



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

ALEX THORNTON

Department of Zoology, University of Cambridge

(Received 2 February 2007; initial acceptance 13 April 2007;  
final acceptance 3 August 2007; published online 17 October 2007; MS. number: 9259R)

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.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

**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 (Metcalf & Monaghan 2001), physiological costs of compensatory growth (Metcalf & 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).

Correspondence: A. Thornton, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, U.K. (email: [jant2@cam.ac.uk](mailto:jant2@cam.ac.uk)).

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

individuals living in semidesert along the dry Kuruman River, 27 km west of Van Zylsrus in the south African Kalahari (26°58'S, 21°49'E). Details of habitat and climate have been published previously (Russell et al. 2002). To facilitate individual identification, unique combinations of hair dye marks (Garnier Nutrisse, Liquorice 1 colour, L'Oréal, Paris, France) were applied to each individual. Marks were applied gently using a paintbrush while meerkats sunned themselves in the morning without the need for capture. The dye dried rapidly (<5 min) and animals did not generally investigate the marks. Groups were located by radiotracking one radiocollared individual within each group. All observations reported here were carried out on groups that had been radiocollared for previous studies (for details of capture and radiocollaring procedures, see Jordan et al. 2007). Individuals were monitored since birth, so the ages of all individuals were known precisely ( $\pm 2$  days). All animals were habituated to close observation (<1 m) and over 90% could be weighed regularly by enticing them onto an electronic top-pan balance using crumbs of hard-boiled egg. Animals were weighed before they started foraging in the morning. To obtain a measure of early body condition, I used the residuals of a regression of body weight when pups first began foraging with the group (hereafter 'weight at first forage') on hind-foot length, which is a good indicator of skeletal size (White 2001). These residuals (henceforth referred to as the body condition index) give a measure of a pup's energy stores relative to its skeletal size when it first began foraging with the group (Jakob et al. 1996). An ordinary least squares regression, with both variables log transformed to achieve homoscedasticity, provided a better fit for the data ( $R^2 = 0.39$ ,  $P < 0.001$ ) than reduced major axis regression (Green 2001) and was therefore used to generate the residuals. As daily fluctuations in weight due to overnight weight loss and food intake may add noise to body condition index calculations, I calculated weight at first forage as pups' mean weight (g) between the ages of 30 and 35 days, when pups first began foraging with the group and could be weighed reliably. Hind-foot length was measured, to the nearest 0.1 mm, using callipers, from the posterior end of the tarsals to the anterior tip of the phalanges, with the foot stretched to standardize measurement. Pups were picked up by hand and held gently but firmly while morphometric measurements were taken, without need for anaesthesia. Pups were returned immediately to the group and showed no outward signs of distress. Hind-foot lengths were taken for all pups born after January 2004 and so are not available for some of the pups included in this study. All hind-foot length measurements were taken before pups first began foraging with the group (mean  $\pm$  SE pup age =  $25 \pm 0.2$  days), and 'hind-foot length' hereafter always refers to the measurements taken at this age. There was no effect of the age at which the measurement was taken on hind-foot length ( $R^2 = 0.06$ ,  $P < 0.104$ ) or body condition index ( $R^2 = 0.06$ ,  $P < 0.118$ ).

To investigate changes in pup time budgets and foraging efficiency with age, I conducted 476 focal watches on 69 pups from 28 litters in 10 groups (mean  $\pm$  SE =  $6.9 \pm 0.6$  focal watches per pup, range 1–23). Focal watches lasted 20 min (1200 s), but if the focal pup was engaged in an activity (e.g. digging) at the end of the 20 min period, the

focal watch was not ended until the pup changed activities (mean  $\pm$  SE focal duration =  $1210 \pm 4$  s). Focal watches were paused if the group ceased foraging for more than 30 s, for example because they had detected a predator. During each focal watch, I recorded the time the focal individual spent engaged in any of three behavioural categories: (1) 'begging', in which pups made repeated food-soliciting calls, either while stationary or while following foraging helpers, without making any attempt to find their own food (Manser & Avey 2000), (2) 'foraging', in which pups actively scratched at the surface or dug in sand (Barnard 2000) or (3) 'other activities', including resting and playing. Data were recorded on a Zire 21 handheld computer (Palm Inc., Sunnyvale, CA, U.S.A.) and times were accurate to 1 s. I also recorded any food items a pup found or was fed during a focal watch. Prey items were divided into five size categories: tiny (items swallowed immediately), small (items fitting entirely in an adult's mouth), medium (less than half the item protruding from an adult's mouth), large (more than half the item protruding from an adult's mouth) and extralarge (more than 80% of the item protruding from an adult's mouth), as per Doolan & Macdonald (1996) and Brotherton et al. (2001). Because the study animals could be observed very closely (<1 m), prey sizes were easily observable. Use of broad prey size categories ensured that there was little risk of misclassification. Mean wet mass values for each category were as follows: tiny = 0.05 g, small = 0.11 g, medium = 0.58 g, large = 2.86 g and extralarge = 9.56 g (M. Scantlebury, unpublished data). These values were used to calculate the total biomass of prey found or fed during each focal watch. Measures of foraging efficiency were calculated in grams per hour of foraging time. Because a single item caught at random may have a disproportionately large influence on measures of foraging efficiency if the pup spent very little time foraging during the focal watch, focal watches in which a pup spent less than 10% of the time foraging were excluded from analyses of foraging efficiency. To investigate whether differences in foraging efficiency were maintained in later life, once individuals were nutritionally independent, I also conducted 387 focal watches on 71 helpers aged 90–360 days (mean  $\pm$  SE =  $5.4 \pm 0.6$  focal watches per individual, range 1–29).

## Statistical Analyses

Unless otherwise indicated, data were analysed in Genstat 8.1 (Rothamsted Experimental Station, Harpenden, U.K.), using linear mixed models (LMM) or generalized linear mixed models (GLMM) for normal and non-normal error structures, respectively. Variance components were estimated using the residual maximum likelihood procedure. Mixed models are similar to general linear models but allow both fixed and random effects to be fitted, with random terms controlling for repeated measures such as individual, group and litter identities (Schall 1991). Initially, all likely explanatory variables were entered into the model. Possible interactions between them were investigated and terms were sequentially dropped until the minimal model contained only terms whose elimination

would significantly reduce the explanatory power of the model. Wald test statistics and probability values for significant terms were derived from having all significant terms in the model, whereas values for nonsignificant terms were obtained by adding each term individually to the minimal model. Residuals for all models were visually inspected to ensure homogeneity of variance, normality of error and linearity. Kolmogorov–Smirnov tests were used to confirm that residuals were normally distributed. All paired analyses were conducted in Minitab 13 (Minitab Inc., State College, PA, U.S.A.). Wherever possible, data were analysed using paired *t* tests. Where data could not be normalized through transformation, Wilcoxon signed-ranks tests were used. All statistical tests were two tailed and means are shown  $\pm$  standard errors. For nonsignificant results of paired analyses, 95% confidence intervals (CI) of the difference are presented. Confidence intervals are considered more informative than power tests in determining the power of statistical tests in light of nonsignificant results, with narrower intervals indicating a higher probability that the true effect size is near zero (Colegrave & Ruxton 2003).

