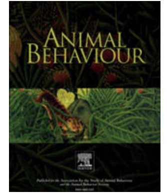
Animal Behaviour 78 (2009) 255–264

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe



Experimental evidence for social transmission of food acquisition techniques in wild meerkats

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ARTICLE INFO

Article history:
Received 9 March 2009
Initial acceptance 20 April 2009
Final acceptance 27 April 2009
Published online 23 June 2009
MS. number: 09-00161

Keywords:
culture
field experiment
meerkat
social learning
Suricata suricatta
tradition

Despite major evolutionary implications, patterns of social information transmission in natural populations remain poorly understood. We used an experiment to examine the spread of novel food acquisition techniques through groups of wild meerkats, *Suricata suricatta*. We trained individual 'demonstrators' in six groups to obtain food from an apparatus using one of two techniques. A further three control groups had no demonstrators. We found evidence for social learning on two levels. First, a greater proportion of individuals in experimental than control groups interacted with the apparatus and obtained food from it. Second, a number of individuals in experimental groups adopted demonstrators' techniques following interactions with demonstrators or other group members that had already learned from demonstrators. Scrounging appeared to be the primary driver of technique acquisition, with naïve individuals being more likely to learn a technique if they had scrounged from an individual performing that technique. Among individuals that never scrounged, observing successful performance of a technique also had a positive effect on technique adoption. Young individuals were more likely than adults to join and scrounge from demonstrators and were consequently more likely to learn. A number of individuals also learned without observing or scrounging from demonstrators, and there was some indication that their techniques subsequently spread to others, leading to the existence of alternative socially learned techniques within groups. These results shed light on patterns of social learning in nature and suggest that a lack of behavioural uniformity within groups need not imply a lack of socially transmitted behaviour.

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Social learning has major evolutionary implications because it can allow the rapid spread of adaptive information through groups and may influence genetic evolution by modifying the selection pressures acting on populations (Laland et al. 2000; Jablonka & Lamb 2005; Richerson & Boyd 2005; Whiten 2005). However, our understanding of the importance of social information transmission in nonhuman animals is limited by a lack of experimental data from natural populations. Most existing studies use one of two main approaches, both of which have important limitations. Ethnographic observational studies documenting behavioural differences between populations (Whiten et al. 1999; Rendell & Whitehead 2001; Perry et al. 2003; van Schaik et al. 2003) cannot determine patterns of social transmission or exclude noncultural explanations of behavioural differences between groups (Galef 2004; Laland & Janik 2006). On the other hand, experiments on captive animals can determine whether information is transmitted through social learning and elucidate the psychological mechanisms involved, but may not reflect patterns of transmission in the wild (Galef 2004; Thornton & Malapert 2009). Controlled field experiments can therefore provide a valuable addition to observational and laboratory studies, allowing researchers to examine patterns of social information transmission within natural groups and determine whether social learning can lead to the establishment of group-typical behavioural patterns or traditions (Fragaszy & Perry 2003).

To date, only a handful of social-learning experiments have been conducted in the wild (reviewed in Galef 2004; Whiten & Mesoudi 2008). One approach, where groups of animals are translocated between sites, has provided compelling evidence for social learning of schooling routes (Helfman & Schultz 1984) and mating sites (Warner 1988) in fish, but provides little information on patterns of information acquisition and is unlikely to be ethical or feasible with larger vertebrates. An alternative approach is the use of diffusion experiments examining whether naïve individuals adopt the behaviour of 'demonstrators' that have been trained, either in

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doi:10.1016/j.anbehav.2009.04.021

captivity (Lefebvre 1986; Langen 1996) or in situ (Midford et al. 2000; Gajdon et al. 2004; Thornton & Malapert 2009) to perform a certain task. A particularly powerful design, loosely based on two-action experiments designed to identify imitation in captive animals, involves exposing different groups to demonstrators trained on different tasks, with additional groups with no demonstrators serving as controls for asocial learning (Whiten & Mesoudi 2008). To our knowledge, only two such experiments have been performed in the wild. In one, white-throated magpie jays, *Calocitta formosa*, were trained in captivity to open one of three doors to obtain food, and then released back into their social groups (Langen 1996). Unfortunately, most demonstrators failed to perform the task following release and most naïve birds were not individually identifiable, so while there was evidence that individuals in groups with demonstrators were more likely to obtain food, the extent to which their behaviour matched that of demonstrators was unclear. In the other experiment, meerkats, *Suricata suricatta*, in control groups chose randomly between two adjacent landmarks indicating the presence of food, while those in experimental groups showed an initial preference for demonstrators' choices, which declined over time (Thornton & Malapert 2009). However, that experiment was designed to examine the establishment and persistence of arbitrary traditions where alternatives are easily discoverable at low cost. The spread of novel food acquisition techniques, which may be more difficult to learn alone and therefore more likely to be adhered to once learned, remains to be investigated in this species.

We used a field experiment to investigate the spread of two alternative food acquisition techniques through habituated groups of meerkats, a cooperatively breeding mongoose species known to show social learning in the wild (Thornton & McAuliffe 2006; Thornton 2008; Thornton & Malapert 2009). Unlike laboratory two-action experiments which test whether subjects imitate one of two different motor patterns to obtain food from the same location (Whiten et al. 2004), the alternative techniques in our apparatus involved access to different locations and we did not focus on the precise motor patterns used. Rather than attempting to identify imitation, our aim was to examine the extent to which techniques could spread through less cognitively demanding mechanisms such as local and stimulus enhancement (Hoppitt & Laland 2008). Although imitation is often thought to enhance the fidelity of social learning (Boyd & Richerson 1985; Galef 1992), its importance in the social transmission of information in nature is unclear. Indeed, many of the most renowned examples of social transmission in the wild, including the spread of milk bottle opening in British titmice (*Parus* spp.) and pine cone stripping in Israeli black rats, *Rattus rattus*, are now thought to have been underpinned by simple, nonimitative social interactions (Sherry & Galef 1984; Terkel 1996). Even some of the putative traditions of wild chimpanzees, *Pan troglodytes*, may be governed by similar mechanisms, despite the species' capacity for imitation in captivity (Whiten et al. 2004). For instance, young individuals appear to acquire nut-cracking skills by having their attention drawn to the objects used in this task by adults, rather than by imitating them (Inoue-Nakamura & Matsuzawa 1997).

