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Social learning about novel foods in young meerkats

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Animals are often neophobic towards novel foods, but will incorporate them into their diet after interacting with experienced conspecifics. Such social learning is likely to be particularly important for young animals, for which most foods are unfamiliar. It has been suggested that in some species adults actively promote learning about unfamiliar foods by teaching offspring, although firm evidence is lacking. I examined social influences on learning about novel foods among wild meerkats, *Suricata suricatta*, a species where older group members teach pups prey-handling skills. In two experiments, naïve pups were significantly more likely to eat hardboiled egg, a food item not normally present in the diet, and scorpions, a common prey type, if they had interacted with experienced conspecifics. I then investigated whether helpers teach pups to eat unfamiliar prey by preferentially feeding rare items and through direct feeding, where food items are transferred mouth to mouth. Rare prey items were fed more frequently than common items, although this may reflect nutritional characteristics. Direct feeding was most commonly used by juvenile helpers, which typically contribute relatively little to cooperative activities, and was more frequent if other helpers were nearby. This suggests that direct feeding may be a means of reducing the costs of feeding by improving the efficiency of energy transfer and minimizing the risks of kleptoparasitism. I conclude that learning about novel foods is likely to occur as a by-product of provisioning by helpers. There was little evidence that helpers actively teach pups what to eat.

Keywords: helping behaviour; meerkat; social learning; *Suricata suricatta*; teaching; tradition

Individuals in many species are neophobic towards unfamiliar foods, but may use information gained by interacting with experienced conspecifics, or cues these leave behind, to learn about profitable or palatable novel foods (Nicol 1995; Galef & Giraldeau 2001; Galef 2003; Visalberghi & Addessi 2003; Lupfer-Johnson & Ross 2007). Social learning about novel foods is likely to be especially useful in generalist species that eat a wide range of different food types (Klopfer 1961; Lefebvre 2000). Within these species, young individuals, for which most foods are unfamiliar, may particularly benefit from the use of socially acquired information. By learning from more experienced individuals, naïve young may reduce the need for time-consuming trial-and-error learning and avoid the risk of sampling items that are toxic or of no nutritional value (Galef 1993).

Social learning about novel foods typically occurs through the use of inadvertent social information (Danchin et al. 2004), without any active involvement of knowledgeable individuals (Visalberghi & Fragaszy 1996; Galef & Giraldeau 2001). Young Norway rats, *Rattus norvegicus*, for example, are attracted to food sites where an adult colony member is present (Gerrish & Alberts 1995) and preferentially consume food items that are marked with chemical cues left by feeding adults (Laland & Plotkin 1993). In many primate species, juveniles may acquire information about unfamiliar foods by scrounging scraps of food found by more experienced group members (King 1999; Visalberghi & Addessi 2003). However, it has also been suggested that in certain species adults may play an active role in promoting learning about suitable foods by infants through teaching (Nicol & Pope 1996; Rapaport 1999; reviewed in Caro & Hauser 1992; Thornton & Raihani 2008).

From an evolutionary perspective, teaching can be considered as a cooperative behaviour that functions to

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promote learning in others (Thornton & Raihani 2008). Under Caro & Hauser's (1992) operational definition, teaching involves a knowledgeable individual modifying its behaviour in the presence of a naïve observer, at some cost or with no immediate benefit to itself, in such a way as to facilitate learning of knowledge or skills by the observer. To date, only three studies, on meerkats, *Suricata suricatta* (Thornton & McAuliffe 2006), tandem-running ants, *Temnothorax albipennis* (Franks & Richardson 2006) and pied babblers, *Turdoides bicolor* (Raihani & Ridley 2008), have provided strong evidence for teaching under this definition, and it is still unclear whether teaching about unfamiliar foods occurs in any nonhuman species (Thornton & Raihani 2008). Teaching about unfamiliar foods may be particularly likely in species where adults donate food to young whose own foraging abilities are poorly developed. By preferentially donating food that is unfamiliar to offspring, adults may promote learning. To date, most research has been conducted on callitrichid primates. Work on golden lion tamarins, *Leontopithecus rosalia*, showed that adults donate novel foods to offspring more frequently than familiar foods (Rapaport 1999). Although this is consistent with a role for adults in teaching infants about novel foods, it is unclear whether social exposure to novel foods promotes their incorporation into the diet. Furthermore, other studies on lion tamarins (Price & Feistner 1993) and marmosets, *Callithrix jaccus* (Brown et al. 2005), have produced contradictory results. Several authors have concluded that patterns of learning in primates are more consistent with the view of infants as adept gatherers of social and asocial information rather than adults as active information donors (King 1994; Visalberghi & Fragaszy 1996; Brown et al. 2004; Voelkl et al. 2006).

Previous studies of social influences on learning about novel foods in wild animals have relied purely on observational data, rendering it difficult to draw firm conclusions as to whether naïve individuals learn as a result of interactions with others (Fragaszy et al. 1997). I used experiments and detailed observational data to examine whether wild meerkat pups learn to eat unfamiliar foods by interacting with adults and whether adults play an active role in promoting learning through teaching. Meerkats are small (<1 kg), cooperatively breeding mongooses that live in groups of 2–50 individuals in the arid regions of southern Africa. Groups comprise a dominant male and female, who monopolize breeding, and a variable number of helpers of both sexes who assist in rearing the young (Clutton-Brock et al. 1998). Pups are born underground and first emerge from their natal burrow at around 3 weeks of age. For the first 10 days following emergence, pups spend several hours a day above ground, and are guarded by one or more babysitters. At this age, pups are rarely fed solid food and are primarily reliant on milk produced by their mother and allolactating helpers (Doolan & Macdonald 1999). Pups begin accompanying the foraging group at around 30 days of age. Until pups reach nutritional independence at around 3 months of age, older group members provision them with invertebrate and small vertebrate prey in response to begging calls (Doolan & Macdonald 1999; Brotherton et al. 2001) and teach them to handle difficult prey items by gradually introducing them to live prey (Thornton & McAuliffe 2006). All group members over 3 months old (referred to hereafter as 'helpers') contribute to pup feeding and teaching, but the contributions of individuals under 6 months are relatively low (Brotherton et al. 2001; Thornton 2008).