#### *Body condition and time budgets*

To investigate factors affecting pup time budgets I conducted two separate LMMs on factors affecting the proportion of time pups spent begging and foraging during focal watches. Proportions were normalized for analysis through arcsine-square-root transformation. Rainfall (measured as the total rainfall, in mm, during the 30 days prior to the day of the focal watch), time of day (morning or afternoon foraging session), pup sex, pup age (in days), litter size, helper number, helper sex ratio, pup body condition index and pup hind-foot length (in mm, log transformed) were fitted as explanatory variables. As all group members above 3 months old are nutritionally independent and can potentially contribute to pup feeding (Brotherton et al. 2001), helper number refers to the total number of individuals over 3 months old present in the group. Sex ratios were categorized as female biased ( $<0.4$ ), male biased ( $>0.6$ ) or equal ( $0.4$ – $0.6$ ). Unless otherwise specified, these explanatory terms were used for all multivariate analyses in this study.

I investigated within-litter effects of body weight on time budgets using paired analyses on the proportions of time spent begging and foraging by pairs of siblings born on the same day in the same litter which differed naturally in weight (hereafter 'natural pairs'). Pairs were chosen such that the heavy individual was greater in weight than its light sibling by an average of at least 10% on days when they were both weighed. The weight at first forage of the heavy pup was on average  $14.0 \pm 2.3\%$  greater than that of its lighter sibling. Among the nine pairs of pups for which data were available, there was no significant difference between the hind-foot lengths of heavy and light pups (means: heavy pups:  $35.5 \pm 1.1$  mm; light pups:  $34.5 \pm 1.3$  mm; 95% CI =  $-1.25$ ,  $3.35$ ; paired *t* test:  $t_9 = 1.05$ ,  $P = 0.322$ ) and heavy pups had a significantly higher body condition index than light pups (means: heavy pups:  $0.0039 \pm 0.025$ ; light pups:  $-0.022 \pm 0.021$ ; paired *t* test:  $t_9 = 2.31$ ,  $P = 0.05$ ). All litters used for these

analyses were born to the dominant female in the group. Over 90% of individuals born to dominant females are fathered by the dominant male in the group (Griffin et al. 2003), so littermates in natural pairs were likely to be full siblings. As focal watches on natural pairs were conducted on the same day, individuals were of the same age and measures of rainfall, litter size, helper number and helper sex ratio were equal. Helper number and rainfall values for the litters used in these analyses did not differ significantly from the rest of the population (analysis of variance (ANOVA): helper number:  $F_{1,50} = 0.52$ ,  $P = 0.476$ ; rainfall:  $F_{1,50} = 0.19$ ,  $P = 0.664$ ), suggesting that group and environmental factors affecting these litters were representative of the population as a whole. Paired analyses were conducted separately for pups in two age categories: 'young' ( $<45$  days) and 'old' ( $\geq 65$  days). Analyses used average values from multiple focal watches on each pup within an age category (mean =  $4.3 \pm 0.6$  focals per pup, range 1–8). I collected data from 12 pairs, but for three of these pairs I was unable to collect data during the young age category, so analyses incorporate data from nine pairs of young siblings and 12 pairs of old siblings. As preliminary analyses indicated no effect of sex on any measure of pup time budgets or foraging efficiency, both same-sex and different-sex pairs were included in the analyses.

#### *Body condition and food intake*

*Feeding by helpers.* If helpers feed pups of differing body condition at different rates, this may affect pups' investment in foraging behaviour and their skill development. To examine whether pup body condition affected the rate at which helpers fed pups during focal watches, I conducted a LMM with feeding rate (in g/h, log transformed) fitted as the response term. Sample sizes and explanatory variables were the same as in the LMM analyses of time budgets above. I also conducted paired analyses to examine whether there were differences in rates of pup feeding to light and heavy littermates from natural pairs. Response terms were normalized for analysis through log transformation.

*Food found by pups.* Pups rarely found prey for themselves in the first 2 weeks after they began foraging with the group, so I examined whether pup body condition index influenced the probability that pups would find any food for themselves when younger than 45 days using a GLMM. Data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether a pup found any prey during a focal watch. The analysis used data from 70 focal watches on 38 pups from 20 litters in 10 groups (mean =  $1.8 \pm 0.2$  focal watches per individual, range 1–6). Total time spent foraging (s) was included as a potential explanatory variable along with the other variables used in LMMs on pup time budgets. For older pups ( $>45$  days), I used a LMM with foraging efficiency (mass of food found by pups, in g/h spent foraging, log transformed) as the response term to investigate whether there was a relationship between pups' body condition index and foraging efficiency, controlling for other potential explanatory variables (as described above). The analysis used data from 394 focal

watches on 62 individuals from 26 litters in 10 groups (mean =  $6.4 \pm 0.5$  focal watches per individual, range 1–29). I further examined whether body weight affected foraging efficiency by conducting paired tests on the foraging efficiency of littermates in natural pairs.

Differences in the foraging efficiency of light and heavy individuals could be due to weight or size alone rather than experience. For example, larger individuals may simply be stronger and better able to displace sand rapidly while foraging. To disentangle the effects of weight and experience, I conducted a LMM on average foraging efficiency of the 15 pups aged 45–55 days with the highest average morning weights ('younger pups') and the 15 pups aged 65–75 days with the lowest average morning weights ('older pups'). Despite the age difference, the younger pups had significantly higher average morning weights than the older pups (ANOVA:  $F_{1,29} = 7.49$ ,  $P = 0.011$ ). At the age when the pups first began foraging with the group, the younger pups had higher weights (ANOVA:  $F_{1,29} = 43.08$ ,  $P < 0.001$ ) than the older pups. Early hind-foot length measurements were available for eight of the younger pups and for all 15 of the older pups. Among these pups, the younger pups had longer hind-feet when they first began foraging with the group than did the older pups (ANOVA:  $F_{1,21} = 7.58$ ,  $P = 0.012$ ). Measures of foraging efficiency (in g/h of foraging) were averaged per pup and normalized for analysis with a log transformation.

*Acquisition of nutritional independence.* Differences in foraging ability of pups of differing body condition may lead to differences in the age at which pups find more food for themselves than is fed to them by helpers. To examine the degree to which pups of differing body condition relied on adults for food, I used a LMM on factors affecting the difference between the total mass of food found by a pup and that fed to it by helpers during a focal watch. These data were normalized by log transforming the mass (g) of food found and fed, and the difference between the two values was used as the response term in the model. The analysis included all pups on which focal watches were conducted between 30 and 90 days of age. Sample sizes and explanatory variables are as in LMM analyses on pup time budgets above.

#### *Early body condition and foraging efficiency later in life*

To investigate whether early body condition had downstream effects on foraging efficiency once individuals had reached full nutritional independence, I conducted a LMM on the foraging efficiency of 71 helpers between 90 and 360 days of age. The analysis used data from 387 focal watches (mean =  $5.4 \pm 0.6$  focal watches per individual, range 1–29). Helper age (days), early body condition index, hind-foot length, sex, rainfall, group size, number of pups in the group and helper sex ratio were fitted as explanatory variables.