In our experiment, demonstrators in six groups were trained, out of sight of other individuals, to obtain food from a 'Box' apparatus using one of two techniques. We then presented the Box when the whole group was present to examine whether naïve individuals acquired the technique of their demonstrators. Three additional groups served as controls, where we presented the Box but had no demonstrators. We predicted that individuals in experimental groups would be more likely to interact with the Box and to obtain food than those in control groups. As all the animals in the population were individually recognizable, we were able to examine whether individuals in experimental groups that observed or scrounged from demonstrators were more likely to learn the same technique. Moreover, as the ages and sexes of all animals were known, we were able to investigate the effects of these characteristics on patterns of learning.

METHODS

Study Population

Experiments were conducted on nine groups of 8–18 free-living meerkats (mean group size = 13.4 ± 1.1) in the Northern Cape, South Africa (see Clutton-Brock et al. 2001 for details of habitat and climate). All individuals had known birth dates (±2 days), were identifiable by unique dye marks and were habituated to close observation (<1 m). Groups were located by radiotracking one collared animal in each group that had been radiocollared for previous studies (see Golabek et al. 2008 and Thornton 2008 for marking and collaring procedures). Animals were categorized as pups (<3 months), juveniles (3–6 months) or adults (>12 months; Brotherton et al. 2001). There were no meerkats between 6 and 12 months present at the time of the study. Work was carried out with ethics approval from the Universities of Cambridge and Pretoria, under a permit issued by the Northern Cape Conservation Authority.

Apparatus

The Box (Fig. 1) consisted of a rectangular plastic box (24 × 35 cm and 18.4 cm high), with two additional boxes (25 × 19 cm and 8 cm high and 10 × 7 cm and 4.5 cm high) attached to the top of the main box, forming steps. Two other steps were attached to the sides of the main box, to allow small pups to climb to the top. The front face of the small box at the top was covered with kitchen paper affixed with adhesive tape on all sides. The front face of the main box had a cat flap at the bottom, hinged at the top. The other three faces were covered by chicken wire so that observers could see into the Box. Inside the main box was affixed a pot of diameter 10 cm and height 4 cm.

Experimental Procedures

Food rewards (crumbs of hardboiled egg and pieces of scorpions freshly killed by applying firm pressure to the head with tongs)

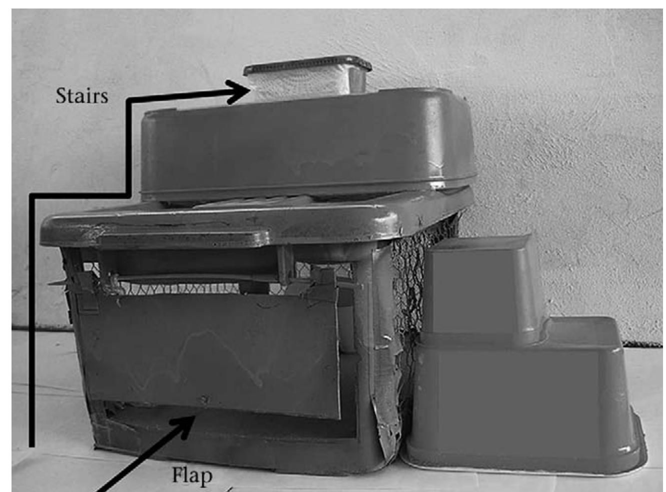

Figure 1. The 'Box'. The 'Stairs' technique involved climbing up the Box and breaking a paper lid to obtain hidden food; the 'Flap' technique involved going through a flap to obtain food inside the Box.

could be obtained from the Box using two methods. Meerkats could either climb up the steps, rip off the paper cover from the small top box and scoop out the rewards contained inside ('Stairs technique') or go through the cat flap in the bottom part of the Box and obtain food from the pot ('Flap technique'). These techniques were designed so that they could be completed using actions from the meerkats' standard behavioural repertoire, but were sufficiently novel that they would not be easily discovered by individual learning. For example, the actions required to break open the paper lid on the Stairs are similar to those meerkats use to dig in sand. However, meerkats do not generally use their claws for ripping and although they commonly climb onto objects to look out for predators, they do not climb to obtain food. Similarly, meerkats do on occasion push through narrow spaces (such as cavities in dead trees) while foraging or hiding from predators, but the act of pushing up a flap is novel.

We trained one individual in three different groups to perform the Stairs technique and one individual in another three groups to perform the Flap technique. A further three groups served as controls, with no trained demonstrators. Groups were randomly assigned to treatments.

Training

All demonstrators were subordinate adult males. We chose adult subordinates because meerkats are less likely to attend to the actions of younger individuals and may avoid approaching dominants so as not to be attacked or displaced (Thornton & Malapert 2009). We used males because, unlike females, they do not run the risk of being evicted from the group by dominants (Clutton-Brock et al. 1998) and so were more likely to be present throughout the experiment. To ensure that only specific individuals were exposed to training, we trained demonstrators when they were foraging out of sight of the rest of the group or when they were babysitting pups that were underground at the breeding burrow while the rest of the group was foraging. It generally took 2 days of training for individuals to reach proficiency in either technique (6–10 training trials per demonstrator).

To train demonstrators on the Stairs technique, we laid trails of hardboiled egg crumbs going up the steps into the top box. Once individuals were readily approaching the Box and climbing up to obtain rewards, we began covering the opening of the top box with kitchen paper. Initially, the cover was only attached at the top, so that the individual could put its paw under the paper to obtain food. As individuals became more competent at obtaining food in this manner, we began to attach the cover more securely on all sides so the paper had to be ripped to reach the food. Training continued until individuals reliably approached the Box, climbed up the steps, ripped the paper and obtained food.

We trained individuals on the Flap technique by propping open the flap and laying trails of hardboiled egg leading to the pot inside the main box. We then began incrementally closing the flap so that meerkats had to push against it to enter or exit the box. Training ceased once individuals consistently approached the Box and pushed through the flap to obtain rewards and subsequently exit the Box.

