

Variation in contributions to teaching by meerkats

Alex Thornton*

*Department of Zoology, University of Cambridge, Downing Street,
Cambridge CB2 3EJ, UK*

Recent evidence from cooperative insect, bird and mammal societies has challenged the assumption that teaching is restricted to humans. However, little is known about the factors affecting the degree to which individuals in such societies contribute to teaching. Here, I examine variation in contributions to teaching in meerkats, where older group members teach pups to handle difficult prey. I show that investment in teaching varies with characteristics of pups, helpers, groups and ecological conditions. Although prior experience in caring for pups did not significantly influence teaching behaviour, younger helpers, which were still investing in growth, contributed less to teaching than older individuals. This suggests that, in common with other cooperative activities, contributions to teaching vary with the costs experienced by individual group members. However, in contrast to other forms of helping in meerkats, I detected no effects of nutritional state on teaching, suggesting that it carries relatively low costs. In species where individuals can potentially gain direct or indirect fitness benefits from facilitating learning in others, low costs divided among multiple group members may help tip the balance towards selection for teaching.

Keywords: helping behaviour; meerkats; parental care; social learning; *Suricata suricatta*; teaching

1. INTRODUCTION

Teaching, whereby knowledgeable individuals actively facilitate learning in others, was commonly assumed to be a uniquely human form of behaviour dependent on a capacity for mental state attribution (Premack & Premack 1996). This view was challenged by Caro & Hauser (1992), who suggested that behaviour that functions to teach may occur in the absence of sophisticated mental faculties. They proposed a definition outlining three criteria for teaching: (i) an experienced individual, A, modifies its behaviour in the presence of a naive observer, B; (ii) A incurs a cost, or derives no immediate benefit; and (iii) as a result of A's behaviour, B acquires knowledge or skills more rapidly than it would otherwise have done, or that it would not have learned at all. From this perspective, teaching is best seen as a form of cooperative behaviour in which individuals incur short-term costs in order to facilitate learning in others (Thornton & Raihani 2008).

Although behaviour suggestive of teaching has been reported in a number of species (reviewed in Thornton & Raihani 2008), only three studies, on tandem running ants, *Temnothorax albipennis* (Franks & Richardson 2006), pied babblers, *Turdoides bicolor* (Raihani & Ridley 2008) and meerkats, *Suricata suricatta* (Thornton & McAuliffe 2006), have provided strong evidence for all the three criteria. In meerkats, the subjects of this study, older individuals, including both parents and helpers, teach pups prey-handling skills by providing them with otherwise unavailable opportunities to practice handling difficult prey (Thornton & McAuliffe 2006). Young pups are typically provisioned with dead or disabled prey, but helpers modify

their prey-provisioning methods in response to age-related changes in pup begging calls, and increasingly donate intact prey. Following provisioning, helpers generally monitor pups' handling attempts, occasionally nudging items to draw pups' attention to them and retrieving prey that escapes. Provisioning live prey is costly, as helpers must spend longer time monitoring pups and run the risk that the pups will be injured or lose the item. However, experience with live prey results in improvements in pups' abilities to rapidly and safely kill and consume difficult prey types (Thornton & McAuliffe 2006). A number of studies on other carnivores, particularly felids, have provided evidence for similar processes (reviewed in Caro & Hauser 1992), although it has proved difficult to establish causal relationships between the behaviour of mothers and the acquisition of hunting skills in young.

Teaching, like any other form of cooperative behaviour, will only be favoured by selection if the long-term fitness benefits of investing in teaching outweigh the short-term costs of assisting others (West *et al.* 2007; Thornton & Raihani 2008). This may be particularly probable in the context of offspring care where adults may benefit from promoting the acquisition of knowledge or skills by offspring in situations where high costs or lack of opportunities limit offspring's capacity to learn without assistance (Thornton & Raihani 2008). In cooperative societies, where individuals incur costs in teaching young that are not their own, teaching can be considered to be a form of helping behaviour. Helpers may gain substantial indirect and/or direct fitness benefits from raising the condition and survival of the young they assist (Emlen 1991; Clutton-Brock 2002; Bergmüller *et al.* 2007), but individual contributions to helping often vary considerably. Considerable evidence suggests that variation in helper behaviour is related to the costs and benefits of

*jant2@cam.ac.uk

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2008.0268> or via <http://journals.royalsociety.org>.

helping. For example, individuals commonly adjust their investment in helping in relation to variables such as relatedness and group size (Komdeur 1994; Heinsohn & Legge 1999), and a number of studies have shown that individuals increase their contributions to helping when nutritional constraints are reduced through experimental provisioning (Eden 1987; Boland *et al.* 1997; Clutton-Brock *et al.* 2000, 2001a; Russell *et al.* 2003). This raises the question of whether individual contributions to teaching also vary facultatively in response to current benefits and costs.