#### *Experiment 1: relaxation of energetic constraints*

To examine whether a relaxation of energetic constraints (i.e. a full stomach) would affect pup time budgets in the short term, I experimentally provisioned 12 pups

from 11 litters in eight groups with 12 g of hard-boiled egg before they commenced foraging in the morning. An assistant and I simultaneously conducted one 3-h foraging focal watch on the fed pup and a randomly allocated unfed control of the same sex from the same litter, beginning as soon as the group left the sleeping burrow and began foraging in the morning. Individuals in a pair were siblings of the same age with similar weight at first forage (means: fed =  $128.4 \pm 7.8$  g, unfed =  $128.7 \pm 6.9$  g; 95% CI =  $-8.37$ ,  $7.87$ ; paired  $t$  test:  $t_{12} = 0.07$ ,  $P = 0.947$ ), early hind-foot length (means: fed =  $36.4 \pm 1.1$  mm, unfed =  $36.1 \pm 1.0$  mm; 95% CI =  $-1.31$ ,  $1.87$ ; paired  $t$  test:  $t_{12} = 0.39$ ,  $P = 0.707$ ) and early body condition index (means: fed =  $0.0082 \pm 0.019$ , unfed =  $0.0059 \pm 0.012$ ; 95% CI =  $-0.016$ ,  $0.021$ ; paired  $t$  test:  $t_{12} = 0.29$ ,  $P = 0.779$ ) and all focal pups were aged 46–63 days. Fed and unfed pups did not differ in preforaging morning weight on the day of focal watches (means: fed =  $219.3 \pm 12.0$  g, unfed =  $218 \pm 9.6$  g; 95% CI =  $-9.90$ ,  $12.40$ ; paired  $t$  test:  $t_{12} = 0.25$ ,  $P = 0.810$ ), and observers were randomly allocated to treatments. I compared the proportion of time spent begging and foraging, foraging efficiency and rate of provisioning by helpers to fed and unfed pups using paired  $t$  tests.

#### *Experiment 2: manipulating body weight*

To test whether experimental manipulation of body weight would affect pups' time budgets and foraging efficiency, I examined whether pups that did not differ in weight initially would develop differing time budgets and foraging efficiency as a result of long-term experimental provisioning. I predicted that greater body weight or improved body condition as a result of provisioning would cause fed pups to invest more time in foraging and thus develop greater foraging efficiency than their unfed siblings. I provisioned nine pups from seven litters in seven groups with 12 g of egg twice daily, every day, beginning soon after the pups first started accompanying the foraging group (mean age =  $36.3 \pm 1.4$  days) and continuing throughout the pup-care period (mean days fed =  $36 \pm 6$ ). Pups were provisioned at the end of foraging sessions, so that hunger during the foraging session was not affected. Each fed pup was paired with an unfed control of the same sex in the same litter. Fed pups did not differ significantly from unfed controls in weight at first forage (means: fed =  $145 \pm 11.3$  g, unfed pups =  $141.2 \pm 12.7$  g; 95% CI =  $-8.23$ ,  $15.71$ ; paired  $t$  test:  $t_9 = 0.72$ ,  $P = 0.492$ ). Morphometric data were available only for the four pairs of pups born after January 2004. Among these four pairs, hind-foot length and body condition index appeared to be similar in fed and unfed pups (hind-foot length means: fed =  $38.5 \pm 1.3$  mm, unfed =  $37.0 \pm 1.9$  mm; body condition index means: fed =  $-0.021 \pm 0.013$ ; unfed =  $-0.020 \pm 0.014$ ). Repeated focal watches were conducted on both individuals at different ages during the pup-care period (mean =  $15.3 \pm 2.9$  focal watches per pup; range 5–28). Owing to the death of one pup, foraging data were available for nine pairs within 15 days of the start of the feeding experiment (<38 days old) and eight pairs older than 65 days (at least 27 days from the start of the experiment). I used average values

from multiple focal watches on each pup within an age category for analysis. The time budgets and foraging efficiency of fed and unfed pups in each of the two age categories were compared using paired *t* tests.

## RESULTS

### Body Condition and Time Budgets

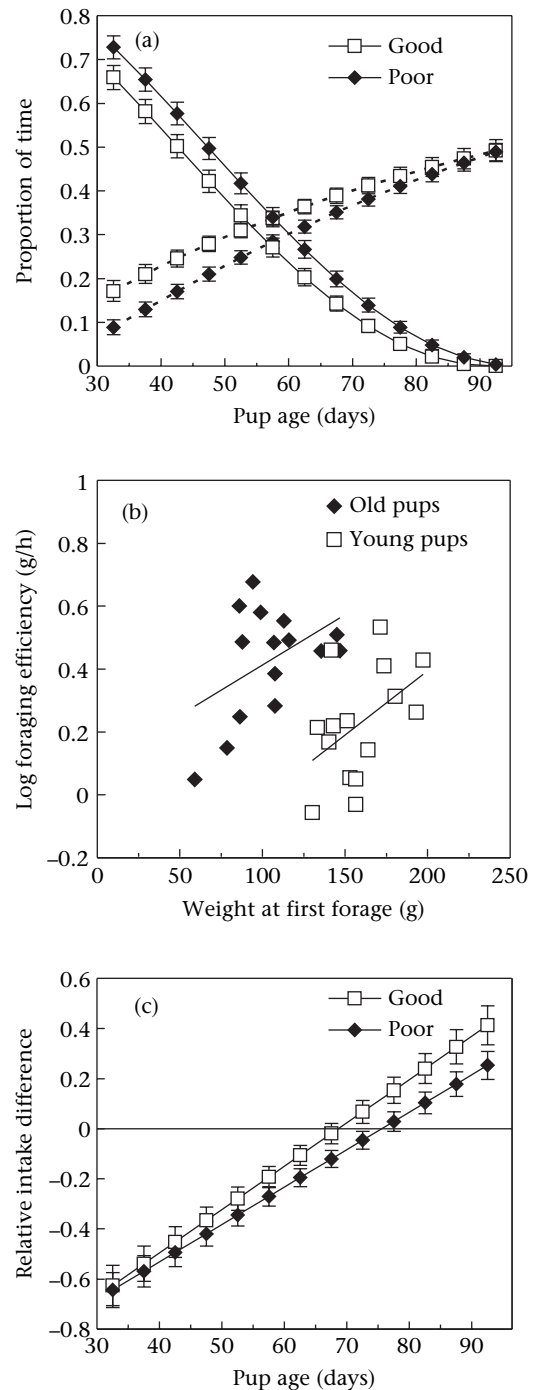
When they first began foraging with the group, pups spent the majority of their time begging for food from helpers. Pups younger than 45 days spent a mean of  $18 \pm 1.5\%$  of their time foraging for themselves, but the proportion of time spent foraging increased to around 45% as they approached 85–90 days (mean =  $43 \pm 1.9\%$ ), while the proportion of time spent begging declined to zero (LMMs: foraging:  $P < 0.001$ ; begging:  $P < 0.001$ ;  $N = 476$  focal watches; Fig. 1a, Table A1). The rest of the time was spent on activities including moving between sites, playing, resting and vigilance.