Group Phase

Once demonstrators were fully trained, we began conducting group sessions during the period in the early morning when the whole group was present around the sleeping burrow. Meerkats commonly spend up to 1 h sunning, grooming and playing around the burrow before they leave the burrow area to forage as a dispersed group. However, they do occasionally look for food around the burrow and will readily eat if food is available (A. Thornton, unpublished data). As meerkats do not eat during the night, motivation to obtain food in the morning should be comparable across all individuals. The Box was placed adjacent to the sleeping burrow entrance such that it was visible by and approximately equidistant to all group members. Sessions lasted 20–90 min depending on how long the group stayed at the burrow, with sessions ending once the first individual moved more than 20 m from the burrow.

We conducted a total of 6–12 sessions at each group (mean $= 8.2 \pm 0.8$), with sessions spaced at least 2 days apart (mean days between sessions $= 7.8 \pm 0.6$). The total number of sessions varied because in groups where new pups emerged from the natal burrow during the experiment, we conducted additional sessions so that all individuals were present for at least three sessions. Sessions were videorecorded using a Panasonic NV-GS80 camcorder (Panasonic Corporation, Kadoma, Japan). From the videos, we later transcribed the identity and behaviour of all individuals that approached the Box, the time (s) they spent interacting with the Box (scratching, pushing or otherwise manipulating it), whether they were successful in obtaining food using either technique, and whether they were joined (approached to within 30 cm) at the Box by other individuals. A bout refers to a discrete period of interaction with the Box or an individual at the Box. When one individual joined another, we noted whether it observed successful acquisition of food or scrounged food. Scrounging involved either following an individual up the stairs and obtaining crumbs of food after the paper lid was broken or following an individual through the flap and obtaining food from the pot inside. Individuals were only classed as having learned to obtain food if they went through the flap or broke the paper lid and obtained food alone (i.e. without scrounging).

Whenever an individual ripped the paper at the top of the stairs, we waited for it to leave the Box and then briefly removed the Box, replaced the paper and replenished the food out of sight of the meerkats. As we did not remove meerkats from the Box, individuals that were on the Box with a group member that ripped the paper had an opportunity to scrounge. Food taken through the Flap technique was replenished as required by opening the lid of the main Box (on the opposite side to the flap) out of sight of the meerkats.

Statistical Analyses

Data were analysed in Genstat v. 8.1 (Rothamstead Experimental Station, Harpenden, U.K.). Multifactorial analyses were conducted using generalized linear models (GLM) or generalized linear mixed models (GLMM) fitted with group and, where necessary, individual identities specified as random terms to control for repeated measures (Schall 1991). Initially, all probable explanatory variables were entered into models. Possible two-way 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, and values for nonsignificant terms were obtained by adding each term individually to the minimal model. All significant results ($P < 0.05$) are reported in the text. Full tables of results for statistical models are in the Appendix. Means are quoted $\pm$ SE throughout.

Interactions with the Box

We used a GLMM with a binary response term (1 or 0) to investigate whether treatment (control or experimental) affected whether individuals ever interacted with the Box during the experiment. Treatment, individual characteristics (age and sex) and the total duration of the experiment were included as explanatory terms. As the total number of individuals present might affect an

individual's tendency to interact with a novel object, group size was included as an additional explanatory term. The number of animals per group could change over time with the emergence of new pups, so we defined group size as the mean number of meerkats in the group during the time each individual was present for the experiment. The analysis used data for all 115 untrained meerkats, with group identity fitted as a random term.

Interactions with Demonstrators

We used a GLMM to examine factors affecting the proportion of bouts in which individuals in experimental groups joined demonstrators. Data were fitted to a binomial distribution, with the number of bouts within a session in which each individual joined the demonstrator as the numerator and the number of bouts of interaction with the Box by the demonstrator as the denominator. The analysis was conducted on data from all 83 individuals in experimental groups, with individual characteristics and demonstrator's technique (Flap or Stairs) fitted as explanatory terms and group and individual identity as random terms. Similar analyses were conducted on the proportion of bouts in which untrained individuals scrounged or were blocked from access to the Box when they joined demonstrators. These analyses included all 68 meerkats that ever joined a demonstrator during the experiment.

Technique Acquisition

We used two separate GLMMs with binary response terms (1 or 0) to investigate whether the trained technique of the demonstrator in their group (Flap or Stairs) affected whether individuals ever pushed the flap or scratched the box at the top of the stairs. Both analyses included all 78 meerkats in experimental groups that ever interacted with the Box. Group identity was included as a random term, with the demonstrator's technique and individual characteristics as explanatory terms. As individuals that spent longer at the Box might have a higher chance of pushing the flap or scratching the top box regardless of interactions with demonstrators, we included time alone with the Box (s), as a proportion of available time, as an additional explanatory variable. For individuals that obtained food, the available time was the total time from the start of the experiment until they first learned to obtain food.

We investigated preferential adoption of the Flap or Stairs technique among untrained individuals that learned to obtain food using a GLM. Data within the three Flap and Stairs groups were pooled owing to the small number of individuals, with the demonstrator's technique and individual characteristics as explanatory terms. Data were fitted to a binomial distribution, with the number of times individuals obtained food using the Flap as the numerator and the total number of times food was obtained using either technique (Stairs + Flap) as the denominator. We also used a GLMM to investigate the importance of scrounging and observing informed individuals on technique acquisition. Binary response terms (1 or 0) indicated whether individuals ever learned the demonstrator's technique. Explanatory terms were: whether an individual had ever scrounged from an informed group member (demonstrator or other individual that had already learned the technique); whether an individual had ever observed a performance of the technique; the demonstrator's technique; individual characteristics; and the proportion of time alone with the Box. Group identity was fitted as a random term. The analysis used all 78 meerkats in experimental groups that ever interacted with the Box.