I carried out two experiments examining whether young pups learn to eat novel foods by interacting with helpers. In experiment 1, I presented naïve pups with hardboiled egg, a food type not normally present in the meerkat diet, in the presence or absence of experienced helpers. I predicted that pups would not eat the egg initially when alone, but would learn to eat egg after interacting with helpers. In experiment 2, I initially presented naïve littermates of the same age with scorpions, a common prey item, in the absence of helpers. I then conducted repeated presentations where the pups were given either unmodified scorpions when alone, scorpions with salivary cues deposited by helpers when alone, or unmodified scorpions in the presence of a helper. I predicted that pups would refuse scorpions initially, and pups that encountered scorpions in the presence of helpers would learn to eat them after fewer trials than pups that encountered scorpions alone. If cues deposited by conspecifics promote learning, as has been found in rats (Laland & Plotkin 1993), pups would be expected to learn more rapidly if they encountered scorpions with salivary cues from helpers than if they encountered only unmodified scorpions.

I also used mixed-model analyses of natural data to investigate whether helpers actively teach pups to eat unfamiliar food items. First, I examined whether helpers preferentially feed items they encounter infrequently to pups. If pups learn to eat foods they are given, helpers may promote learning about uncommon prey by biasing pups' food encounters towards those prey types. Second, I considered whether helpers facilitate learning by modifying their method of prey provisioning. When provisioning, helpers generally drop prey items on the floor in front of a pup, but occasionally a helper will approach a pup with a food item and allow the pup to take the item directly from its mouth (personal observation). I refer to this method of provisioning as 'direct feeding'. Pups sometimes fail to interact with food on the ground in front of them (Thornton & McAuliffe 2006), but respond to the sight of a helper with food in its mouth by approaching the helper and attempting to snatch the food (Ewer 1963). Ewer (1963) suggested that by allowing pups to take food directly from their mouths, helpers may promote the incorporation of novel foods into the diet. If direct feeding is a form of teaching, helpers would be expected to use this method preferentially when donating prey types that were rarely given to pups, particularly when pups were young. However, similar effects may arise if rare prey types are particularly palatable or nutritious. It is also possible that rather than serving to facilitate learning, direct feeding provides helpers with immediate benefits, and cannot therefore be considered a form of teaching (Thornton et al. 2007; Thornton & Raihani 2008). For example, by feeding pups mouth to mouth, helpers may lower the costs of provisioning by reducing the time they must spend monitoring pups handling prey following provisioning. Direct feeding may also help to reduce the risk that other helpers will take the food item before the pup can eat it.

METHODS

Study Site and Population

Data were collected from December 2003 to April 2006 on meerkats in 13 groups of 6–41 individuals living in xeric savannah along the dry Kuruman River in the South African Kalahari (Clutton-Brock et al. 1998). The study was carried out with ethics approval from the University of Cambridge and the University of Pretoria, under a permit issued by the Northern Cape Conservation Authority, South Africa. Groups were located by radiotracking one radiocollared animal within each group. All work reported here was conducted on groups that had been radiocollared for previous studies (see Jordan et al. 2007 for details of capture and collaring procedures). All individuals were identifiable through unique marks of hair dye (Garnier Nutrisse, Liquorice 1 colour, L'Oréal, Paris, France) that were applied gently with 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. Individuals were monitored since birth, so the ages of all individuals were known precisely (±2 days). All animals were habituated to close observation (<1 m) and over 90% could be weighed regularly by using crumbs of hardboiled egg to entice them onto an electronic balance. Animals were weighed at dawn, before the beginning of the morning foraging session. 'Helper relative weight', measured as the difference between a helper's weight on the day of a pup feed and its average weight for the 10 surrounding days, was included in multifactorial analyses as a measure of a helper's energy balance on the day of a feed (Thornton & McAuliffe 2006). I defined pups as individuals less than 3 months old. Helpers were divided into three categories: juveniles (3–6 months), subadults (6–12 months) and adults (>12 months; Brotherton et al. 2001).

Statistical Analyses

Permutation tests to compare differences between groups in experiments 1 and 2 were conducted with R (www.r-project.org); P values were generated by calculating the proportion out of 10 000 random permutations that produced the observed distribution of results. All other data were analysed in Genstat 8.1 (Rothamstead Experimental Station, Harpenden, U.K.). Multifactorial analyses were conducted with linear mixed models (LMM) or generalized linear mixed models (GLMM) for normal and non-normal error structures, respectively. Mixed models are similar to general linear models (GLM), 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 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 statistics and probability values for significant terms were derived from having all significant terms in the model, while values for nonsignificant terms were obtained by adding each term individually to the minimal model.

Novel Food Experiments

Experiment 1: egg learning

I was not able to use entirely novel food items for social-learning experiments as meerkats showed a high degree of food neophobia and would not consistently eat unfamiliar foods (see Appendix), so individuals could not be trained to act as demonstrators for naïve group members. I therefore examined social learning of hardboiled egg, which is used at the study site to entice meerkats onto electronic balances for weighing. Although meerkats do occasionally find and eat bird and reptile eggs (0.03% of recorded items found by helpers, $N = 12\,150$ items; A. Thornton, unpublished data), pups that have never encountered hardboiled egg before generally make no attempt to eat it. All pups at the study site must therefore be trained to eat hardboiled egg so that they can be weighed regularly. Informal observations suggested that pups generally began to eat egg after joining and feeding with older individuals that had already been trained. To confirm the role of social interactions in learning, I introduced a protocol using 61 pups from 22 litters in 10 groups. Experiments began when pups were between 25 and 30 days old, and were reliably emerging from their natal burrow but not yet joining the foraging group. I presented small quantities of crumbled hardboiled egg (<2 g) under two conditions: in the 'alone' condition no helpers were present within 2 m, whereas presentations in the 'helper' condition were carried out when pups were next to helpers. Initially, all pups were tested under the 'alone' condition and I noted whether they ate any egg. The egg was placed on the ground directly in front of the pup (<5 cm). All pups involved in the presentation were extremely well habituated to close observation. Pups showed no fear of human observers when the egg was placed in front of them and all pups clearly oriented towards the egg and sniffed it, even when no attempt was made to eat. Following the first presentation, I sprinkled hardboiled egg next to a helper known to eat egg when the pup was present (within 20 cm) and noted whether the pup fed with the helper ('helper' condition). Finally, I presented the pup with egg when alone again. The three presentations were carried out within 30 min on the same day. The next day, all pups were tested alone again. If the pup ate egg, it was given another trial alone. Pups that ate egg alone on three consecutive occasions were judged to have learned. Pups that did not eat egg alone were given another trial with a helper. Each 'helper' trial was followed by an 'alone' trial until the pup completed three consecutive trials eating egg alone.