Multivariate analyses showed that early body condition index was a significant predictor of pup time budgets (LMMs: foraging:  $P = 0.001$ ; begging:  $P = 0.002$ ;  $N = 476$  focal watches; Fig. 1a), even after controlling for the effects of skeletal size (hind-foot length), time of day and rainfall (Table A1). Pups with high early body condition indexes spent more time foraging and less time begging than pups in poorer condition. For ease of graphical presentation, Fig. 1a shows early body condition indexes factorized as above or below average (i.e. above or below zero). As they approached nutritional independence, all pups converged on around 50% of their time spent foraging (Fig. 1a; pup age\*body condition index:  $P = 0.010$ ). Paired analyses of littermates that differed naturally in weight at first forage and early body condition index produced similar results. Among pairs of both young (<45 days) and old ( $\geq 65$  days) pups, light pups spent a greater proportion of their time begging than their heavier siblings (paired *t* tests, young:  $t_9 = 2.43$ ,  $P = 0.041$ , Fig. 2a; old:  $t_{12} = 2.49$ ,  $P = 0.030$ , Fig. 2b). In young pairs, heavy pups invested a greater proportion of time in foraging than light pups (paired *t* test:  $t_9 = 2.92$ ,  $P = 0.019$ , Fig. 2c), but among older pairs there was no significant difference in the proportion of time spent foraging (95% CI =  $-0.052$ ,  $0.11$ ; Wilcoxon signed-ranks test:  $T = 37$ ,  $N = 12$ ,  $P = 0.910$ , Fig. 2d).

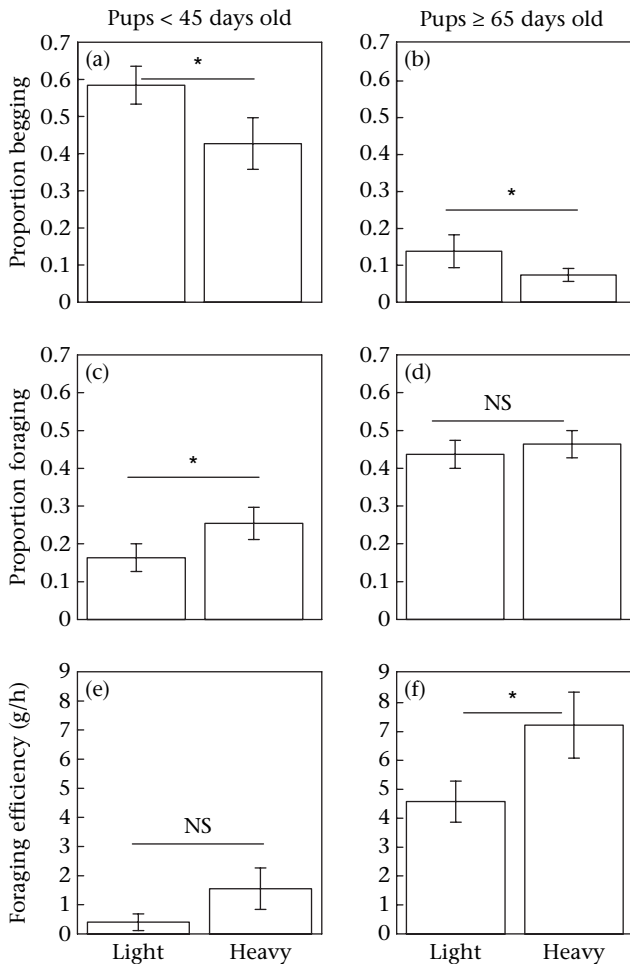
### Body Condition and Food Intake

#### Feeding by helpers

I found no evidence that pups' early body condition influenced the amount of food they received from helpers. Overall, the mass of food received was highly variable, ranging 0–65 g/h (mean =  $4.37 \pm 0.41$ ,  $N = 476$  focal watches). A LMM showed that pup age had a quadratic effect on the amount of food received (age:  $P = 0.264$ ; age<sup>2</sup>:  $P = 0.049$ ), but body condition index had no significant influence ( $P = 0.273$ ; Table A2). Pups received more food from helpers in the morning than in the afternoon and when rainfall in the previous 30 days was high (Table A2).



**Figure 1.** (a) Proportion of time pups spent begging (solid lines) or foraging (dashed lines) by pups in good or poor condition. Lines represent predicted means  $\pm$  SE from separate LMMs. (b) Foraging efficiency (in g/h, log transformed) of the 15 heaviest young pups (45–55 days) and the 15 lightest old pups (65–75 days) against their weight at first forage. (c) Effect of pup age and body condition index on the relative difference between the mass of food found by pups and the mass fed by helpers per hour during a focal watch. Lines represent predicted means from a LMM  $\pm$  SE.



**Figure 2.** Paired comparisons of light and heavy pups in the same litter. Separate analyses were conducted on nine pairs of young pups (<45 days old) and 12 pairs of old pups (≥65 days). In analysis of the foraging efficiency of young pairs, two pairs were excluded as pups spent less than 120 s of the focal foraging. Graphs show means of raw data ± SE for the proportion of time spent begging (a) and (b), the proportion of time spent foraging (c) and (d) and foraging efficiency (g/h) (e) and (f).

There were no significant differences in the rate of pup feeding to littermates which differed naturally in weight (pups <45 days means: heavy pups =  $0.37 \pm 0.15$  log g/h, light pups =  $0.14 \pm 0.11$  log g/h; 95% CI =  $-0.23, 0.69$ ; paired *t* test:  $t_9 = 1.85$ ,  $P = 0.284$ ; pups ≥65 days means: heavy pups =  $-0.074 \pm 0.11$  log g/h, light pups =  $-0.15 \pm 0.13$  log g/h; 95% CI =  $-0.43, 0.12$ ; paired *t* test:  $t_{12} = 1.22$ ,  $P = 0.248$ ).

**Food found by pups**

Pups younger than 45 days old gained few immediate benefits from attempting to forage for themselves, finding on average only  $0.41 \pm 0.19$  g/h spent foraging ( $N = 70$  focal watches), and helpers provided on average  $95.2 \pm 0.20\%$  of the prey biomass consumed by pups during this time (average feeding rate =  $6.27 \pm 1.17$  g/h). In 58 of 70 focal watches (82.9%) conducted during this period, the focal pup found no food. Early body condition index had no significant effect on the probability that

a pup would find any food during a focal watch during this time (GLMM:  $\chi^2_1 = 2.12$ ,  $P = 0.146$ ), controlling for a significant positive effect of rainfall ( $\chi^2_1 = 7.31$ ,  $P = 0.007$ ). No other variable proved significant in the analysis ( $P > 0.3$ ). Paired *t* test analysis supported this result: there was no significant difference in the mass of food found per hour of foraging by heavy and light pups in young natural pairs (<45 days: 95% CI:  $-0.74, 3.05$ ;  $t_7 = 1.49$ ,  $P = 0.188$ ; Fig. 2e).

Among older pups (≥45 days), LMM analysis revealed a significant positive effect of body condition index on pup foraging efficiency ( $P = 0.047$ ) even after controlling for significant positive effects of early hind-foot length, pup age and rainfall (Table A3). Similarly, heavy pups in old natural pairs (≥65 days) showed significantly higher foraging efficiency than their lighter siblings (paired *t* test:  $t_{12} = 4.21$ ,  $P = 0.001$ ; Fig. 2f).

The lower foraging efficiency of light compared to heavy pups could be due to physical constraints on foraging imposed by small size rather than differences in experience. However, a LMM of the foraging efficiency of old but currently light pups and young but currently heavy pups showed that the older pups showed significantly higher foraging efficiency despite their lower body weight ( $P < 0.001$ ,  $N = 30$  pups; Fig. 1b, Table A4), suggesting that high foraging efficiency does not result from high body weight alone.