Studies of the factors affecting variation in teaching behaviour are now needed to assess the magnitude of the costs involved and further our understanding of the circumstances under which teaching may evolve. Although it has been shown that *T. albipennis* ants evaluate their investment into a particular bout of teaching according to the time already invested in that bout (Richardson *et al.* 2007), it is not yet known whether overall investment in teaching varies with the current costs experienced by individual teachers. This paper provides the first examination of the factors influencing individual contributions to teaching, using longitudinal data from meerkats. These are small (less than 1 kg) mongooses from the arid regions of southern Africa. They are obligate cooperative breeders, living in groups of 2–50 individuals consisting of a dominant male and female and a variable number of helpers of both sexes that aid in rearing the young (Clutton-Brock *et al.* 2001b). Pups are born underground and begin accompanying the foraging group at approximately 30 days of age. All helpers feed pups with invertebrate and small vertebrate prey in response to begging calls until the pups reach nutritional independence at around three months of age, but the contributions of juvenile helpers (three to six months) are typically low (Brotherton *et al.* 2001).

I use multivariate analyses to examine the factors affecting investment in two components of teaching behaviour in meerkats: prey modification (i.e. whether mobile prey items are provisioned dead, disabled or intact) and the amount of time helpers spend monitoring pups handling prey following provisioning. Previous studies of meerkats have shown that individual investment in raised guarding (Clutton-Brock *et al.* 1999), baby-sitting (Clutton-Brock *et al.* 2000) and pup-feeding (Clutton-Brock *et al.* 2001a) decreases with increasing group size. I therefore examined whether group size had similar effects on contributions to teaching, predicting that individual contributions to costly elements of teaching should decline when there are larger numbers of helpers to share the burden. Nutritional state has been shown to affect helping behaviour in many species (Heinsohn & Legge 1999), and in cheetahs, where there is evidence suggestive of a similar form of teaching to that found in meerkats (Caro & Hauser 1992), hungry mothers are less likely to give away intact prey to cubs (Caro 1994). I therefore investigated whether meerkat helpers' absolute weight and that which they put on during foraging sessions affected provisioning methods and monitoring time. Both of these factors have been shown to have significant positive effects on other forms of helping behaviour in meerkats (Clutton-Brock *et al.* 2000, 2001a, 2002). In addition, I considered the effects of rainfall, which affects prey availability and foraging intake (Doolan & Macdonald 1996), and litter

size, which may influence helpers' levels of investment in individual pups. Finally, I examined the effects of age and prior experience. Younger individuals may be less likely to invest in helping behaviour if, for example, they are still investing in growth (Brotherton *et al.* 2001; Clutton-Brock *et al.* 2001a) or if their foraging skills are not yet fully developed (Heinsohn 1991). I therefore examined changes in helper weight with age and investigated whether helper age had effects on teaching behaviour. As parental and helping behaviour may also improve with experience (Tardif *et al.* 1984; Komdeur 1996; Margulis *et al.* 2005), I compared the teaching behaviour of experienced and inexperienced helpers, controlling for any effects of age.

2. MATERIAL AND METHODS

I collected data on 13 groups consisting of 6–41 meerkats living in semi-desert along the dry Kuruman River in the South African Kalahari (Clutton-Brock *et al.* 1998) between December 2003 and April 2006. Where suitable, additional data from the Kalahari Meerkat Project database were included, so some analyses are based on data from 15 groups. Groups were located by radio-tracking collared individuals (see Jordan *et al.* 2007 for details of collaring procedures) and all individuals were identifiable by unique marks of black hair dye. Individuals were monitored from birth, so the ages of all animals were known precisely (± 2 days). All animals were habituated to close observation (less than 1 m) and over 90% could be weighed regularly by using crumbs of hard-boiled egg to entice them on to an electronic top-pan balance. Animals were weighed at dawn, before the start of the morning foraging session, and again after the cessation of foraging in the middle of the day (mean time between 'morning' and 'afternoon' weighing = 3.4 ± 0.03 hours). The residuals of a regression of pre-foraging morning weights (in grams) against age (in days) were used to obtain a measure of how heavy a helper was for its age (hereafter 'age-related weight'). I also conducted a regression of morning weight gain (measured as the change in mass, in grams per hour, between morning and afternoon weights) against helper age and used the residuals as a measure of 'age-related weight gain' that provides a measure of a helper's proficiency at finding food for its age. To obtain an estimate of a helper's foraging proficiency around the time of a pup feed, I averaged measures of age-related weight gain for the 10 days surrounding the feed.

Helpers were classed as all individuals over three months old. Every time a helper fed a pup, I noted the identity of the donor and the recipient, the type of prey (e.g. scorpion, gecko) and whether it was provisioned dead, disabled or intact. The disabled prey items were those that were modified, but not killed, prior to provisioning. For scorpions, this typically involved a helper removing the sting. Prey items were divided into three size classes: small (fitting entirely in an adult's mouth), medium (less than half that is protruding from an adult's mouth) and large (more than half that is protruding; Brotherton *et al.* 2001).