As it is imperative for long-term data collection at the study site that all pups rapidly learn to eat egg, I could not introduce a control treatment with pups that were never given egg in the presence of helpers. However, for eight pups from six litters in five groups, I followed the first 'alone' presentation with another 'alone' presentation. The responses of these pups on the second trial were compared to those of pups whose second experience with egg was with a helper to examine whether a tendency to eat egg results from social influences rather than simply the number of exposures. To examine further whether feeding with helpers, rather than simply the total number of exposures, led to pups eating egg, I conducted a GLMM on factors affecting the probability that a pup would eat egg presented to it when alone for the 61 pups in the main experiment. Data were fitted to a binomial distribution with a logit link function and whether or not the pup ate the egg fitted as a binary response term (1 or 0). Pup, litter and group identity were fitted as random factors and pup sex, age, number of prior exposures to egg and whether the previous exposure was with a helper were fitted as explanatory variables.

Experiment 2: scorpion learning

To examine whether social cues facilitate learning about a common prey item in the meerkat diet, I presented scorpions to young pups before they began foraging with the group (25–30 days). Scorpions of the genus *Opistophthalmus* were collected at the field site and killed immediately prior to presentations by applying firm pressure to the head with tongs. They were then placed on the ground 5 cm in front of the experimental pup during presentations. Three littermates from 11 litters in six groups were randomly allocated to three treatments: 'control', 'helper' and 'saliva'. Pups from all three treatments were first presented with a single dead scorpion when no helper was within 2 m and I noted whether the pup bit the scorpion. Control pups that did not bite the scorpion received further identical presentations until they bit the scorpion, up to a maximum of seven presentations in total. All presentations were conducted within 20 min of each other on the same day. For pups in the 'helper' and 'saliva' treatments, the first control presentation was followed by an experimental presentation. For pups in the 'helper' treatment, this involved placing the scorpion next to a helper when the pup was present within 20 cm. For pups in the 'saliva' treatment, the scorpion was first held in tongs and presented to a helper when the pup was not present, so that the helper would bite the scorpion and deposit saliva on it. The scorpion was then removed and presented to the focal pup when there were no helpers within 2 m to examine whether helper salivary cues promoted eating. Experimental treatments were followed by another control treatment. If the pup bit the scorpion, the experiment was ended for that pup. If the pup did not bite the scorpion, it was given another experimental treatment and then another control treatment until it bit the scorpion when alone. This was repeated up to a maximum of seven presentations in total (Table 1).

Table 1. Protocol for scorpion learning experiment

Trial	Treatment		
	Control	Helper	Saliva
1	Alone	Alone	Alone
2	Alone	Expt	Expt
3	Alone	Alone	Alone
4	Alone	Expt	Expt
5	Alone	Alone	Alone
6	Alone	Expt	Expt
7	Alone	Alone	Alone

Control pups were always presented with scorpions when there were no helpers within 2 m. 'Expt' denotes experimental trials. For pups in the 'helper' treatment, experimental trials involved presentation of a scorpion when with a helper. Pups in the 'saliva' treatment were given scorpions with helper saliva with no helpers present during experimental trials. Trials ceased once the pup had bitten the scorpion when alone.

The responses of pups from the three treatments in the second trial were compared using a permutation test. To examine the effect of treatment on the number of trials required for pups to bite the scorpion when alone, I conducted a one-way analysis of variance (ANOVA), blocking for litter. Pups that never bit the scorpion in any of the seven trials were assigned a score of eight. The response term (number of trials) was normalized for analysis using a square-root transformation and multiple post hoc tests were conducted to examine pairwise differences between treatments.

Teaching About Unfamiliar Foods?

Do helpers preferentially feed pups uncommon prey types?

I conducted 919 20 min focal watches (=306 h) on 122 helpers from 11 groups when 46 different litters of dependent pups were present in the group ($\overline{X} \pm \mathrm{SE} = 7.5 \pm 0.7$ focal watches per helper). Every time a helper found a food item, I noted the type of item (e.g. scorpion, gecko), its size, whether the helper ate the item itself or fed it to a pup and, for items donated to pups, the method of provisioning ('direct feeds', where a helper approached a pup and allowed it to take food directly from its mouth; or 'indirect feeds', where food was dropped on the floor). Prey items were divided into three size classes: small (items fitting entirely in an adult's mouth); medium (less than half the item protruding from the mouth) and large (more than half the item protruding), as per Brotherton et al. (2001).

To investigate whether helpers preferentially feed prey types they encounter infrequently to pups, I conducted a GLMM using the 5773 prey items found by helpers during focal watches. Helpers found 18 different prey types. Abundance for different prey types did not increase linearly, but rather clumped naturally into discrete categories constituting less than 5%, 5–10% or more than 10% of all items found by helpers. For analysis, data were fitted to a binomial distribution with a logit link function and binary response terms (1 or 0) indicating whether or not the item was fed to a pup. To control for repeated measures within a focal watch, each focal watch was assigned a unique identity which was entered into the analysis as a random term, along with the identity of individual helpers, groups, and pup litters. In addition to prey abundance, explanatory terms were: helper number, helper characteristics (age category (juvenile, subadult and adult), sex and relative weight), rainfall, prey size, the age of pups in the group (in days) and the number of pups in the litter. Rainfall refers to the total rainfall (in mm) during the 30 days prior to the day of the focal watch and helper number is the total number of individuals over 3 months present in the group.