**Acquisition of nutritional independence**

As pups of different early body condition received similar amounts of food from helpers, differences in the foraging efficiency of pups with different early body condition generated discrepancies in the degree to which pups relied on helpers for food. LMM analysis of the difference between the mass of food found by a pup and the mass of food received from helpers during focal watches revealed a significant interaction between pup age and body condition index ( $P = 0.017$ ,  $N = 476$  focal watches, Table A5), controlling for other significant terms in the model. For ease of graphical presentation, Fig. 1c shows early body condition indices factorized as above or below average (i.e. above or below zero). Pups that were in good condition when they first began foraging with the group reached the point at which the mass of food they found themselves exceeded the mass fed by helpers earlier than pups in poor condition (Fig. 1c).

**Early Body Condition and Foraging Efficiency Later in Life**

A LMM of focal watches on nutritionally independent meerkats revealed that differences in foraging efficiency were maintained because individuals that were in good condition when they first began foraging with the group as pups showed higher foraging efficiency than individuals who were in poor condition in early life ( $P = 0.038$ ,  $N = 387$  focal watches), controlling for the effects of age and rainfall (Table A6).

## Experiment 1: Relaxation of Energetic Constraints

During focal watches, experimentally fed pups spent a significantly higher proportion of time foraging and a lower proportion of time begging than their unfed siblings (mean proportion of time spent foraging: fed =  $0.37 \pm 0.022$ , unfed =  $0.31 \pm 0.020$ ; paired *t* tests:  $t_{12} = 2.73$ ,  $P = 0.003$ ; mean proportion of time spent begging: fed =  $0.20 \pm 0.028$ , unfed =  $0.27 \pm 0.031$ ;  $t_{12} = 2.73$ ,  $P = 0.020$ ). There was no significant difference in the foraging efficiency of fed and unfed pups (means: fed =  $2.87 \pm 0.77$  g/h, unfed =  $3.10 \pm 0.77$  g/h; 95% CI =  $-3.22, 2.74$ ;  $t_{12} = 0.18$ ,  $P = 0.864$ ) or in the rate of feeding by helpers (means: fed =  $3.72 \pm 0.80$  g/h, unfed =  $3.47 \pm 0.70$  g/h; 95% CI =  $-0.95, 1.45$ ;  $t_{12} = 0.46$ ,  $P = 0.652$ ). Pups received a significantly greater mass of food from helpers during focal watches than they obtained for themselves (means: received =  $7.78 \pm 0.80$  g, found =  $2.31 \pm 0.46$  g;  $t_{24} = 4.55$ ,  $P < 0.001$ ), with no effect of treatment (fed or unfed) on the difference between the mass of food received and found (means: fed pups:  $5.38 \pm 2.13$  g, unfed pups:  $5.57 \pm 1.24$  g; ANOVA, blocking for litter identity:  $F_{1,12} = 0.01$ ,  $P = 0.921$ ).

## Experiment 2: Manipulating Body Weight

Long-term supplementary feeding increased the weight of pups: whereas fed pups did not differ significantly from unfed controls in weights at first forage or morning weights collected within 15 days of the start of the experiment (means: fed =  $195.7 \pm 14.5$  g, unfed =  $184.4 \pm 16.7$  g; 95% CI =  $-4.3, 26.9$ ; paired *t* tests:  $t_9 = 1.67$ ,  $P = 0.133$ ), they were significantly heavier after the age of 65 days (means: fed =  $382.5 \pm 10.4$  g, unfed =  $339.4 \pm 5.2$  g;  $t_8 = 5.08$ ,  $P = 0.001$ ). The proportional increase in weight over the course of the time period was greater for fed than unfed pups (means: fed =  $0.94 \pm 0.12$ , unfed =  $0.78 \pm 0.11$ ;  $t_8 = 3.43$ ,  $P = 0.011$ ). However, fed and unfed pups did not differ significantly in the average proportion of time spent begging or foraging within 15 days of the start of the experiment (begging: fed =  $0.34 \pm 0.077$ , unfed =  $0.35 \pm 0.072$ ; 95% CI =  $-0.11, 0.092$ ;  $t_9 = 0.17$ ,  $P = 0.866$ ; foraging: fed =  $0.21 \pm 0.023$ , unfed =  $0.23 \pm 0.031$ ; 95% CI =  $-0.073, 0.024$ ;  $t_9 = 1.18$ ,  $P = 0.274$ ) or when older than 65 days (begging: fed =  $0.15 \pm 0.050$ , unfed =  $0.17 \pm 0.053$ ; 95% CI =  $-0.077, 0.040$ ;  $t_8 = 0.77$ ,  $P = 0.467$ ; foraging: fed =  $0.45 \pm 0.014$ , unfed =  $0.47 \pm 0.023$ ; 95% CI =  $-0.077, 0.044$ ;  $t_8 = 0.64$ ,  $P = 0.542$ ). There were no differences in the foraging efficiency of fed and unfed pups in either age category (means <15 days from the start of the experiment: fed =  $-0.026 \pm 0.14$  log g/h; unfed =  $-0.17 \pm 0.10$  log g/h; 95% CI =  $-0.29, 0.058$ ;  $t_9 = 0.76$ ,  $P = 0.466$ ; means >65 days old: fed =  $11.7 \pm 3.08$  g/h; unfed =  $11.2 \pm 3.13$  g/h; 95% CI =  $-2.77, 3.81$ ;  $t_8 = 0.37$ ,  $P = 0.720$ ) or in the rate at which they were provisioned by helpers (means <15 days from start: fed =  $2.23 \pm 0.64$  g/h; unfed =  $0.88 \pm 0.29$  g/h; 95% CI =  $-0.48, 3.17$ ;  $t_9 = 1.70$ ,  $P = 0.128$ ; means >65 days old: fed =  $0.24 \pm 0.16$  g/h; unfed =  $0.22 \pm 0.11$  g/h; 95% CI =  $-0.42, 0.46$ ;  $t_8 = 0.19$ ,  $P = 0.855$ ).

## DISCUSSION

As they grew older, meerkat pups reduced the time they spent begging and spent more time foraging for themselves. After controlling for the effect of hind-foot length (a measure of skeletal size), pups with high body condition indexes spent more time foraging and less time begging than pups with low body condition indexes. Paired analyses of littermates produced similar results, with heavier pups investing more time in foraging and less time in begging than their lighter siblings. Among pups in paired analyses for which skeletal measurements were available, the heavier pups showed significantly higher body condition indexes. As the body condition index provides a measure of an individual's energetic reserves relative to its skeletal size, these results suggest that investment in foraging behaviour by pups may be energetically constrained, such that individuals with higher energy reserves can afford to forage more. Among young pups, who still receive milk in addition to solid food (Russell et al. 2002), investment in foraging may be influenced by the quantity of milk received. For example, if pups that are larger or in better condition can outcompete siblings for access to teats, they may be less hungry and more able to devote time to unproductive foraging. Short-term provisioning experiments confirm that a reduction in energetic constraints affects investment in foraging because fed pups with full stomachs spent more time foraging and less time begging than unfed control siblings. However, this raises the question of why pups should increase their investment in foraging when energy reserves are high rather than resting to conserve energy.