(a) Statistical analyses

All data were analysed in GENSTAT v. 8.1 (Rothamstead Experimental Station, Harpenden, UK). I used linear mixed models (LMMs) or generalized linear mixed model (GLMMs) for normal error structure or non-normal error structure, respectively. Mixed models are similar to general

Table 1. GLMMs of factors affecting the probability that scorpions would be provisioned dead, disabled or intact. (Data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether a scorpion was provisioned in a given state.)

| full model | d.f. | dead feeds | | disabled feeds | | intact feeds | |
|----------------------------------|------|-----------------------------|----------|-----------------------------|----------|-----------------------------|----------|
| | | Wald statistic (χ^2) | <i>p</i> | Wald statistic (χ^2) | <i>p</i> | Wald statistic (χ^2) | <i>p</i> |
| pup age (days) | 1 | 10.53 | 0.001 | 13.65 | <0.001 | 50.45 | <0.001 |
| helper number | 1 | 4.82 | 0.028 | 1.02 | 0.314 | 3.19 | 0.074 |
| helper age (days) | 1 | 3.24 | 0.072 | 0.91 | 0.341 | 5.87 | 0.015 |
| pup sex | 1 | 2.72 | 0.099 | 6.21 | 0.082 | 0.72 | 0.397 |
| litter size | 1 | 2.44 | 0.118 | 0.01 | 0.915 | 2.29 | 0.130 |
| prey size (small, medium, large) | 2 | 0.46 | 0.481 | 26.80 | <0.001 | 21.67 | <0.001 |
| age-related weight gain | 1 | 0.27 | 0.605 | 0.21 | 0.650 | 0.13 | 0.717 |
| helper sex | 1 | 0.18 | 0.668 | 0.10 | 0.752 | 0.07 | 0.797 |
| age-related weight | 1 | 0.06 | 0.809 | 0.31 | 0.577 | 0.01 | 0.904 |
| rainfall | 1 | 0.00 | 0.977 | 0.78 | 0.377 | 0.74 | 0.389 |
| helper experience (yes, no) | 1 | 0.00 | 0.998 | 1.06 | 0.303 | 0.98 | 0.323 |
| minimal model | | effect size | s.e. | effect size | s.e. | effect size | s.e. |
| constant | | -0.75 | 0.093 | -1.12 | 0.16 | -0.36 | 0.16 |
| pup age | | -0.016 | 0.0050 | -0.018 | 0.0048 | 0.038 | 0.0053 |
| helper number | | 0.031 | 0.014 | -0.013 | 0.013 | -0.029 | 0.017 |
| helper age: ≥ 1 yr | | -0.0010 | 0.00055 | -0.00049 | 0.00051 | 0.0014 | 0.00058 |
| prey size | | | | | | | |
| small | | 0 | 0 | 0 | 0 | 0 | 0 |
| medium | | -0.21 | 0.20 | 0.86 | 0.19 | -0.76 | 0.18 |
| large | | -0.17 | 0.17 | 0.85 | 0.16 | -0.80 | 0.21 |
| significant | | litter identity | | litter identity | | litter identity | |
| random terms ($p < 0.05$) | | | | | | | |

linear models, but allow both fixed and random effects to be fitted (Schall 1991), with random terms controlling for repeated measures such as individual, group and litter identities. Initially, all probable 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 statistics and probability values for significant terms were derived from having all significant terms in the model, while values for non-significant terms were obtained by adding each term individually to the minimal model. I visually inspected the residuals for all models to ensure homogeneity of variance, normality of error and linearity, applying log transformations where necessary. Kolmogorov-Smirnov tests were used to confirm that residuals were normally distributed.

To investigate the factors affecting the probability that prey would be provisioned dead, disabled or intact, I constructed three GLMMs. Data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether a provisioned item was in a given state. Pup age, helper and pup sex, helper age-related weight and weight gain, helper number, litter size and rainfall were fitted as explanatory variables. Helper number is the total number of individuals over three months present in the group and rainfall refers to the total rainfall (in mm) over the 30 days preceding a pup feed. The analysis also included measures of helper age and experience. As pups' prey-handling competence improves with age (Thornton & McAuliffe 2006), it is probable that, if experience is necessary for the development of teaching behaviour, helpers would have to care for a litter from emergence until nutritional independence in order to

learn about the methods of provisioning and monitoring required for pups of different ages. Consequently, any effects of experience should be evident through comparisons of helpers caring for their first or subsequent litters. I therefore classified inexperienced helpers as all individuals over three months of age that had never before been in a group with foraging pups. The helpers were classed as experienced if they had previously cared for pups. All experienced helpers had cared for at least one litter that foraged with the group for at least 40 days. To verify the results, I also reran all analyses with helper experience included as a continuous variable (the number of days a helper was present in a group with foraging pups). The helpers were divided into three age categories: juveniles (3–6 months), subadult (6–12 months) and adults (more than 12 months). As all helpers older than 2 years were experienced and all juveniles were inexperienced, I restricted the analysis to subadult and adult yearling (age 1–2 years) helpers. To reduce the number of potential confounding variables, I used only feeds of scorpions, which account for 9.3% of all pup feeds (A. Thornton 2003–2006, unpublished data) and are the most difficult and potentially dangerous prey items with which pups are provisioned. Final analyses were conducted on 1070 feeds by 347 helpers to 339 pups from 137 litters in 15 groups.