As the most common prey types are overrepresented in the data set, they may have disproportionate effects on the model. I therefore conducted a second GLMM to investigate whether prey abundance among the 14 prey types that constituted less than 5% of all items found by helpers had any effect on helpers' tendency to donate items to pups. This analysis was conducted on 626 prey items found during 414 focal watches on 99 helpers from 11 groups when 43 different litters of pups were present in the group. Prey abundance was treated as a continuous variable, normalized for analysis through log transformation. All other variables were the same as in the main analysis above.

Distribution of direct feeds

In addition to the pup feeds recorded during focal watches on helpers, I also recorded feeds during 1070 focal watches on 165 pups ($\overline{X} \pm \mathrm{SE} = 6.5 \pm 0.3$ focal watches per pup). Provisioning data were supplemented by recording pup feeds ad libitum (Altmann 1974). For each pup feed, I noted the identity of the donor and the recipient, the type and size of the item and whether it was a 'direct' or an 'indirect' feed. To investigate whether the potential for parasitism by other helpers affects feeding method, I also noted whether or not another helper was present within 2 m at the time of a feed.

I investigated factors affecting the distribution of direct feeding using a GLMM on 5102 pup feeds by 267 helpers to 235 pups from 68 litters in 13 groups. Data were fitted to a binomial distribution with a logit link function and binary response terms (1 or 0) indicating whether or not the food item was transferred directly to the pup's mouth, rather than being dropped by the helper. Individual, group and litter identities were fitted as random terms to control for repeated measures of each. Explanatory terms fitted were: helper number, helper age category, sex and relative weight, pup age (in days) and sex, litter size, rainfall, prey size and prevalence, and whether there was another helper present within 2 m at the time of a pup feed (yes or no). In contrast to prey abundance in the analysis on factors affecting whether helpers fed a found item to a pup (described above), prey prevalence refers to the number of feeds of a given type (e.g. scorpions) as a percentage of the total number of prey items fed to pups. Prey types were categorized as accounting for less than 5%, 5−10% or more than 10% of all feeds.

Helper monitoring behaviour

Helpers commonly remained with pups and monitored them handling prey after giving them a food item. Monitoring was defined as a helper standing next to a pup after provisioning it with a food item, with its head oriented towards the pup, while the pup handled the prey (Thornton 2008). I used a stopwatch to record the duration of monitoring (±1 s) following pup feeds. Rather than being a form of teaching, direct feeding may serve to increase the efficiency of food transfers, for example by reducing the time helpers must spend monitoring pups with prey. I therefore conducted a linear mixed model (LMM) to investigate whether feeding method (direct or indirect) affects monitoring duration. As previous work has shown that the duration of monitoring is affected by characteristics of the prey (Thornton & McAuliffe 2006; Thornton 2008), I reduced the number of confounding variables by restricting the analysis to the single most common prey type, insect larvae, which are immobile and cannot escape. The analysis was conducted on 1408 pup feeds by 193 helpers to 166 pups from 49 litters in 12 groups and the response term was normalized for analysis using a log transformation. As direct feeds are most likely when pups are young, I used only feeds to pups younger than 45 days. Characteristics of the donor and recipient were fitted as potential explanatory variables, along with feeding method and whether or not there was another helper present within 2 m at the time of the feed.

RESULTS

Novel Food Experiments

Experiment 1: egg learning

None of the 61 pups tested ate egg the first time they were presented with it, but during the 'helper' treatment that followed, 30 pups ate egg once the helper began eating. In contrast, none of eight pups whose first exposure was followed by another exposure alone ate egg during either the first or second exposure. The presence of experienced helpers on the second exposure therefore significantly increased the probability that pups would eat egg (permutation test on pups whose second exposure was with or without helpers: $P = 0.007$). Helpers always allowed pups to feed on the egg if the pups attempted to do so. On two occasions, the helper picked up a chunk of egg and actively fed the pup. Feeding with helpers significantly increased the probability that pups would eat egg again on the subsequent trial in the absence of helpers. Of the 30 pups that fed with helpers, 25 subsequently ate egg again when they were presented with it alone, whereas none of the 31 pups that did not eat egg in the presence of feeding helpers ate egg on the subsequent 'alone' trial (25 out of 30 versus 0 out of 31; chi-square test: $\chi^2_1 = 43.77$, $P < 0.001$; Table 2).

The total number of prior exposures required for pups to learn to eat egg (i.e. eat egg alone on three consecutive occasions) varied considerably. Seventeen individuals learned to continue eating egg alone after a single

Table 2. Results of egg experiment

Ate?	Before	Helper	After
Yes	0	30	25
No	61	31	36

Number of pups that ate egg on their first exposure to egg, in the absence of helpers ('Before'), when exposed to egg in the presence of a helper ('Helper') and when tested again alone ('After').

experience of eating egg with a helper (total prior exposures = 2; one alone and one with a helper), whereas six individuals, none of which ate egg with a helper on the first trial of the experiment, required over 20 exposures before they learned to eat egg (mean for these six pups ± SE = 30.7 ± 5.91 previous exposures). A GLMM analysis of whether a pup would eat egg when it was presented with it alone revealed no effect of pup age or sex (age: $P = 0.917$; sex: $P = 0.741$), but pups were significantly more likely to eat egg alone if their previous exposure to egg was with a helper ($\chi^2_1 = 49.53$, $P < 0.001$), even when the total number of prior exposures to egg (alone and with helpers) was controlled for ($\chi^2_1 = 4.61$, $P < 0.001$). Pup identity was a significant random term in the model ($P < 0.05$), but group and litter identity were not significant random terms.