Research on optimal foraging has shown that animals' time budget allocation and foraging strategies are complex. Where the mean rewards of different foraging options are equal, but the variance is different, animals frequently show a preference for a particular option (Kacelnik & Bateson 1996). In the current case, however, the two options available to pups, foraging for themselves or begging from helpers, differ greatly in their rewards. Young pups gain little from foraging because they rarely find food for themselves and obtain the great majority of their food intake from provisioning by adults. Furthermore, digging is likely to be highly energetically costly because it involves displacing large volumes of sand and may increase predation risk because individuals are unable to scan for predators and dig simultaneously. Why, then, do young pups invest on average 18% of their time on an activity that produces little current benefit and why should investment in foraging vary with early body condition or hunger?

One possibility is that investment in foraging in early life promotes the development of foraging skills, thereby producing long-term downstream benefits. Pups in better condition may be able to spend less time begging and more time foraging without a reduction in feeding rate by adults because pups in better condition can produce higher maximal rates of begging calls (J. R. Madden & T. H. Clutton-Brock, unpublished data). As a result, they may gain additional foraging experience and hence develop high foraging efficiency. Correlational evidence presented here provides support for this suggestion. All pups were equally

incompetent foragers initially, but pups with good early body condition invested more time in foraging and developed higher foraging efficiency than pups in poorer condition. Similar results emerged from paired analyses of full siblings, so differences in foraging efficiency are unlikely to be entirely dependent on genetic differences. As a result of their higher foraging efficiency, pups with good early body condition reached nutritional independence earlier and continued to show high foraging efficiency later in life, when they were nutritionally independent. Although greater skeletal size may account in part for differences in foraging efficiency, opportunities for learning as a result of foraging practice may produce important additional effects. The finding that older but lighter pups had higher foraging efficiency than younger but heavier individuals suggests that bulk alone does not explain foraging efficiency and that experience has important effects on the development of foraging skills.

The results of the long-term feeding experiment appear surprising in light of the hypothesis advanced here. In the experiment, fed pups became heavier than their unfed siblings as a result of provisioning. I predicted that fed pups would increase their investment in foraging and develop greater foraging efficiency as a result, but fed and unfed pups did not show different time budgets or foraging efficiency in either time period tested. This contrasts with the finding that long-term nutritional status is positively correlated with time spent playing and that both short- and long-term experimental provisioning of pups results in increased investment in play (Sharpe et al. 2002). It is possible that investment in play may have effects on the development of foraging skills, for example by promoting neuromuscular development (Byers & Walker 1995) or brain development (Ferchmin & Eterovic 1982), but as yet data to test this idea are lacking. Another possibility is that differences in foraging efficiency may be predetermined by effects very early in life, before pups first leave their natal burrow. For example, as has been suggested for song learning in passerines (Nowicki et al. 1998), high energy reserves very early in life may promote the development of neural structures associated with learning during the development of foraging behaviour. If the trajectory of pups' foraging skill development is predetermined in this way, before pups first begin to forage with the group, this may explain why long-term supplemental provisioning did not affect foraging efficiency. However, this does not explain why pups with high early body condition or a full stomach invest more time in foraging or why older more experienced pups have higher foraging efficiency than younger pups, even if the younger pups are heavier and had a better start in life. Weight differences as a result of long-term supplemental provisioning took time to emerge, so fed and unfed pups in the early stage of the experiment were of similar weight and body condition and showed similar time budgets and foraging efficiency. Differences in weight became apparent as pups approached independence, when the proportion of time spent foraging tends to converge for naturally heavy and light pups. Fed pups therefore did not gain additional foraging practice, which may explain why they did not develop greater foraging efficiency. Further research is clearly necessary to

ascertain the validity of the hypothesis presented here. Beginning supplementary feeding at an earlier age may ensure that differences in pup weight and condition are present when pups first begin to join the foraging group. Furthermore, the use of a  $2 \times 2$  experimental design, with pairs of fed and unfed siblings that were initially in poor condition and other pairs who were initially in good condition, may help to elucidate the extent to which influences in very early life predetermine pups' future behaviour and skill development. More work is also needed to determine the magnitude of the fitness benefits conveyed by high foraging efficiency. It may be that high efficiency is not particularly important during periods when food is abundant but allows individuals to gain advantages over competitors during times of low rainfall when food abundance drops and prey are typically found deeper in the sand (Turbé 2006).

The results of this study lend some support to a novel hypothesis linking early body condition to the development of critical skills. Although it is not possible to rule out additional explanations for the differences in time budgets and foraging efficiency of different pups, it is difficult to explain all the results presented here without invoking a role for variation in opportunities for learning mediated by early body condition. It is likely that this effect works in tandem with other processes, including differential neural development in early life, to affect young meerkats' development of foraging skills. Early experience can have important effects on foraging skill acquisition (e.g. Heinsohn 1991; Slagsvold & Wiebe 2007). My work raises the possibility that the experience that individuals accrue is influenced by their condition in early life. Good early condition could therefore have positive impacts on future fitness because it allows individuals to invest time in practice and thus rapidly acquire skills of critical fitness value. These effects may also have important implications for the elucidation of maternal effects and phenotypic inheritance. For example, in meerkats maternal weight relates to pup weight at weaning (Russell et al. 2003), and similar relationships are found in several other species (Lindström 1999). If large females with efficient foraging skills produce large offspring which are able to learn skills rapidly then the possibility of non-genetic inheritance of foraging skills is raised. In cooperative societies, large offspring with high foraging efficiency may thus contribute more to the care of their mothers' future litters (Russell et al. 2002) and have a higher probability of breeding (Russell et al. 2007).

### Acknowledgments

H. and J. Kotze kindly allowed me to work on their land and the Northern Cape Conservation Authority granted permission to conduct the research. Work was carried out with ethics approval from the University of Cambridge and the University of Pretoria. I am grateful for the support of the Mammal Research Institute at the University of Pretoria and for the help of T. Flower, N. Jordan, K. McAuliffe and N. Tayar. I thank T. H. Clutton-Brock for supervision and access to the meerkats and M. Manser for technical support and discussion. S. English, S. Hodge, K. Isvaran, N. Jordan, K. McAuliffe, A. Radford, N. Raihani

and A. Young provided invaluable advice. N. Metcalfe and three anonymous referees made useful comments on earlier drafts of the paper. This work was funded by the Natural Environment Research Council and the Cambridge Philosophical Society.