I defined monitoring time as the combined time during which a helper stood next to a pup after provisioning it with a food item, with its head oriented towards the pup while the pup handled the prey, and the time taken to retrieve lost prey and return it to pups. I noted monitoring time (to the nearest s) using a stopwatch. In total, I collected accurate monitoring times for 6148 feeds by 300 helpers to 244 pups from 65 litters in 13 groups. I investigated factors

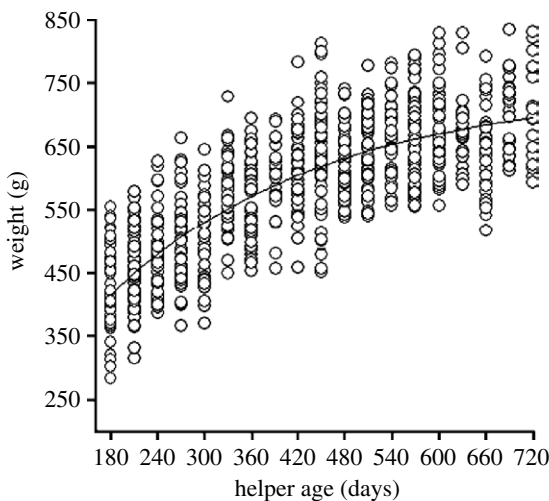


Figure 1. Morning weights of subadult and yearling helpers (asymptotic regression: $r^2=63.9$, $F_{2,841}=746.61$, $p<0.001$). Points show morning weights every 30 days for all helpers included in the analysis of provisioning behaviour.

affecting the monitoring time using a LMM. The response term (in s) was log-transformed to achieve normality of residuals. I included pup age and sex, helper sex and age category (juvenile, subadult or adult), helper number, litter size, whether another helper was present within 2 m, rainfall and prey size and mobility as potential explanatory terms. Prey items that were immobile (e.g. beetle larvae) and items that were killed prior to provisioning were classified as ‘stationary’, and mobile prey items (e.g. crickets and scorpions) provisioned alive were classified as ‘moving’. To investigate the effects of helper experience on monitoring time, I conducted a separate LMM using only feeds by subadult and yearling helpers and fitted helper age (in days) and helper experience as explanatory terms in addition to the core variables described above. To reduce the number of potential confounding factors in the model, I included only feeds of large moving prey. The final model was based on 308 feeds by 131 helpers to 126 pups from 51 litters in 12 groups.

3. RESULTS

Characteristics of the prey, pups, helpers and groups all affected the state in which scorpions were provisioned to pups (table 1). Larger scorpions were more likely to be disabled prior to provisioning and less likely to be given intact than small scorpions. The probability that a scorpion would be fed dead or disabled declined with pup age, while the probability that the item would be fed intact increased, controlling for other significant terms in the model (table 1). The weight of subadult and yearling helpers increased with age, but began to plateau as helpers grew older (figure 1). The older helpers were more likely to provision pups with intact scorpions (figure 2), and there was a non-significant trend for the probability of provisioning dead scorpions to decline with helper age (table 1). However, controlling for helper age and other significant variables, I found no evidence that experienced helpers provisioned scorpions in a different way to inexperienced helpers ($p>0.3$; table 1). Repeating the analyses with helper experience treated as a continuous variable produced qualitatively similar results: there was no significant effect of helper experience on the probability of prey being provisioned dead ($\chi^2=0.53$, $p=0.467$),

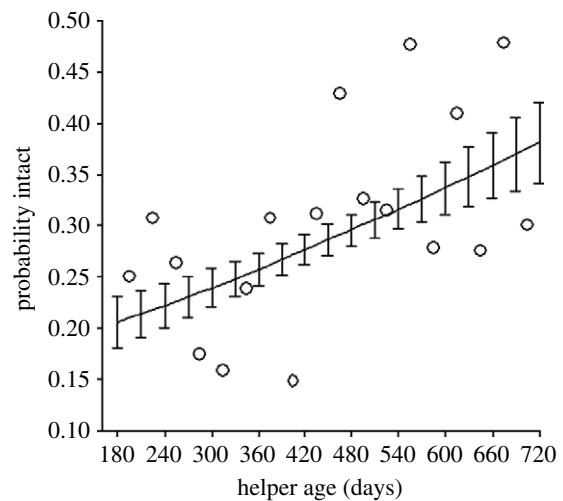


Figure 2. Helper age had a significant positive effect on the probability that helpers would provision scorpions intact to pups (GLMM: $\chi^2=5.87$, $p=0.015$; table 1). Points are mean values from raw data. Line shows predicted means \pm s.e. from a GLMM, controlling for other significant terms in the model.