Experiment 2: scorpion learning

Of the 33 experimental pups, 13 (39.4%; 5 of 11 pups from the control treatment and 4 of 11 pups from each of the helper and saliva treatments; permutation test: $P = 0.302$) bit the scorpion the first time they were presented with one. In the second trial, all 11 pups in the 'helper' treatment bit the scorpion, but only five pups in each of the saliva and control treatments bit the scorpion (permutation test: $P = 0.006$; Table 3). All 11 pups in the helper treatment bit scorpions alone by the end of the experiment, but only nine pups in each of the other two treatments ever bit scorpions alone. Among the six litters in which no pup ate scorpions on its first exposure, all six pups from the helper treatment subsequently bit the scorpion when tested alone after the first experimental trial (i.e. on the third trial), but pups in the other two treatments required a greater number of trials before they bit a scorpion in control presentations (ANOVA: $F_{1,5} = 11.05$, $P = 0.003$). Multiple post hoc comparisons revealed that pups in the helper treatment bit scorpions alone after significantly fewer trials those in the saliva ($F_1 = 8.30$, $P = 0.016$) and control treatments ($F_1 = 21.70$, $P < 0.001$), but the difference between the saliva and control treatments was not significant ($F_1 = 3.16$, $P = 0.106$; Fig. 1). In the helper treatments, two of the six helpers involved picked up the scorpion and fed it to the pup and three nudged the scorpion repeatedly with their nose until the pup bit the scorpion. One helper simply ate the scorpion, but the accompanying pup approached the helper once it was eating, made begging calls and attempted to take the scorpion from the helper's mouth.

Table 3. Results of scorpion experiment

	Trial	
Treatment	1	2
Control	5	5
Saliva	4	5
Helper	4	11

Number of pups in the three treatments that bit the scorpion in the first and second trial. There were 11 pups in each treatment.

Teaching About Unfamiliar Foods?

Do helpers preferentially feed pups uncommon prey types?

As has been shown in previous studies (Brotherton et al. 2001; Clutton-Brock et al. 2001) helpers were more likely to donate found items to pups when helper number was low (GLMM: $\chi^2_1 = 12.46$, $P < 0.001$; see Supplementary material, Table S1), when litter size was high ($\chi^2_1 = 29.15$, $P < 0.001$), and when the item was large ($\chi^2_2 = 39.68$, $P < 0.001$), and juveniles were less likely than older helpers to donate prey to pups ($\chi^2_2 = 30.80$, $P < 0.001$). When these effects were controlled for, the age of the pups in the group had a quadratic effect on the probability that helpers would donate food ($\chi^2_1 = 27.73$, $P < 0.001$) and prey types that made up less than 5% of all prey found by helpers were more likely to be given to pups than more common prey items ($\chi^2_2 = 58.59$, $P < 0.001$; Fig. 2; see Supplementary material, Table S1). If helper behaviour constitutes a form of teaching, one might expect rare prey items to be fed more often than common items when pups were young, but these differences should disappear as pups grow older and more familiar with different prey types. However, there was no significant interaction between prey abundance and pup age in the GLMM analysis (prey abundance*pup age: $P = 0.426$; prey abundance*pup age^2: $P = 0.470$).

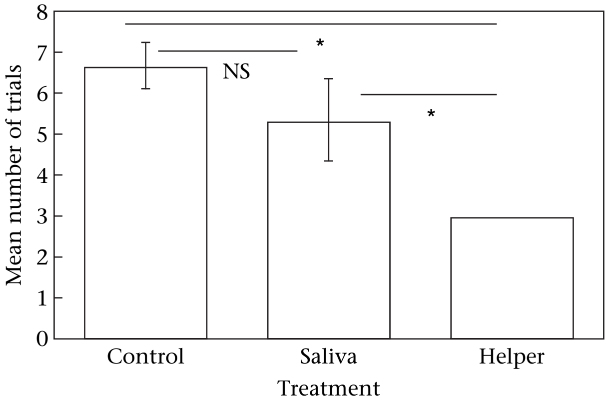

Figure 1. Mean number of exposures to scorpions ± SE before pups in the control, saliva and helper treatments ate a scorpion alone. Pups that failed to eat a scorpion in all seven trials of the experiment were allocated a score of eight. *$P < 0.05$; NS $P = 0.106$.

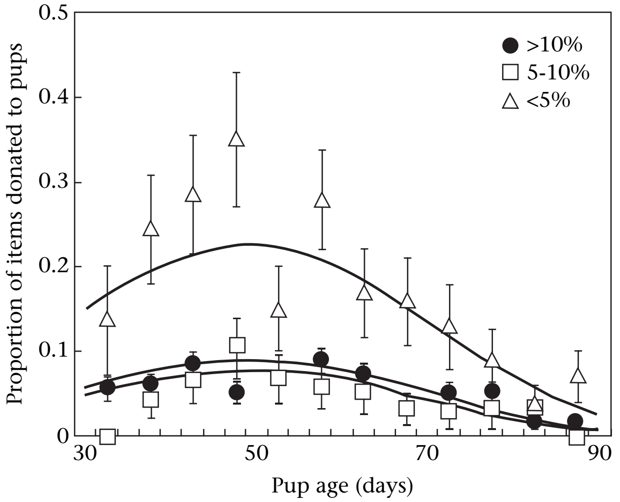

Figure 2. Effects of pup age and prey abundance on the proportion of items donated to pups. Points show average values from raw data ± SE. Lines show predicted means from a GLMM analysis.

GLMM analysis using only prey types that constituted less than 5% of all items found by helpers produced qualitatively similar results to the larger model, but I found no effect of prey abundance on the probability an item would be fed to a pup ($\chi^2_1 = 0.77$, $P = 0.381$). Treating prey abundance as a categorical variable, factorized according to the upper and lower quartiles of the distribution, also produced no significant effect ($\chi^2_2 = 0.57$, $P = 0.567$).