## References

- Barnard, J. A. 2000. Costs and benefits of group foraging in cooperatively breeding meerkats. Ph.D. thesis, University of Cambridge.
- Brotherton, P. N. M., Clutton-Brock, T. H., O'Riain, M. J., Gaynor, D., Sharpe, L., Kansky, R. & McIlrath, G. M. 2001. Offspring food allocation by parents and helpers in a cooperative mammal. *Behavioral Ecology*, **12**, 590–599.
- Brown, J. L. 1987. *Helping and Communal Breeding in Birds*. Princeton, New Jersey: Princeton University Press.
- Byers, J. A. & Walker, C. 1995. Refining the motor training hypothesis for the evolution of play. *American Naturalist*, **146**, 25–40.
- Caro, T. M. 1980. Effects of the mother, object play and adult experience on predation in cats. *Behavioral and Neural Biology*, **29**, 29–51.
- Clutton-Brock, T. H., Brotherton, P. N. M., Russell, A. F., O'Riain, M. J., Gaynor, D., Kansky, R., Griffin, A., Manser, M., Sharpe, L., McIlrath, G. M., Small, T., Moss, A. & Monfort, S. 2001a. Cooperation, control, and concession in meerkat groups. *Science*, **291**, 478–481.
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Brotherton, P. N. M., McIlrath, G. M., White, S. & Cameron, E. Z. 2001b. Effects of helpers on juvenile development and survival in meerkats. *Science*, **293**, 2446–2449.
- Colegrave, N. & Ruxton, G. D. 2003. Confidence intervals are a more useful complement to nonsignificant tests than are power calculations. *Behavioral Ecology*, **14**, 446–447.
- Cuthill, I. C. & Houston, A. I. 1997. Managing time and energy. In: *Behavioural Ecology: an Evolutionary Approach* (Ed. by J. R. Krebs & N. B. Davies), pp. 97–120. Oxford: Blackwell Scientific.
- Doolan, S. P. & Macdonald, D. W. 1996. Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *Journal of Zoology*, **239**, 697–716.
- Ferchmin, P. A. & Eterovic, V. A. 1982. Play stimulated by environmental complexity alters brain and improves learning-abilities in rodents, primates, and possibly humans. *Behavioral and Brain Sciences*, **5**, 164.
- Glaser, A. S. 2006. Prey detection and foraging strategies in meerkats. M.Sc. thesis, University of Zurich.
- Green, A. J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology*, **82**, 1473–1483.
- Griffin, A. S., Pemberton, J. M., Brotherton, P. N. M., McIlrath, G., Gaynor, D., Kansky, R., O'Riain, J. & Clutton-Brock, T. H. 2003. A genetic analysis of breeding success in the cooperative meerkat (*Suricata suricatta*). *Behavioral Ecology*, **14**, 472–480.
- Gustafsson, L., Qvarnstrom, A. & Sheldon, B. C. 1995. Trade-offs between life-history traits and a secondary sexual character in male collared flycatchers. *Nature*, **375**, 311–313.
- Heinsohn, R. G. 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged couds. *American Naturalist*, **137**, 864–881.
- Holekamp, K. E. & Smale, L. 1998. Behavioral development in the spotted hyena. *Bioscience*, **48**, 997–1005.
- Jakob, E. M., Marshall, S. D. & Uetz, G. W. 1996. Estimating fitness: a comparison of body condition indices. *Oikos*, **77**, 61–67.
- Johnsson, J. I. & Bohlin, T. 2006. The cost of catching up: increased winter mortality following structural growth compensation in the wild. *Proceedings of the Royal Society of London, Series B*, **273**, 1281–1286.
- Jordan, N. R., Cherry, M. I. & Manser, M. B. 2007. Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Animal Behaviour*, **73**, 613–622.
- Kacelnik, A. & Bateson, M. 1996. Risky theories: the effects of variance on foraging decisions. *American Zoologist*, **36**, 402–434.
- Kruuk, L. E. B., Clutton-Brock, T. H., Rose, K. E. & Guinness, F. E. 1999. Early determinants of lifetime reproductive success differ between the sexes in red deer. *Proceedings of the Royal Society of London, Series B*, **266**, 1655–1661.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Oxford: Oxford University Press.
- Lindström, J. 1999. Early development and fitness in birds and mammals. *Trends in Ecology & Evolution*, **14**, 343–348.
- Lummaa, V. 2003. Early developmental conditions and reproductive success in humans: downstream effects of prenatal famine, birthweight, and timing of birth. *American Journal of Human Biology*, **15**, 370–379.
- Manser, M. B. & Avey, G. 2000. The effect of pup vocalisations on food allocation in a cooperative mammal, the meerkat (*Suricata suricatta*). *Behavioral Ecology and Sociobiology*, **48**, 429–437.
- Metcalfe, N. B. & Monaghan, P. 2001. Compensation for a bad start: grow now, pay later? *Trends in Ecology & Evolution*, **16**, 254–260.
- Mittelbach, G. C., Osenberg, C. W. & Wainwright, P. C. 1999. Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? *Evolutionary Ecology Research*, **1**, 111–128.
- Nowicki, S., Peters, S. & Podos, J. 1998. Song learning, early nutrition and sexual selection in songbirds. *American Zoologist*, **38**, 179–190.
- Rovero, F., Hughes, R. N. & Chelazzi, G. 1999. Effect of experience on predatory behaviour in dogwhelks. *Animal Behaviour*, **57**, 1241–1249.
- Russell, A. F., Clutton-Brock, T. H., Brotherton, P. N. M., Sharpe, L. L., McIlrath, G. M., Dalerum, F. D., Cameron, E. Z. & Barnard, J. A. 2002. Factors affecting pup growth and survival in co-operatively breeding meerkats, *Suricata suricatta*. *Journal of Animal Ecology*, **71**, 700–709.
- Russell, A. F., Brotherton, P. N. M., McIlrath, G. M., Sharpe, L. L. & Clutton-Brock, T. H. 2003. Breeding success in cooperative meerkats: effects of helper number and maternal state. *Behavioral Ecology*, **14**, 486–492.
- Russell, A. F., Young, A. J., Spong, G., Jordan, N. R. & Clutton-Brock, T. H. 2007. Helpers raise the reproductive potential of offspring in cooperative meerkats. *Proceedings of the Royal Society of London, Series B*, **274**, 513–520.
- Schall, R. 1991. Estimation in generalized linear models with random effects. *Biometrika*, **78**, 719–727.
- Sharpe, L. L., Clutton-Brock, T. H., Brotherton, P. N. M., Cameron, E. Z. & Cherry, M. I. 2002. Experimental provisioning increases play in free-ranging meerkats. *Animal Behaviour*, **64**, 113–121.
- Slagsvold, T. & Wiebe, K. L. 2007. Learning the ecological niche. *Proceedings of the Royal Society of London, Series B*, **274**, 19–23.
- Stephens, D. W. & Krebs, J. R. 1986. *Foraging Theory*. Princeton, New Jersey: Princeton University Press.
- Thornton, A. 2007. Social influences on the development of foraging behaviour in meerkats. Ph.D. thesis, University of Cambridge.
- Thornton, A. & McAuliffe, K. 2006. Teaching in wild meerkats. *Science*, **313**, 227–229.
- Turbé, A. 2006. Foraging decisions and space use in a social mammal, the meerkat. Ph.D. thesis, University of Cambridge.
- Verhulst, S., Holveck, M. J. & Riebel, K. 2006. Long-term effects of manipulated brood size on metabolic rate in zebra finches. *Biology Letters*, **2**, 478–480.
- West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.
- White, S. M. 2001. Juvenile development and conflicts of interest in meerkats. Ph.D. thesis, University of Cambridge.
- Worthman, C. M. & Kuzara, J. 2005. Life history and the early origins of health differentials. *American Journal of Human Biology*, **17**, 95–112.