Finally, we used a GLMM to examine the proportion of young (pups and juveniles) and adult individuals that learned to obtain food. Data were fitted to a binomial distribution, with the number of individuals that learned as the numerator and the total number of individuals in the group in that age category as the denominator. Age category was fitted as an explanatory variable, with group as a random term. Two similar models were conducted to investigate the proportion of individuals in different age categories that learned following interactions with informed group members and without such interactions.

RESULTS

Interactions with the Box

Patterns of interaction with the Box were significantly affected by treatment (experimental or control groups). While 78 of 83 (94%) untrained individuals in experimental groups interacted with the Box at some point during the experiment, only 24 of 32 (75%) individuals in control groups did so (Table A1 in the Appendix). In total, 18 individuals in experimental groups (22%; 1–6 individuals per group; mean $= 3.0 \pm 0.73$) and three individuals in control groups (9%; 0–2 individuals per group; mean $= 0.67 \pm 0.33$) successfully learned to obtain food from the Box (Table 1). Meerkats that learned a given technique generally performed it repeatedly (mean number of times used $= 9.4 \pm 2.3$) and continued to use it over a number of sessions (technique performed during 1–8 experimental sessions per individual; mean of 2.8 ± 0.4), spread over a mean of 19.5 ± 4.2 days.

Interactions with Demonstrators

When demonstrators were at the Box in experimental groups, pups and juveniles were significantly more likely to join them than were adults (Fig. 2a, Table A2 in the Appendix). Young animals were also more likely to scrounge when they joined demonstrators (Fig. 2b, Table A3 in the Appendix). Overt aggression by demonstrators when joined at the Box was never seen, but demonstrators occasionally used their bodies to block other individuals' access to the Box (6.2% of occasions where a demonstrator was joined). Demonstrators were more likely to block pups than juveniles or adults that joined them at the Box (Fig. 2c, Table A4 in the Appendix).

Technique Acquisition

Individuals in Flap groups were more likely to push the flap during the experiment than were individuals in Stairs groups (Table A5 in the Appendix). Age also had a significant effect in this analysis, with pups and juveniles being more likely than adults to push the flap (Fig. 3a, Table A5). Young animals were also more likely to scratch the small box at the top of the stairs, but there was no significant difference in this tendency between individuals in Flap and Stairs groups (Table A6 in the Appendix). The proportion of time spent at the box in the absence of demonstrators had no significant effect on either the probability of pushing the flap (Table A5) or scratching the top box (Table A6).

There was some evidence that techniques used by demonstrators were preferentially adopted by other group members, with use of the Flap technique (number of times individuals obtained food using Flap/times obtained food using either technique) being significantly higher in Flap than Stairs groups (pooled data for Flap and Stairs groups; Table A7 in the Appendix). In the Stairs groups, five individuals (two pups and one adult in AZ group, one adult in F group and one juvenile in W group) adopted the Stairs technique after observing or scrounging from a demonstrator. In one of these groups, W, two pups subsequently observed and scrounged from the juvenile that had learned the Stairs technique, and also began to use the same technique. A third pup then observed and scrounged from one of these

Table 1
Individuals that learned to obtain food from the Box

Individual	Group	Treatment	Sex & age	Stairs				Flap			
				N	Informed individual	O	SCR	*N*	Informed individual	O	SCR
DEM	AZ	Stairs	MA	7	Trained	—	—	1	None	—	—
AZM001	AZ	Stairs	MP	17	DEM	2	0	0	—	—	—
AZM004	AZ	Stairs	MP	8	DEM	3	1	29	DEM	1	0
VM032	AZ	Stairs	MA	2	DEM	1	0	0	AZM004	1	0
					AZM004	1	0				
DEM	F	Stairs	MA	19	Trained	—	—	0	—	—	—
FM136	F	Stairs	MA	10	DEM	4	0	0	—	—	—
DEM	W	Stairs	MA	13	Trained	—	—	0	—	—	—
WM123	W	Stairs	MJ	29	DEM	1	3	0	—	—	—
WF128	W	Stairs	FP	2	WM123	4	5	0	—	—	—
WM126	W	Stairs	MP	2	WM123	12	5	0	—	—	—
					VF128	2	0				
WF127	W	Stairs	FP	7	WM126	3	1	0	—	—	—
DEM	CD	Flap	MA	0	—	—	—	84	Trained	—	—
CDF019	CD	Flap	FA	1	None	—	—	0	—	—	—
CDF036	CD	Flap	FP	0	—	—	—	18	DEM	2	8
CDF041	CD	Flap	FP	3	None	—	—	2	DEM	2	1
									CDF042	2	0
CDF042	CD	Flap	FP	0	—	—	—	10	DEM	2	2
WM096	CD	Flap	MA	2	None	—	—	0	—	—	—
CDM037	CD	Flap	MP	0	—	—	—	1	DEM	2	3
									CDF036	2	0
DEM	D	Flap	MA	0	—	—	—	46	Trained	—	—
DF122	D	Flap	FJ	6	None	—	—	0	DEM	4	0
DF121	D	Flap	FJ	17	DF122	0	1	0	DEM	7	0
DEM	E	Flap	MA	18	None	—	—	33	Trained	—	—
EM126	E	Flap	MP	1	None	—	—	0	DEM	4	2
EM129	E	Flap	MJ	13	DEM	2	0	0	DEM	6	2
KUM006	KU	Control	MP	35	None	—	—	0	—	—	—
GGF014	KU	Control	FA	0	—	—	—	3	None	—	—
LF133	L	Control	FP	10	None	—	—	0	—	—	—

DEM = trained demonstrator; F = female, M = male; A = adult, J = juvenile, P = pup. *N* = number of times technique performed alone; informed individual = identity of informed group member interacted with. 'Trained' indicates that a demonstrator was trained to perform the technique. 'None' indicates no instances of observing or scrounging from informed group members prior to first successful performance. O = number of times observed an individual obtaining food using that technique; SCR = number of times scrounged from an individual using that technique. Where individuals learned a technique, O and SCR refer to the number of interactions with informed group members prior to the first performance of the technique. Where individuals were not successful, O and SCR are the total number of interactions during the whole experiment.