Distribution of direct feeds

The frequency of direct feeds varied with characteristics of the feeder, the pup being fed and the prey item. Large prey items were more likely than smaller items to be fed directly across all age categories of helpers. Direct feeding was most likely when the prey item was large and the helper was a juvenile (GLMM: helper age*prey size: $\chi^2_4 = 11.22$, $P = 0.024$; Fig. 3a; see Supplementary material, Table S2). Direct feeding declined with pup age ($\chi^2_1 = 34.21$, $P < 0.001$) and, among young pups, less prevalent prey items were fed directly more often than more prevalent items (pup age*prey prevalence: $\chi^2_2 = 7.24$, $P = 0.027$; Fig. 3b; see Supplementary material, Table S2). When these effects were controlled for, direct feeds were more common when there was another helper present within 2 m at the time of a feed ($\chi^2_1 = 16.68$, $P < 0.001$; Fig. 3c; see Supplementary material, Table S2).

Helper monitoring behaviour

Juvenile helpers spent less time monitoring pups handling prey following a pup feed than did subadults and adults (LMM: $\chi^2_1 = 13.53$, $P < 0.001$; Fig. 4a). Monitoring duration declined with pup age ($\chi^2_1 = 57.92$, $P < 0.001$), and was longer if the prey item was large ($\chi^2_1 = 127.51$, $P < 0.001$; Fig. 4b) and if the feed was indirect rather than direct ($\chi^2_1 = 11.77$, $P < 0.001$; Fig. 4c). As in previous work (Thornton 2008), I found a negative effect of litter size on monitoring duration ($\chi^2_1 = 8.28$, $P = 0.004$), and

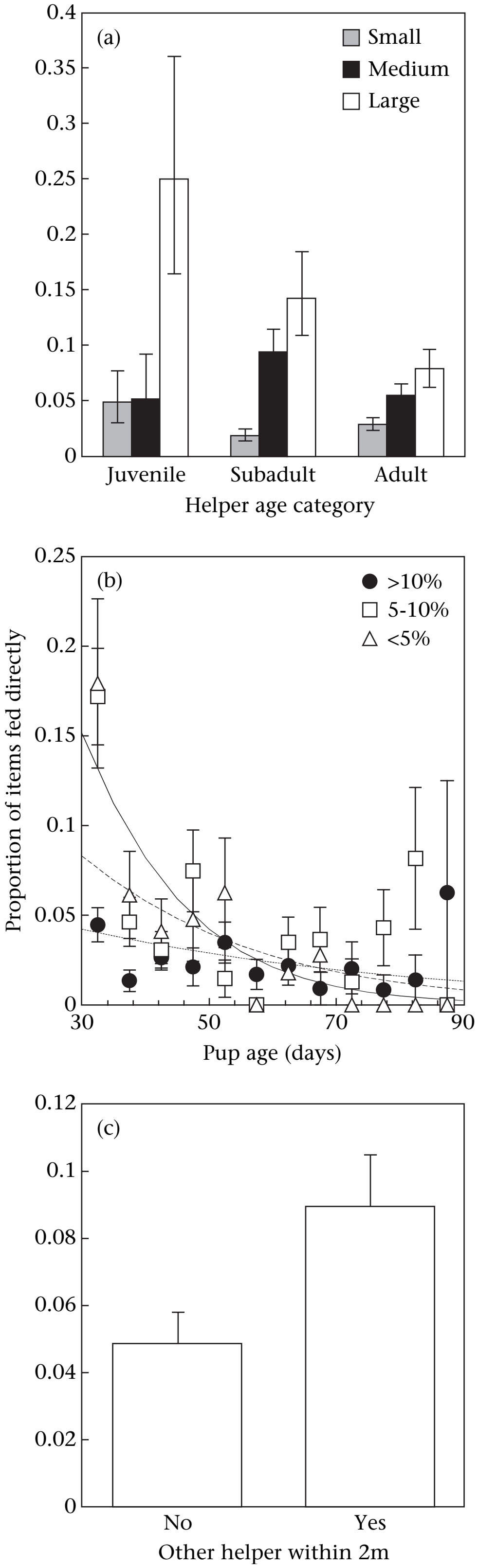

Figure 3. Proportion of items fed directly to the pup's mouth rather than being dropped. Graphs show effects of (a) helper age category and prey size, (b) pup age and prey prevalence (points show means ± SE from raw data; lines show predicted means from a GLMM analysis; dotted line: >10%; broken line: 5–10%; solid line: <5%) and (c) the presence of another helper within 2 m at the time of the pup feed.