disabled ($\chi^2=0.65$, $p=0.421$) or intact ($\chi^2=3.12$, $p=0.077$). Neither helper age-related weight nor age-related weight gain had significant effects on whether scorpions were given to pups dead, disabled or intact (table 1). Finally, the number of helpers in the group influenced whether helpers killed scorpions prior to provisioning: helpers in large groups were more likely to provision pups with dead scorpions and there was a non-significant negative trend for helpers in larger groups to be less likely to provision live scorpions (table 1).

The duration of monitoring following pup feeds was also affected by prey, pup, helper and group characteristics, as well as by recent rainfall. Monitoring duration was greater if the prey item was moving and larger in size and declined as pups grew older (table 2). Among helpers, age-related weight and weight gain did not have a significant effect, but juvenile helpers invested less time in monitoring pups than subadults and adults (table 2; figure 3). Finally, monitoring time declined with increasing litter size and rainfall, and when another helper was present within 2 m (table 2). In a restricted analysis of monitoring time following feeds of large, mobile prey by subadult and yearling helpers, pup age, litter size, rainfall and the proximity of another helper all had significant effects, as described above, and there was a trend for a longer monitoring time if the prey item was intact than if it was disabled ($p=0.070$; see table S1 in the electronic supplementary material). Again, there was no significant effect of helper age-related weight ($\chi^2=0.65$; $p=0.421$) or weight gain ($\chi^2=0.29$; $p=0.529$). I found no effect of helper age ($\chi^2=0.01$; $p=0.986$) or experience ($\chi^2=0.73$; $p=0.392$; see table S1 in the electronic supplementary material). Quantitatively similar results were produced if the helper’s experience was treated as a continuous variable ($\chi^2=0.01$; $p=0.954$).

4. DISCUSSION

Helpers gradually introduced pups to intact scorpions, thus providing them with otherwise unavailable opportunities to learn how to handle these difficult prey items. As

Table 2. LMM on factors affecting the duration of monitoring. (The response term was log-transformed. Adult and litter identity constituted significant repeatability ($p < 0.05$), but group and pup identity were not significant random terms.)

| full model | Wald statistic (χ^2) | d.f. | p |
|---|-----------------------------|---------|--------|
| prey mobility (moving, stationary) | 565.58 | 1 | <0.001 |
| prey size (small, medium, large) | 565.58 | 2 | <0.001 |
| pup age (days) | 545.42 | 1 | <0.001 |
| other helper: < 2 m | 21.92 | 1 | <0.001 |
| litter size | 16.62 | 1 | <0.001 |
| rainfall (mm) | 8.14 | 1 | 0.004 |
| helper age category (juvenile, subadult, adult) | 8.68 | 2 | 0.013 |
| helper number | 1.92 | 1 | 0.166 |
| pup sex | 1.13 | 1 | 0.288 |
| age-related weight | 0.83 | 1 | 0.362 |
| helper sex | 0.55 | 1 | 0.458 |
| age-related weight gain | 0.31 | 1 | 0.580 |
| minimal model | effect size | s.e. | |
| constant | 0.56 | 0.028 | |
| prey mobility | | | |
| moving | 0 | 0 | |
| stationary | -0.26 | 0.011 | |
| prey size | | | |
| small | 0 | 0 | |
| medium | 0.14 | 0.0091 | |
| large | 0.29 | 0.013 | |
| pup age (days) | -0.0078 | 0.00033 | |
| other helper: < 2 m | | | |
| no | 0 | 0 | |
| yes | -0.039 | 0.0083 | |
| litter size | -0.018 | 0.045 | |
| rainfall (mm) | -0.00052 | 0.00018 | |
| helper age category | | | |
| juvenile | 0 | 0 | |
| subadult | 0.073 | 0.026 | |
| adult | 0.072 | 0.025 | |

pups grew older, the proportion of scorpions fed dead or disabled declined, as shown previously (Thornton & McAuliffe 2006). However, the method of provisioning scorpions was affected by characteristics of the helpers, prey and group, as well as the age of pups. When younger helpers fed scorpions to pups, they were less likely to give them away intact than the older helpers. However, controlling for age effects, I found no significant effect of prior experience on provisioning methods, regardless of whether helper experience was treated as categorical or continuous. It is probable that the effects of helper age on prey-provisioning methods in meerkats occur due to differential costs to helpers of differing ages, and that experience acquired in caring for previous litters does not play a major role. Subordinate and yearling helpers increased in weight with age, but the rate of growth declined as helpers grew older. The costs of provisioning and teaching are, therefore, likely to be highest for younger helpers, which must invest considerably in growth. The hypothesis that provisioning methods are affected by costs is supported by the effects of prey and group sizes. The helpers were less likely to give scorpions intact and more likely to disable items prior to provisioning if they were large. This is likely to be because intact prey is more likely to escape; larger items represent a greater loss of investment if pups lose them and helpers must invest greater amounts of time monitoring pups handling prey if