pups and subsequently also acquired the technique (Fig. 4a). In the Flap groups, four individuals in CD group (all pups) adopted the Flap technique after observing and scrounging from the demonstrator (mean number of times observed $= 2.0 \pm 0.0$; mean times scrounged $= 3.5 \pm 1.6$, range 1–8). No untrained individuals in either of the two other Flap groups used the Flap technique. Untrained individuals were more likely to obtain food independently using the demonstrator's technique if they had previously scrounged from the demonstrator or another untrained individual that had already learned the same technique (Fig. 3b, Table A8 in the Appendix). Observing the demonstrator's technique without scrounging did not have an additional significant effect (Table A8). However, in a restricted analysis using meerkats that never scrounged from an individual performing the Stairs technique, observing successful performance of the Stairs technique had a significant positive effect on the probability that untrained individuals would perform the same technique (Table A9 in the Appendix). The proportion of available time spent at the box in the absence of informed individuals had an additional positive effect (Table A9). An equivalent analysis on performance of the Flap technique was not possible owing to the small number of successful individuals.

Some individuals learned to obtain food without observing or scrounging from others. Five individuals from Flap groups (two adults and one pup in group CD, one juvenile in group D and one pup in group E) independently discovered the Stairs technique without ever previously having observed or scrounged from a group member performing this technique. In addition, the demonstrators in Stairs group AZ and Flap group E discovered the opposite technique to the one on which they were trained. Three untrained meerkats later began performing the same techniques following interactions with these individuals. In group AZ, one pup (individual code AZM004), which had already learned the Stairs technique after observing and scrounging from the demonstrator (trained on Stairs), also observed the demonstrator on the one occasion it performed the Flap technique. In the next session, this pup began performing the Flap technique as well as the Stairs technique, and continued to use both techniques for the duration of the experiment (Fig. 4b). In Flap group E, one juvenile observed the demonstrator performing the Stairs technique and subsequently began performing the same technique, and in Flap group D, one juvenile began performing the Stairs technique after scrounging from the juvenile that had discovered the technique independently (details of technique performance and interactions with informed individuals are in Table 1).

Overall, a greater proportion of young individuals (pups and juveniles) than adults learned to obtain food (14 of 38 young individuals versus 4 of 45 adults; GLMM: $\chi^2_1 = 8.77$, $P = 0.003$). This difference holds if we consider only individuals that learned after observing or scrounging from informed group members (GLMM: $\chi^2_1 = 8.84$, $P = 0.003$), but there was no significant difference in the proportion of young and adult meerkats that learned without interactions with others (GLMM: $\chi^2_1 = 0.45$, $P = 0.500$).

DISCUSSION

This study provides evidence for social learning of novel methods of food acquisition on two levels. First, there were strong indications that individuals exposed to the activities of trained demonstrators

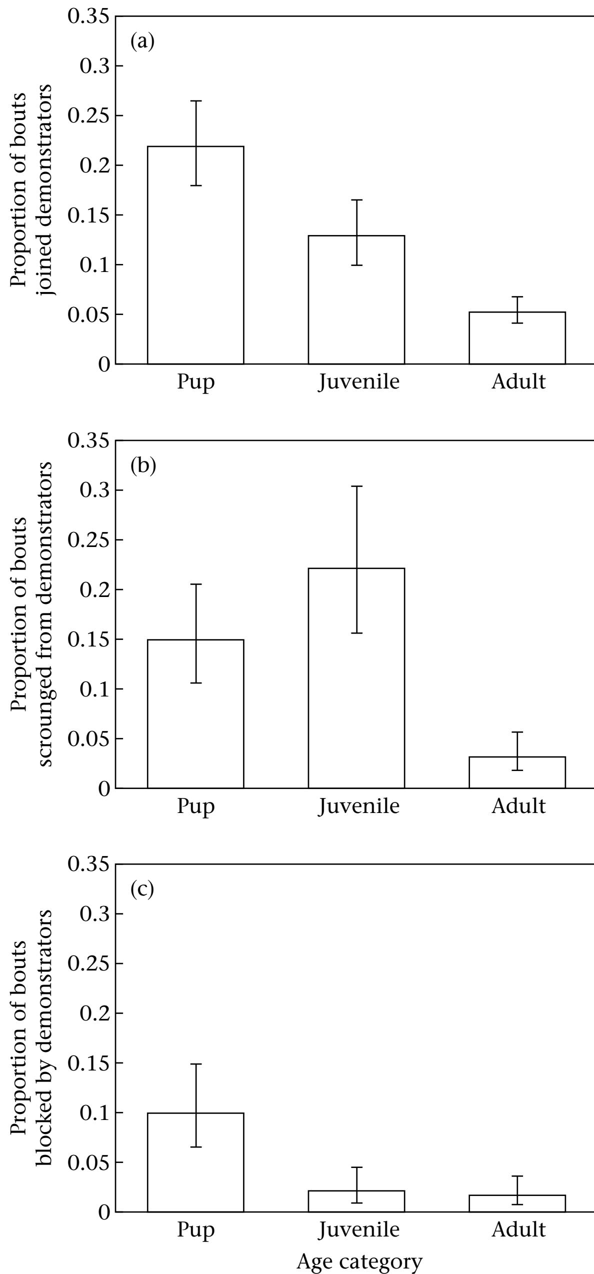

Figure 2. Effects of age on patterns of interaction with demonstrators in experimental groups. (a) The proportion of bouts in which individuals joined demonstrators at the Box ($N = 83$ individuals), (b) the proportion of bouts in which individuals scrounged from demonstrators when they joined them at the Box ($N = 68$ individuals), (c) the proportion of bouts in which demonstrators blocked group members' access to the Box ($N = 68$ individuals). Bars are means $\pm$ SE.