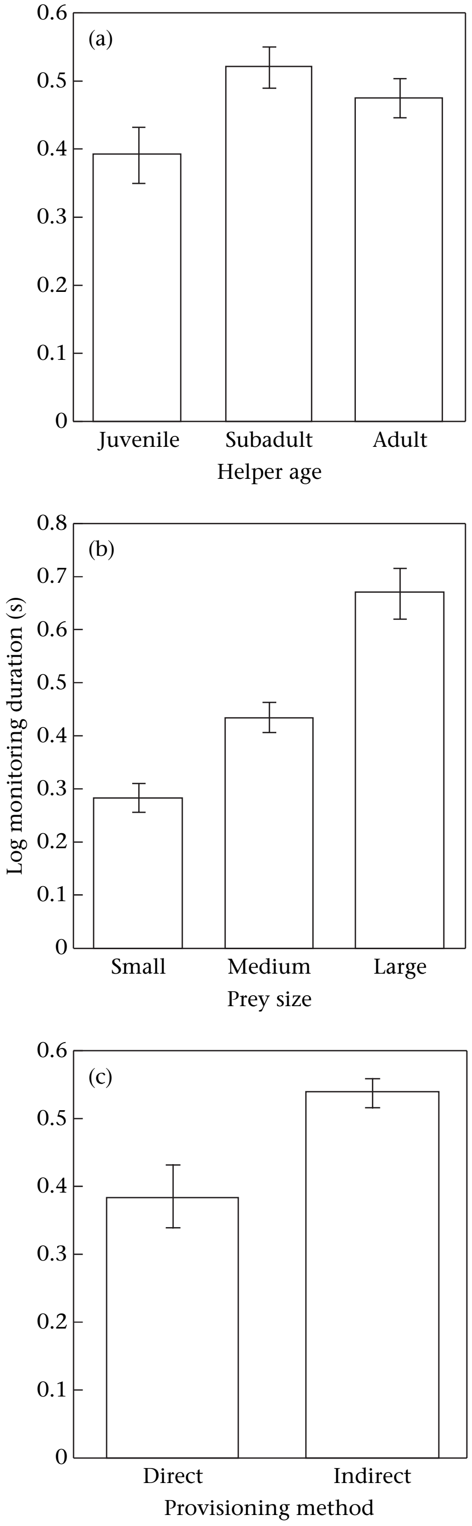

Figure 4. Duration of monitoring by helpers (s, log transformed). Graphs show effects of (a) helper age category, (b) prey size and (c) provisioning method. Bars show predicted means ± SE from an LMM analysis.

there was a positive effect of helper number ($\chi^2_1 = 4.82$, $P = 0.028$). On 12.1% of occasions when prey were fed indirectly, the pup failed to interact with the item and the feeder repeatedly nudged the food until the pup approached and ate it. Nudging was never seen when prey was fed directly (chi-square test: $\chi^2_1 = 6.03$, $P = 0.014$).

DISCUSSION

Theoretical and empirical work suggests that social learning can allow individuals to acquire information of critical fitness value, reducing the need for costly asocial learning (Galef 1995; Giraldeau & Caraco 2000). Young animals may benefit from showing neophobia towards unfamiliar foods, particularly if potentially toxic items are present in the environment, and incorporating novel foods into their diet only after encountering them in the context of interactions with adults (Galef 1993). Here, two experiments showed that social interactions with helpers promote the incorporation of novel foods into the diet of meerkat pups. To my knowledge, this is the first study to demonstrate such effects experimentally in a wild population.

In experiment 1, the presence of a helper eating egg significantly increased the probability that pups too would eat egg. It appears that seeing a helper interacting with egg draws pups' attention to the food and stimulates them to sample the food themselves. Clayton (1978) termed such processes 'social facilitation'. It was not possible in this study to test whether the presence of nonfeeding helpers would stimulate pups to eat, as helpers always ate egg placed next to them. However, this seems unlikely, as pups began to sample egg only once they observed helpers eating. Feeding with helpers appeared to promote learning about the novel food, as pups were significantly more likely to eat egg when alone after they had fed with a helper. For almost 30% of the pups tested, a single presentation of egg in the presence of a helper was sufficient to promote learning. Moreover, mixed-model analysis revealed that across all pups, individuals were more likely to learn to eat egg alone if their previous exposure was with a helper, even after controlling for the total number of exposures. These results strongly suggest that interacting with experienced helpers facilitates learning about hardboiled egg, an item not normally present in the meerkat diet.

In contrast with experiment 1, almost 40% of the pups in experiment 2 bit the scorpion on the first presentation. Although it is unlikely that the pups were ever fed scorpions by helpers before the experiment, it is impossible to rule this out. Other possible explanations for this result may be acquisition of food preferences through prenatal experiences in the womb (Hepper 1988), from the milk of mothers and allolactating helpers (Galef & Sherry 1973) or unlearned responses to visual or olfactory cues. Among the pups that did not recognize scorpions immediately, there was strong evidence that social interactions promoted learning. In all cases, pups were attracted by helpers' interactions with scorpions and bit the prey. These pups all subsequently bit the scorpion in control presentations in the absence of helpers. In contrast, pups in the control and saliva treatments required more presentations before they bit the scorpion. These results suggest that while pups may learn to bite scorpions after repeated presentations, interactions with helpers help to accelerate the process. In rats, it is known that chemical cues left on food by adults promote feeding by juveniles (Laland & Plotkin 1993). In the current study, there is some suggestion that pups that were exposed to scorpions with adult saliva learned more rapidly than pups from the control group, but as the trend was nonsignificant this conclusion must remain tentative.

Experiments 1 and 2 strongly suggest that social interactions play a role in promoting learning about unfamiliar foods by pups. In experiment 1, helpers were seen to feed pups hardboiled egg on only two occasions, suggesting that feeding with helpers is sufficient to promote learning. However, in natural situations feeding together with helpers is very rare because the majority of meerkat prey items occur singly and are indivisible. Learning about food is therefore most likely to occur when helpers donate food to pups. To examine whether helpers play an active role in facilitating this learning process, I investigated whether helpers preferentially feed items they encounter infrequently, and analysed patterns of direct-feeding and postprovisioning behaviour.

Helpers appeared to prefer to feed prey types that constituted less than 5% of all items found. Although this is initially suggestive of an active role for adults in promoting learning about rare prey, the tendency to feed rare items rather than more common items persisted throughout the period of pup dependence. If feeding rare prey is a costly form of active information transfer, as required under Caro & Hauser's (1992) definition of teaching, helpers might be expected to do so only when pups are young, as young pups have little experience of food and are incapable of finding their own prey. It is possible that the tendency to feed rare prey items is driven, not by their rarity, but by other characteristics of the prey. Prey types that made up less than 5% of items found included scorpions, spiders, solifuges and geckos, all of which are high in energy, are typically found deeper in the sand than more common items such as insect larvae, and are difficult to catch (Glaser 2006; Turbé 2006). An analysis conducted using the 14 rarest prey types found no effect of abundance on helpers' tendency to feed items to pups. It therefore appears unlikely that helpers actively teach pups about unfamiliar food. Rather, I would suggest that the primary function of provisioning pups is likely to be nutritional, and pups may learn about unfamiliar foods as a by-product.