Appendix: Tables for Multivariate Analyses

Table A1. Linear mixed model on factors influencing pup time budgets

	df	Time begging		Time foraging	
		Wald statistic ( $\chi^2$ )	P	Wald statistic ( $\chi^2$ )	P
Full model					
Pup age (days)	1	786.55	<0.001	224.51*	<0.001
Log hind-foot length (mm)	1	19.59	<0.001	7.85	0.005
Time of day (a.m., p.m.)	1	13.85	<0.001	11.97	<0.001
Body condition index	1	10.02	0.002	10.12	0.001
Pup sex	1	6.27	0.012	1.25	0.263
Rainfall (mm)	1	5.06	0.024	0.88	0.349
Pup age*body condition index	1	0.40	0.529	6.66	0.010
Helper sex ratio	2	0.68	0.710	1.55	0.460
Helper number	1	0.06	0.813	0.00	0.986
Litter size	1	0.03	0.872	0.82	0.367
Minimal model		Average effect	SE	Average effect	SE
Constant		0.47	0.022	0.60	0.014
Pup age (days)		-0.016	0.00057	0.89	0.060
Log hind-foot length (mm)		-1.66	0.38	0.67	0.28
Time of day					
a.m.		0	0	0	0
p.m.		-0.061	0.017	0.044	0.013
Body condition index		-1.15	0.36	0.79	0.25
Pup sex					
Female		0	0	0	0
Male		0.042	0.017	0.00025	0.00027
Rainfall (mm)		-0.00076	0.00034	0.00025	0.00027
Pup age*body condition index		-0.0080	0.013	-3.29	1.27
Significant random terms ( $P < 0.05$ )		Litter		Litter, individual	

Analysis conducted on the proportion of time spent begging and foraging in 476 focal watches on 69 pups from 28 litters in 10 groups (mean = 6.9 ± 0.6 focal watches per pup, range 1–23). Pup age was log transformed in the analysis on proportion of time spent foraging as the response term asymptotes with age.

Table A2. Linear mixed model on factors influencing rate of pup provisioning by helpers

	Wald statistic ( $\chi^2$ )	df	P
Full model			
Time of day (a.m., p.m.)	12.47	1	<0.001
Log rainfall (mm)	5.25	1	0.022
Pup age <sup>2</sup> (days)	3.87	1	0.049
Pup sex	2.34	1	0.126
Log hind-foot length (mm)	2.10	1	0.148
Pup age (days)	1.25	1	0.264
Body condition index	1.20	1	0.273
Helper number	1.05	1	0.306
Litter size	0.08	1	0.778
Helper sex ratio	0.31	2	0.857
Minimal model	Average effect	SE	
Constant	0.32	0.034	
Time of day			
a.m.	0	0	
p.m.	-0.18	0.051	
Pup age <sup>2</sup>	-0.00020	0.00010	
Log rainfall (mm)	0.085	0.037	
Pup age	0.014	0.013	

Analysis conducted on the rate (in g/h, log transformed) at which pups received food from helpers in 476 focal watches on 69 pups from 28 litters in 10 groups (mean = 6.9 ± 0.6 focal watches per pup, range 1–23). Individual, group and litter identity did not constitute significant repeatability.

Table A3. Linear mixed model on factors influencing pup foraging efficiency

	Wald statistic ( $\chi^2$ )	df	P
Full model			
Pup age (days)	163.06	1	<0.001
Rainfall (mm)	7.94	1	0.005
Log hind-foot length (mm)	4.03	1	0.045
Body condition index	4.03	1	0.047
Time of day (a.m., p.m.)	2.82	1	0.093
Helper number	0.67	1	0.414
Pup sex	0.49	1	0.482
Number of pups	0.43	1	0.514
Helper sex ratio	1.11	2	0.573
Minimal model	Average effect	SE	
Constant	0.41	0.038	
Pup age (days)	0.024	0.0019	
Rainfall (mm)	0.0025	0.00089	
Log hind-foot length (mm)	1.81	0.90	
Body condition index	1.57	0.79	

Analysis conducted on the foraging efficiency (in g/h, log transformed) of pups 45–90 days old in 394 focal watches on 62 pups from 26 litters in 10 groups (mean = 6.4 ± 0.5 focal watches per pup, range 1–29). Litter identity constituted significant repeatability ( $P < 0.005$ ), but individual and group identity were not significant random terms ( $P > 0.05$ ).

**Table A4.** Linear mixed model on average foraging efficiency of old but light and young but heavy pups

	Wald statistic ( $\chi^2$ )	df	P
Full model			
Pup age (45–55, 65–75 days)	18.60	1	<0.001
Weight at first forage (g)	15.49	1	<0.001
Pup age*rainfall	9.39	1	0.002
Rainfall (mm)	1.57	1	0.210
Helper number	0.69	1	0.408
Pup sex	1.09	1	0.298
Litter size	0.06	1	0.801
Helper sex ratio	1.18	2	0.555
Minimal model	Average effect	SE	
Constant	-0.22	0.16	
Pup age			
45–55 days	0	0	
65–75 days	0.39	0.092	
Weight at first forage	0.0044	0.0012	
Pup age*rainfall			
45–55 days	0	0	
65–75 days	0.010	0.0038	
Rainfall (mm)	0.0018	0.0014	

Analysis conducted on the average foraging efficiency (in g/h, log transformed) of the 15 heaviest pups between 45 and 55 days old (from 10 litters in six groups) and the 15 lightest pups between 65 and 75 days old (from nine litters in six groups). Group and litter identity did not constitute significant repeatability ( $P > 0.05$ ).

**Table A5.** Linear mixed model on factors influencing pup acquisition of foraging independence

	Wald statistic ( $\chi^2$ )	df	P
Full model			
Pup age (days)	129.87	1	<0.001
Time of day (a.m., p.m.)	10.05	1	0.002
Rainfall <sup>2</sup> (mm)	5.70	1	0.017
Pup age*body condition index	5.65	1	0.017
Rainfall (mm)	3.91	1	0.048
Body condition index	2.44	1	0.118
Helper number	1.87	1	0.171
Pup sex	1.67	1	0.197
Helper sex ratio	2.00	2	0.368
Log hind-foot length (mm)	0.20	1	0.655
Number of pups	0.04	1	0.838
Minimal model	Average effect	SE	
Constant	-0.017	0.030	
Pup Age (days)	0.016	0.0014	
Time of day			
a.m.	0	0	
p.m.	0.14	0.043	
Rainfall <sup>2</sup> (mm)	0.000044	0.000018	
Pup age*body condition index	0.074	0.031	
Rainfall (mm)	-0.0040	0.0020	
Body condition index	0.92	0.59	

Analysis conducted on the factors affecting the difference in intake (in g, log transformed) from self-feeding and being fed in 476 focal watches on 69 pups from 28 litters in 10 groups (mean = 6.9 ± 0.6 focal watches per pup, range 1–23). Individual identity constituted significant repeatability ( $P < 0.05$ ), but individual and group identity were not significant random terms ( $P > 0.05$ ).

**Table A6.** Linear mixed model on factors influencing foraging efficiency of helpers

	Wald statistic ( $\chi^2$ )	df	P
Full model			
Pup age (days)	11.49	1	<0.001
Log rainfall (mm)	5.54	1	0.019
Body condition index	4.32	1	0.038
Helper number	2.96	1	0.085
Log hind-foot length (mm)	1.31	1	0.252
Number of pups	0.34	1	0.557
Helper sex ratio	0.89	2	0.639
Time of day (a.m., p.m.)	0.26	1	0.607
Pup sex	0.10	1	0.746
Minimal model	Average effect	SE	
Constant	1.12	0.028	
Pup age (days)	0.00093	0.00027	
Log rainfall (mm)	0.093	0.039	
Body condition index	1.43	0.069	

Analysis conducted on the foraging efficiency (in g/h, log transformed) of helpers aged 90–360 days in 387 focal watches on 71 individuals from 31 litters in nine groups (mean = 5.4 ± 0.6 focal watches per individual, range 1–29). Litter identity constituted significant repeatability ( $P < 0.005$ ), but individual and group identity were not significant random terms ( $P > 0.05$ ).