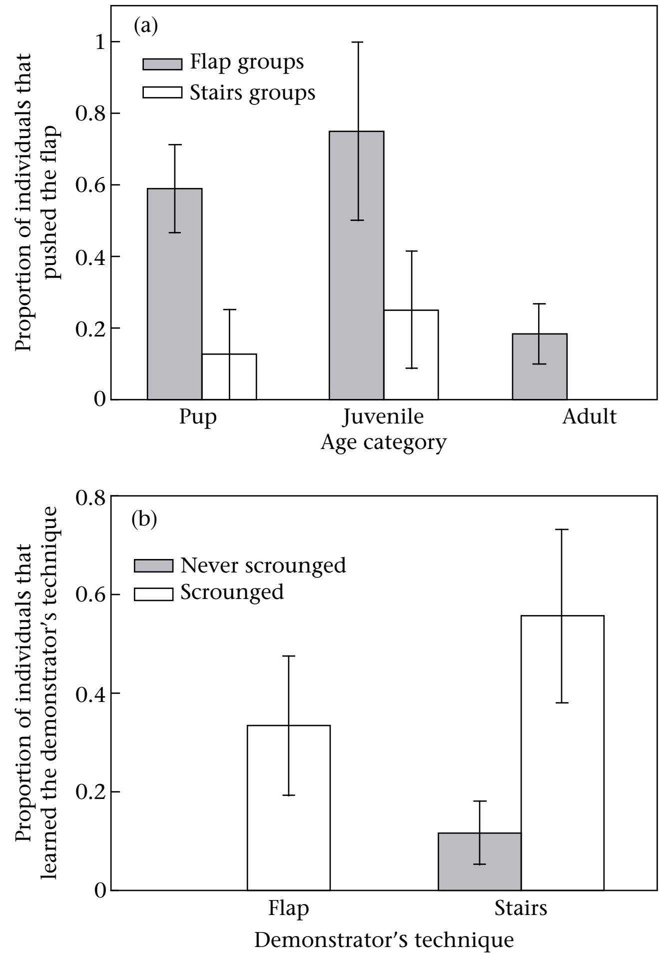

Figure 3. (a) Proportion of pups, juveniles and adults in Flap and Stairs groups that pushed the flap ($N = 78$ individuals). (b) Proportion of individuals in Flap and Stairs groups that learned the demonstrator's technique, showing meerkats that did and did not scrounge from an informed group member performing that technique ($N = 78$ individuals). Bars are means $\pm$ SE.

were more likely to interact with the apparatus and obtain food. Second, there was some evidence for limited transmission of specific techniques from informed individuals to others, although individual learning prevented uniform spread through groups.

While a quarter of the individuals in control groups never interacted with the Box, only 6% of those in experimental groups failed to do so. Moreover, a greater proportion of meerkats in experimental groups learned to obtain food from the Box, with at least one individual in each group being successful, whereas in one of the control groups no meerkat ever obtained food. These results strongly suggest that the presence of trained demonstrators had an important effect on group members' tendency to explore the apparatus. As no meerkat was ever seen to display mobbing behaviour, produce alarm calls or otherwise display fearful responses towards the Box, it is unlikely that the effect of demonstrators was to reduce neophobia among their group members. Rather, demonstrators' actions probably served to attract others' attention to the Box and its contents and thereby promote interaction.

The evidence for social transmission of specific techniques through experimental groups was weaker, but none the less suggestive. Although relatively few individuals successfully obtained food, meerkats in Flap groups were significantly more likely than those in Stairs groups to push the Flap, indicating that they paid attention to the functional parts of the apparatus used by demonstrators. Whether this effect was caused by attraction to the specific stimulus (the flap) or its general location is unclear. We did not find an equivalent effect on the tendency to scratch the small box at the top of the stairs. This is likely to be because individuals in all groups often climbed onto the Box to look out for predators and were therefore fairly likely to smell the food and explore the area.

Even though only 18 meerkats across the experimental groups learned to obtain food, there was some evidence that exposure to informed individuals affected technique acquisition. Among the successful individuals, there was an overall effect of preferential adoption of demonstrators' techniques, with use of the Flap technique being significantly higher in Flap than Stairs groups. Following

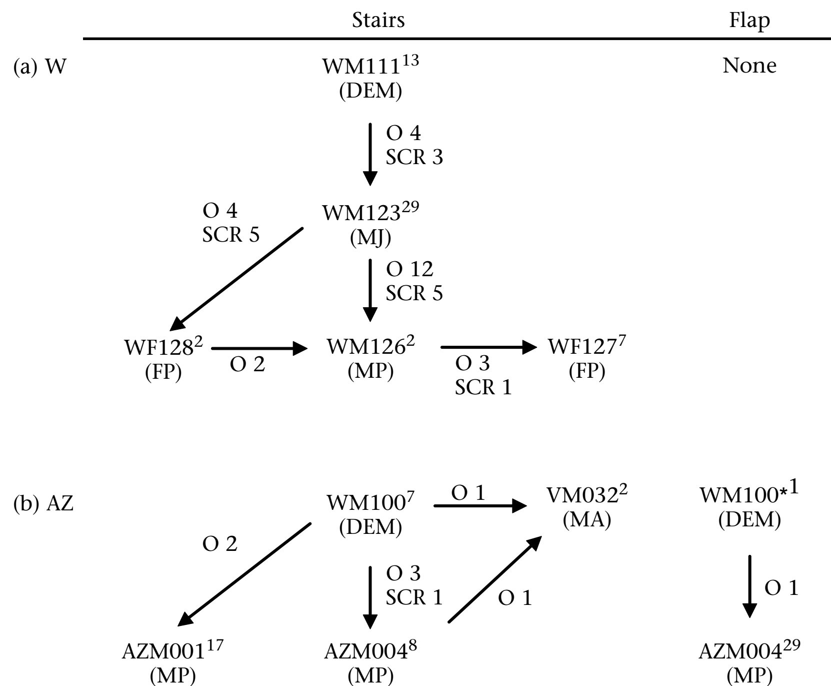

Figure 4. Patterns of technique acquisition in (a) group W and (b) group AZ. Letters in parentheses under individual codes refer to individual characteristics: DEM = demonstrator, M = male, F = female, A = adult, J = Juvenile, P = Pup. Arrows indicate direction of putative information transmission. O = number of times observed a knowledgeable individual performing a technique prior to first successful performance; SCR = number of times scrounged from a knowledgeable individual performing a technique prior to first successful performance.