the prey is large (Thornton & McAuliffe 2006). The helpers in large groups were more likely to provision pups with dead scorpions and there was a trend for a negative effect of group size on the probability of provisioning intact scorpions. This is consistent with the previous finding that helpers reduce their individual contributions to caring for pups when there are more helpers available to share the burden of care (Clutton-Brock *et al.* 2000, 2001a).

Examination of the second component of teaching, post-provisioning monitoring of pups handling prey, further supported the idea that differential costs, rather than prior experience, account for variation in teaching investment by meerkats. The primary predictors of monitoring time were the age of the pup and the difficulty presented by the prey item. The helpers monitored pups for longer if the prey was large and alive, and monitoring time declined as pups grew older. These effects are likely to occur in response to improvements in pup competence, as pup prey-handling times and the probability of losing prey decline as pups grow older (Thornton & McAuliffe 2006). There was a negative effect of the presence of another helper within 2 m, suggesting that monitoring does not function to deter kleptoparasitism attempts by other helpers. Controlling for other significant effects, I found that juveniles invested less time in monitoring than older helpers. However, when I examined the duration of monitoring by subadult and yearling helpers, I found no

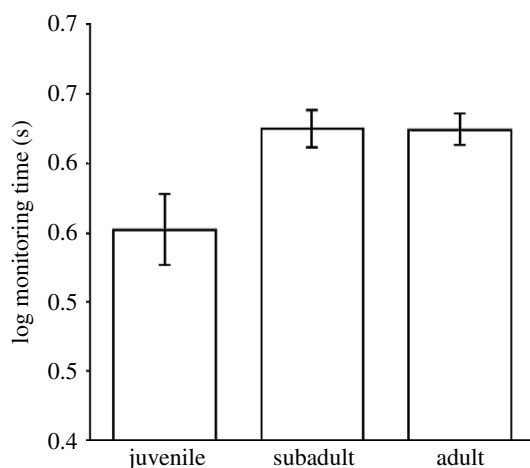


Figure 3. Juveniles spent less time monitoring pups following provisioning than older helpers (LMM: $\chi^2=8.68$, $p=0.008$; see table S1 in the electronic supplementary material). Graph shows predicted means \pm s.e. controlling for other significant terms in the model.

significant difference between helpers that did or did not have prior experience in caring for pups. The same conclusion held if helper experience was treated as a continuous variable. This suggests that the low investment of juveniles in monitoring is due to the costs of growth and the fact that juveniles' foraging skills are not yet fully developed (Barnard 2000), rather than a lack of experience. The lack of an effect of helper age on monitoring duration by subadult and yearling helpers may be because growth rates are lower and foraging behaviour is more developed than in juveniles. The effects of litter size and rainfall on monitoring duration support the suggestion that monitoring duration varies with individual costs. The decline in monitoring time with increasing litter size is likely to occur because helpers can afford to invest more time in supporting a given pup's handling attempts if there are fewer other pups to feed and teach. The negative effect of rainfall may occur because when rainfall is high and food is more readily available it is of less importance if a pup loses a particular prey item.

Together, these results indicate that, in common with other forms of helping behaviour (Heinsohn & Legge 1999), individuals vary their contributions to teaching in response to differential costs. However, unlike previous studies of helping in meerkats (Clutton-Brock *et al.* 2000, 2001a, 2002), I found no effects of body weight or weight gained through foraging on the method of provisioning or the duration of monitoring. This suggests that, relative to the costs of babysitting or pup-feeding, the costs of teaching are low. Babysitting involves individuals foregoing foraging for up to 24 hours when guarding pups at the natal burrow (Clutton-Brock *et al.* 1998), and pup-feeding involves helpers relinquishing a significant proportion of the food they find (Clutton-Brock *et al.* 2001a). By contrast, teaching entails the relatively minor costs to helpers of pups losing donated prey items and time spent monitoring pups. This may explain why, in mixed model analyses, age differences between growing juvenile helpers and adults produce detectable effects on contributions to teaching, while finer-scale variations in nutritional state do not. In future studies, measures of individual helpers' current condition, taking into account their skeletal size, and experimental manipulations of

nutritional state may allow more detailed investigation of the effects of nutritional state on investment in teaching.