An analysis of patterns of direct feeding showed that the probability that a feed would be transferred directly rather than being dropped on the floor declined with pup age and, when pups were young, items were more likely to be transferred directly if they made up a relatively low proportion of all feeds. This pattern is consistent with direct feeding as a form of teaching: as young pups are neophobic towards novel prey, helpers may actively promote the incorporation of unfamiliar food into the diet by exploiting pups' tendency to snatch any food they see in a helper's mouth. However, when pups first begin foraging with the group, all prey items are novel, yet direct feeding makes up only around 15% of all feeds, even for the rarest prey types. Rather than being a costly form of active information transfer, it may be that direct feeding allows helpers to reduce the costs of pup feeding. Young pups occasionally fail to notice prey on the ground (Thornton & McAuliffe 2006) and often struggle to pick items up because of the small size of their jaws. If food is transferred directly from mouth to mouth, however, the process of locating and picking up prey is eliminated, so helpers need to spend less time monitoring the pup handling the prey and nudging prey items to draw the pups' attention to them. The pattern of feeding among helpers of different ages is consistent with direct feeding as a way of reducing investment in postprovisioning monitoring. Juvenile helpers, which are still investing in growth, and typically contribute little to pup care (Clutton-Brock et al. 2000, 2001; Brotherton et al. 2001) and teaching (Thornton 2008), showed a greater tendency to feed directly than older helpers, particularly if the prey item was large. Direct feeding was also more likely when there was another helper present nearby, suggesting that transferring food directly to a pup's mouth may also help to reduce the risk of lost investment as a result of kleptoparasitism from other helpers. As the primary function of direct feeding does not appear to be to promote learning in pups, it cannot be meaningfully classified as teaching (Thornton & Raihani 2008). In fact, direct feeding may actually reduce opportunities for learning. Previous work in this species and others has shown that repeated experience in handling prey promotes learning of handling skills (Caro 1980; Rovero et al. 1999; Thornton & McAuliffe 2006). As pups fed directly do not have to locate and pick up prey from the ground, opportunities to practise processing food are reduced. The finding that less common prey items are fed directly to young pups more than other prey may be explained by trade-offs between a helper's own requirements and signals of need from pups (cf. Clutton-Brock et al. 2005). When a pup sees a helper with food, it produces 'high-pitched' calls which typically cause the helper to drop the food item (Manser & Avey 2000; Kunc et al. 2007). It is possible that these calls are less intense if the pup does not recognize the prey item, so helpers are less likely to drop it. This may be particularly true among juvenile helpers whose motivation to feed must be balanced against the demands of growth.

The results presented here suggest that pups learn to eat unfamiliar prey by interacting with more experienced group members. Young pups are neophobic towards novel food types, but learn to eat them by feeding with or being fed by helpers. However, the results suggest that helpers are unlikely to play an active role in teaching pups about novel food. Teaching about novel foods would involve the transmission of specific units of information: that particular food types are safe to eat. Such teaching of declarative information is classed as 'fixed' teaching (Thornton & Raihani 2008), and is similar to the form of teaching reported in ants, where tandem leaders teach naïve followers specific routes (Franks & Richardson 2006) and pied babblers, where adults teach young to associate specific 'purr' calls with food (Raihani & Ridley 2008). In contrast, previous work on teaching in meerkats describes 'progressive' teaching of procedural knowledge of how to handle difficult prey (Thornton & McAuliffe 2006; Thornton & Raihani 2008). It has been commonly assumed that a capacity for teaching is underpinned by specific cognitive capacities, in particular the ability to attribute mental states, or know what your pupils know (Premack & Premack 1996; Strauss et al. 2002; Wellman & Lagattuta 2004). If teaching were underpinned by such abilities, one would expect individuals to be able to demonstrate teaching across different contexts. However, evidence suggests that rather than being contingent on complex cognitive faculties, teaching in nonhuman animals is an adaptation to specific contexts where high costs or lack of opportunities limit the capacity for individual learning or standard social learning and where experienced individuals can gain delayed fitness benefits through promoting learning in others (Thornton & Raihani 2008). In meerkats, young pups rarely find mobile prey, so opportunities to practise handling skills are lacking. The acquisition of these skills is critical for survival, so helpers actively invest in teaching by providing pups with opportunities to handle live prey. Selection for teaching about novel foods, on the other hand, may be less strong. Although it could be beneficial for helpers to teach pups about rare foods, the benefits of this teaching would be relatively low simply owing to the fact that such items make up a low portion of the diet and pups can acquire inadvertent social information when they are fed. Social learning plays a valuable role in pups' learning about food, but active teaching in this case would seem unnecessary.

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Supplementary Material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.anbehav.2008.07.007.

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Appendix: Responses to Novel Foods

Methods

To investigate whether meerkats are neophobic towards unfamiliar foods, I presented 108 individuals from seven groups (53 adults, 32 subadults, six juveniles and 17 pups) with raw and cooked chicken pieces, cooked minced beef and raw bacon. Each individual was presented with each of the food types on five occasions over the course of a week. In addition, I presented 51 individuals from eight groups (10 adults, six subadults, one juvenile and 34 pups) with commercially available black crickets, *Gryllus bimaculatus* (Herpetology Africa (Pty) Ltd, Hillcrest, South Africa). Meerkats often eat dune crickets (*Comicus* sp.) and other gryllid and locustid Orthoptera (Doolan & Macdonald 1996), but black crickets are not found at the study site. Food items were presented on the ground 5 cm in front of target individuals. Crickets were killed immediately prior to presentation to prevent them from escaping. Meerkats showed no fear of human observers when items were placed in front of them and all individuals clearly noticed the items, even when no attempt was made to eat them.

Results

Of the 108 individuals tested, none ate raw or cooked chicken or cooked minced beef. Six individuals (5.6%; two subadults, one juvenile and three pups) ate bacon on the first occasion it was presented to them, but only two of these sampled bacon again on the next presentation, and both individuals refused the bacon on subsequent presentations. Only six of 51 individuals (11.7%; two adults, one subadult and three pups) ate the black crickets presented to them on the first trial. Three of these individuals ate black crickets again on subsequent trials, while the other three never ate black crickets again. As meerkats would not consistently eat any of the novel food types I presented them with, I was not able to train individuals to act as demonstrators for social-learning experiments.