informed group members and scrounging food from them appeared to be the primary driver of technique acquisition, as animals were significantly more likely to adopt the demonstrator's technique if they had scrounged from an individual performing that technique. This effect is likely to have occurred because the act of going through the flap or climbing up the stairs with an informed conspecific was reinforced, making individuals more likely to repeat it when alone. Scrounging appears to have similar effects promoting learning about novel foods in this and other species (Visalberghi & Addessi 2003; Thornton 2008), where young animals acquire information by taking food that adults are eating. However, the impact of scrounging on social learning appears to be highly variable between species and contexts, with some studies reporting positive effects (Midford et al. 2000; Caldwell & Whiten 2003) and others indicating that scrounging inhibits information transmission (e.g. Giraldeau & Lefebvre 1987; Lefebvre & Helder 1997). This variation is likely to reflect both differences in experimental design and in levels of social tolerance in different species. For instance, in cases where individuals are likely to be attacked for approaching demonstrators or can scrounge food that has spilled out of the apparatus, they may not be reinforced for attempting to get access to food themselves and learning may not occur. In our experiment, all individuals that scrounged also saw successful performance of a technique, making it difficult to determine whether observation alone was sufficient to promote learning. Nevertheless, some support is provided by the finding that among individuals that did not scrounge, those that witnessed a group member performing the Stairs technique were more likely to learn that technique.

Despite the evidence that social interactions promoted technique acquisition, a number of individuals learned to obtain food without having observed or scrounged from others. Although we cannot rule out the possibility that a minority of these animals could have witnessed performance of a technique from a distance, our observations indicated that meerkats that attended to the activities of others tended to approach, so this seems unlikely. Of the 10 individuals classed as having learned independently (including three from control groups and two demonstrators that learned the opposite technique to that on which they were trained), eight performed the Stairs technique, implying that this was the easier of the two techniques to learn. There was some suggestion that a number of naïve group members subsequently adopted these techniques after observing or scrounging from these individuals, although the evidence is difficult to quantify so the claim must remain tentative. For instance, the only untrained individual in a Stairs group that learned to perform the Flap technique was one that observed its demonstrator (trained on Stairs) on the one occasion that it obtained food through the Flap. In contrast to a two-action study on chimpanzees, where individuals preferred their groups' predominant tool use technique (using a stick to poke or lift a blockage and obtain food) even if they discovered alternatives (Whiten et al. 2005), and a recent field experiment where marmosets, *Callithrix jacchus*, tended to continue to use the first of two techniques they learned (pushing or pulling a door; Pesendorfer et al. 2009), two of the three meerkats that learned both techniques alternated between them throughout the experiment. Rather than conforming to the behaviour of others or forming inflexible habits, these meerkats appeared to choose between the two techniques to avoid other meerkats feeding at the Box.

Patterns of successful food acquisition and technique adoption reflected variation in the tendency to join informed individuals at the Box. Young meerkats were more likely to join demonstrators at the Box and to scrounge from them, and were also significantly more likely to learn to obtain food. When we considered only individuals that learned without observing or scrounging from informed group members, we found no such age effect, suggesting that learning by young meerkats is related to their interest in the activities of others. Although individuals were generally tolerant of the close presence of others at the Box, which may have facilitated learning, it was not the case that demonstrators were particularly tolerant of young group members. Indeed, demonstrators were

more likely to block access to the Box when they were joined by pups than by adults. This is likely to be a response to young meerkats' greater determination to join and scrounge from more experienced group members. In contrast to a recent study on chimpanzees (Lonsdorf et al. 2004), we found no sex differences in learning. This probably reflects the fact that while young female chimpanzees spend more time than males watching their mothers fish for termites and consequently develop the skill more rapidly and proficiently, meerkats' attention to the activities of others did not differ between the sexes.

A number of important conclusions can be drawn from this study. First, observing and, in particular, scrounging from knowledgeable individuals can promote exploration of a novel food source and the acquisition of techniques to extract the food in free-living meerkats. To our knowledge, this is the first experimental demonstration of such effects in a wild mammal population. More tentatively, there is some evidence that, where alternative techniques of food acquisition are possible, social learning may result in the transmission of techniques from knowledgeable animals to other members of their social groups. Further field experiments across a variety of taxa, combined with observations of group-typical behaviour patterns and controlled laboratory studies, will be essential in determining the degree to which cultural variants may spread and be maintained in different nonhuman animal species.

Second, this study supports the growing body of evidence that young individuals in meerkat societies are the most likely to acquire information from social interactions (Thornton & McAuliffe 2006; Thornton 2008; Thornton & Hodge 2009; Thornton & Malapert 2009). This pattern is likely to result not because the young have a greater capacity for social learning, but because they are dependent on adults for food and protection (Brotherton et al. 2001; Clutton-Brock et al. 2001) and so are more likely to attend to and learn from them. Consequently, social transmission in meerkats may principally occur between rather than within age cohorts. In cooperative breeders such as meerkats where nonparents contribute to care, both vertical (parent to offspring) and oblique (helper to offspring) transmission are likely to be important in the acquisition of skills by the young (Rapaport & Brown 2008; Thornton & Raihani 2008). In captivity, where animals are confined in close proximity with few pressing requirements (such as foraging or predator avoidance) and few stimuli to attend to other than each other, such patterns of transmission may be less evident. For example, contrary to suggestions from studies in the wild (Biro et al. 2003; Lonsdorf 2006), laboratory experiments have found that juvenile and adult chimpanzees are equally likely to learn socially (Whiten et al. 2005). Further experimental studies on free-living populations will be essential to determine the routes through which social information flows in nature.

Finally, this study suggests that in natural situations opportunities for individual learning may often interfere with the establishment of group-level traditions. In our experiment, a number of individuals learned asocially to acquire food from the Box. Moreover, there was some suggestion that the techniques learned by these individuals subsequently spread to others, leading to the existence of two alternative socially learned techniques of food acquisition within groups. These findings, along with the indication that social learning may be limited to a subset of the group, indicate that we must be cautious in using behavioural uniformity within groups as a criterion for identifying socially transmitted traits in the wild (e.g. McGrew 2004). It is possible that a capacity for imitation in certain species may promote the establishment of more homogeneous and widespread traditions, but until more is known about patterns and mechanisms of social learning in nature, no firm claims can be made. It is therefore prudent to assume that a lack of behavioural uniformity need not imply an absence of socially transmitted behaviour.