I suggest that relatively low costs may be a major factor favouring selection for teaching in meerkats and other species. Individual costs of investment in teaching may be particularly low among cooperative species where the burden of teaching is shared among multiple helpers. This may help to account for the fact that the strongest evidence for teaching to date is found in meerkats (Thornton & McAuliffe 2006), pied babblers (Raihani & Ridley 2008), ants (Franks & Richardson 2006) and humans (Gergely *et al.* 2007), all of which live in cooperative societies. Indirect fitness benefits resulting from high levels of relatedness between helpers and the young they assist (Emlen 1991; Bourke 1997) may further tip the balance towards selection for teaching in cooperative breeders. Although work demonstrating a lack of consistent correlation between investment in helping and relatedness to young in meerkats (Clutton-Brock *et al.* 2000, 2001a), and several other cooperatively breeding vertebrates (Brown 1987; Jacobs & Jarvis 1996; Cockburn 1998), cautions against overemphasis on the role of indirect fitness benefits (Clutton-Brock 2002), it is probable that kin selection plays an important role in the evolution of teaching. Direct benefits, including benefits of increased group size (Kokko *et al.* 2001) and reductions in the costs of rearing young by accelerating development (Thornton & Raihani 2008) are also likely to play a major role. Together, these indirect and direct benefits are particularly likely to outweigh the costs of teaching when the costs are low and the burden of teaching is shared with other group members.

I thank Mr and Mrs H. Kotze and the Northern Cape Conservation Services for permission to work at the study site. Work was carried out with ethics approval of the University of Cambridge and 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 advice and access to the meerkats and M. Manser for their technical support and discussion. M. Bell, C. Cyrus-Kent, S. English, S. Hodge, K. McAuliffe, A. Radford, N. Raihani and two anonymous referees provided useful comments. This work was funded by the Natural Environment Research Council, the Cambridge Philosophical Society and Pembroke College, Cambridge.

