components, including handling and finding prey. Prey handling skills in meerkat pups develop as a result of teaching, whereby adults provide pups with otherwise unavailable opportunities to handle difficult prey (Thornton & McAuliffe 2006). I therefore concentrated on pups' abilities to find prey items for themselves. Optimal foraging theory indicates that the currency that individuals seek to maximize may vary between contexts and that individual strategies and sensitivities to variance in rewards may vary with individuals' current energetic states (Stephens & Krebs 1986). Here, the aim was to examine meerkats' general abilities to find food for themselves, rather than investigating day-to-day variation in foraging strategies. I therefore used the mass of food found by individuals per hour invested in digging as a measure of foraging efficiency. Meerkats feed on a wide range of invertebrate and small vertebrate prey, which they find by digging in sand (Doolan & Macdonald 1996). Digging demands considerable energy and time expenditure, with individuals sometimes spending over 5 min to capture a single prey item and displacing their own body weight in sand (Barnard 2000). Digging may also raise predation risk as individuals are unable to dig and scan for predators simultaneously. It is therefore likely to be beneficial for individuals to develop the ability to find the greatest mass of food in the least amount of time. Although this measurement (referred to hereafter as 'foraging efficiency') does not take into account possible variation in the nutritional value of different prey types, it provides a simple and useful measure of individuals' abilities to find the greatest mass of food for the lowest investment in digging and hence their ability to gain weight. This ability is likely to have important fitness consequences. For example, it is known that pups' weight at independence is associated with high daily weight gain, which in turn has beneficial consequences for subsequent development, including increased survival (Clutton-Brock et al. 2001b). Russell et al. (2007) have shown that weight at independence has important effects on key fitness components including the probability of gaining reproductive success and the age of first breeding attempt. Furthermore, dominant individuals, who monopolize breeding, typically show high foraging success and daily weight gain (Barnard 2000; Glaser 2006), suggesting that high foraging efficiency may provide large fitness payoffs.

I investigated the relationships between body condition in early life, time budgets and development of foraging efficiency using longitudinal data from focal observations. I used multivariate analyses to examine general patterns of time allocation, foraging efficiency and helper provisioning rate to pups of varying body condition. Differences in foraging efficiency could be due to genetic and/or maternal effects rather than differences in body condition in early life. To reduce the potential influence of these confounding factors, I also conducted paired analyses on time budgets and foraging efficiency of siblings that were born on the same day to the same mother and reared in the same rearing environment but differed naturally in body weight. If foraging is costly but practising foraging can produce downstream benefits, pups would be expected to increase their investment in foraging if energetic constraints are reduced. I investigated this possibility using short-term feeding experiments to manipulate hunger and comparing the investment in foraging by fed pups to that of unfed siblings of similar weight. Finally, I conducted long-term feeding experiments to manipulate pup body weight. Here, I predicted that fed pups would increase in weight relative to unfed siblings and would therefore invest more time in foraging and develop higher foraging efficiency.

## METHODS

During three field seasons, December 2003 to May 2004, September 2004 to May 2005 and October 2005 to April 2006, I collected data on meerkats in 11 groups of 6–41