REFERENCES

- Barnard, J. A. 2000 Costs and benefits of group foraging in cooperatively breeding meerkats. PhD thesis, University of Cambridge, UK.
- Bergmüller, R., Johnstone, R. A., Russell, A. F. & Bshary, R. 2007 Integrating cooperative breeding into theoretical concepts of cooperation. *Behav. Process.* **76**, 61–72. (doi:10.1016/j.beproc.2007.07.001)
- Boland, C. R. J., Heinsohn, R. & Cockburn, A. 1997 Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. *J. Anim. Ecol.* **66**, 683–691. (doi:10.2307/5921)
- Bourke, A. F. G. 1997 Sociality and kin selection in insects. In *Behavioural ecology: an evolutionary approach* (eds J. R. Krebs & N. B. Davies), pp. 203–227. Oxford, UK: Blackwell Science.
- 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. *Behav. Ecol.* **12**, 590–599. (doi:10.1093/beheco/12.5.590)
- Brown, J. L. 1987 *Helping and communal breeding in birds*. Princeton, NJ: Princeton University Press.
- Caro, T. M. 1994 *Cheetahs of the Serengeti plains: grouping in an asocial species*. Chicago, IL: University of Chicago Press.
- Caro, T. M. & Hauser, M. D. 1992 Is there teaching in nonhuman animals? *Q. Rev. Biol.* **67**, 151–174. (doi:10.1086/417553)
- Clutton-Brock, T. H. 2002 Breeding together: kin selection and mutualism in cooperative vertebrates. *Science* **296**, 69–72. (doi:10.1126/science.296.5565.69)
- Clutton-Brock, T. H. *et al.* 1998 Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. R. Soc. B* **265**, 185–190. (doi:10.1098/rspb.1998.0281)
- Clutton-Brock, T. H., O’Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S. & Manser, M. 1999 Selfish sentinels in cooperative mammals. *Science* **284**, 1640–1644. (doi:10.1126/science.284.5420.1640)
- Clutton-Brock, T. H., Brotherton, P. N. M., O’Riain, M. J., Griffin, A. S., Gaynor, D., Sharpe, L., Kansky, R., Manser, M. B. & McIlrath, G. M. 2000 Individual contributions to babysitting in a cooperative mongoose, *Suricata suricatta*. *Proc. R. Soc. B* **267**, 301–305. (doi:10.1098/rspb.2000.1000)
- Clutton-Brock, T. H., Brotherton, P. N. M., O’Riain, M. J., Griffin, A. S., Gaynor, D., Kansky, R., Sharpe, L. & McIlrath, G. M. 2001a Contributions to cooperative rearing in meerkats. *Anim. Behav.* **61**, 705–710. (doi:10.1006/anbe.2000.1631)
- Clutton-Brock, T. H. *et al.* 2001b Cooperation, control, and concession in meerkat groups. *Science* **291**, 478–481. (doi:10.1126/science.291.5503.478)
- Clutton-Brock, T. H., Russell, A. F., Sharpe, L. L., Young, A. J., Balmforth, Z. & McIlrath, G. M. 2002 Evolution and development of sex differences in cooperative behavior in meerkats. *Science* **297**, 253–256. (doi:10.1126/science.1071412)
- Cockburn, A. 1998 Evolution of helping behavior in cooperatively breeding birds. *Annu. Rev. Ecol. Syst.* **29**, 141–177. (doi:10.1146/annurev.ecolsys.29.1.141)
- Doolan, S. P. & Macdonald, D. W. 1996 Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *J. Zool.* **239**, 697–716.
- Eden, S. F. 1987 When do helpers help? Food availability and helping in the moorhen, *Gallinula chloropus*. *Behav. Ecol. Sociobiol.* **21**, 191–195. (doi:10.1007/BF00303210)
- Emlen, S. T. 1991 Evolution of cooperative breeding in birds and mammals. In *Behavioural ecology: an evolutionary approach* (eds J. R. Krebs & N. B. Davies), pp. 301–337. Oxford, UK: Blackwell Science.
- Franks, N. R. & Richardson, T. 2006 Teaching in tandem-running ants. *Nature* **439**, 153. (doi:10.1038/439153a)
- Gergely, G., Egyed, K. & Király, I. 2007 On pedagogy. *Dev. Sci.* **10**, 139–146. (doi:10.1111/j.1467-7687.2007.00576.x)
- Heinsohn, R. G. 1991 Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *Am. Nat.* **137**, 864–881. (doi:10.1086/285198)
- Heinsohn, R. & Legge, S. 1999 The cost of helping. *Trends Ecol. Evol.* **14**, 53–57. (doi:10.1016/S0169-5347(98)01545-6)
- Jacobs, D. S. & Jarvis, J. U. M. 1996 No evidence for the work–conflict hypothesis in the eusocial naked mole-rat (*Heterocephalus glaber*). *Behav. Ecol. Sociobiol.* **39**, 401–409. (doi:10.1007/s002650050307)
- 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. *Anim. Behav.* **73**, 613–622. (doi:10.1016/j.anbehav.2006.06.010)
- Kokko, H., Johnstone, R. A. & Clutton-Brock, T. H. 2001 The evolution of cooperative breeding through group augmentation. *Proc. R. Soc. B* **268**, 187–196. (doi:10.1098/rspb.2000.1349)
- Komdeur, J. 1994 The effect of kinship on helping in the cooperative breeding Seychelles warbler, *Acrocephalus sechellensis*. *Proc. R. Soc. B* **256**, 47–52. (doi:10.1098/rspb.1994.0047)
- Komdeur, J. 1996 Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behav. Ecol.* **7**, 326–333. (doi:10.1093/beheco/7.4.417)
- Margulis, S. W., Nabong, M., Alaks, G., Walsh, A. & Lacy, R. C. 2005 Effects of early experience on subsequent parental behaviour and reproductive success in oldfield mice, *Peromyscus poliolotus*. *Anim. Behav.* **69**, 627–634. (doi:10.1016/j.anbehav.2004.04.021)
- Premack, D. & Premack, A. J. 1996 Why animals lack pedagogy and some cultures have more of it than others. In *Handbook of education and human development: new models of learning, teaching and schooling* (eds D. R. Olson & N. Torrance), pp. 302–323. Cambridge, MA: Blackwell.
- Raihani, N. J. & Ridley, A. R. 2008 Experimental evidence for teaching in wild pied babblers. *Anim. Behav.* **75**, 3–11. (doi:10.1016/j.anbehav.2007.07.024)
- Richardson, T. O., Sleeman, P. A., McNamara, J. M., Houston, A. I. & Franks, N. R. 2007 Teaching with evaluation in ants. *Curr. Biol.* **17**, 1520–1526. (doi:10.1016/j.cub.2007.08.032)
- Russell, A. F., Sharpe, L. L., Brotherton, P. N. M. & Clutton-Brock, T. H. 2003 Cost minimization by helpers in cooperative vertebrates. *Proc. Natl Acad. Sci. USA* **100**, 3333–3338. (doi:10.1073/pnas.0636503100)
- Schall, R. 1991 Estimation in generalized linear models with random effects. *Biometrika* **78**, 719–727. (doi:10.1093/biomet/78.4.719)
- Tardif, S. D., Richter, C. B. & Carson, R. L. 1984 Effects of sibling-rearing experience on future reproductive success in 2 species of Callitrichidae. *Am. J. Primatol.* **6**, 377–380. (doi:10.1002/ajp.1350060408)
- Thornton, A. & McAuliffe, K. 2006 Teaching in wild meerkats. *Science* **313**, 227–229. (doi:10.1126/science.1128727)
- Thornton, A. & Raihani, N. J. 2008 The evolution of teaching. *Anim. Behav.* (doi:10.1016/j.anbehav.2007.12.014)
- West, S. A., Griffin, A. S. & Gardner, A. 2007 Social semantics: altruism, cooperation, mutualism, strong reciprocity and group selection. *J. Evol. Biol.* **20**, 415–432. (doi:10.1111/j.1420-9101.2006.01258.x)