Acknowledgments

We thank T. Clutton-Brock and M. Manser for their support and access to the meerkats and Mr and Mrs J. Kotze for permission to work on their land. We are grateful to D. Bell, C. Cyrus-Kent, J. Newsom, R. Sutcliffe and the Mammal Research Institute for their help in the field and to K. Moyes for statistical advice. A. Radford, N. Raihani and two anonymous referees provided useful comments on the manuscript. This research was funded by Pembroke College, Cambridge.

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APPENDIX

Coefficient estimates in all tables represent the change in the dependent variable relative to the baseline category and can thus be interpreted as measures of effect size.

Table A1
GLMM on factors affecting the probability that individuals would interact with the Box during the experiment

	Wald statistic (χ^2)	*df*	*P*
Full model			
Treatment (control, experimental)	7.16	1	0.009
Total duration (s)	1.70	1	0.199
Age category (adult, juvenile, pup)	0.68	2	0.711
Sex	0.03	1	0.864
Group size (number of individuals)	0.00	1	0.973
Minimal model	Coefficient estimate	SE	
Constant	1.10	0.41	
Treatment			
Control	0	0	
Experimental	1.65	0.62	

Data were fitted to a binomial distribution with a logit-link function and binary response terms (1 or 0) indicating whether or not an individual interacted with the Box (i.e. approached and inspected the Box or tried to obtain food from it). The analysis used data from 115 meerkats, with group identity fitted as a random term (estimated variance component = 0.0, SE = 0.0).

Table A2
GLMM on factors affecting the proportion of bouts in which individuals joined demonstrators

	Wald statistic (χ^2)	*df*	*P*
Full model			
Age category (adult, juvenile, pup)	22.84	2	<0.001
Sex	1.97	1	0.165
Demonstrator's technique (Flap, Stairs)	0.10	2	0.766
Minimal model	Coefficient estimate	SE	
Constant	−1.27	0.25	
Age category			
Pup	0	0	
Juvenile	−0.64	0.26	
Adult	−1.61	0.38	

Data were fitted to a binomial distribution with a logit-link function, with the number of bouts within a session in which individuals joined the demonstrator as the numerator and the number of bouts of interaction with the Box by the demonstrator as the denominator. The analysis was conducted on data from all 83 individuals in experimental groups, with group and individual identity fitted as random terms (estimated variance components: group = 0.013, SE = 0.116; individual = 1.62, SE = 0.41).

Table A3
GLMM on factors affecting the proportion of bouts in which individuals scrounged from demonstrators

	Wald statistic (χ^2)	*df*	*P*
Full model			
Age category (adult, juvenile, pup)	11.68	2	0.003
Sex	0.29	1	0.588
Demonstrator's technique (Flap, Stairs)	0.02	1	0.892
Minimal model	Coefficient estimate	SE	
Constant	−3.46	0.62	
Age category			
Adult	0	0	
Juvenile	2.20	0.64	
Pup	1.71	0.40	

Data were fitted to a binomial distribution with a logit-link function, with the number of bouts within a session in which individuals scrounged from the demonstrator as the numerator and the total number of bouts in which they joined the demonstrator as the denominator. The analysis was conducted on data from the 68 individuals in experimental groups that joined a demonstrator during the experiment, with group and individual identity fitted as random terms (estimated variance components: group = 0.46, SE = 0.47; individual = 0.42, SE = 0.34).

Table A4
GLMM on factors affecting the proportion of bouts in which individuals were blocked by demonstrators

	Wald statistic (χ^2)	*df*	*P*
Full model			
Age category (adult, juvenile, pup)	9.36	2	0.009
Sex	3.37	1	0.054
Demonstrator's technique (Flap, Stairs)	0.55	1	0.459
Minimal model	Coefficient estimate	SE	
Constant	−4.10	0.81	
Age category			
Adult	0	0	
Juvenile	0.23	1.03	
Pup	1.88	0.77	

Data were fitted to a binomial distribution with a logit-link function, with the number of bouts within a session in which individuals were blocked by the demonstrator as the numerator and the total number of bouts in which they joined the demonstrator as the denominator. The analysis was conducted on data from the 68 individuals in experimental groups that joined a demonstrator during the experiment, with group and individual identity fitted as random terms (estimated variance components: group = 0.71, SE = 0.70; individual = 0.0, SE = 0.0).

Table A5
GLMM on factors affecting the probability that individuals would push the flap

	Wald statistic (χ^2)	*df*	*P*
Full model			
Age category (adult, juvenile, pup)	12.67	2	0.002
Demonstrator's technique (Flap, Stairs)	5.72	1	0.017
Sex	0.08	1	0.782
Proportion of time alone with Box	0.04	1	0.837
Minimal model	Coefficient estimate	SE	
Constant	−1.83	0.75	
Age category			
Adult	0	0	
Juvenile	3.45	1.08	
Pup	2.14	0.74	
Demonstrator's technique			
Flap	0	0	
Stairs	−2.70	1.12	

Data were fitted to a binomial distribution with logit-link function and binary response terms (1 or 0) indicating whether an individual ever scratched or pushed the flap. The analysis was conducted on data from the 78 untrained individuals in experimental groups that interacted with the Box during the experiment, with group identity included as a random term (estimated variance component = 0.75, SE = 1.10). Proportion of time alone with Box refers to the total time an individual spent interacting with the box in the absence of informed individuals, as a proportion of the total time available. For individuals that obtained food, the available time was the total time from the start of the experiment until they first obtained food.

Table A6
GLMM on factors affecting the probability that individuals would scratch the top box during the experiment

	Wald statistic (χ^2)	*df*	*P*
Full model			
Age category (adult, juvenile, pup)	11.79	2	0.003
Sex	0.78	1	0.378
Proportion of time alone with Box	0.42	1	0.518
Demonstrator's technique (Flap, Stairs)	0.39	1	0.531
Minimal model	Coefficient estimate	SE	
Constant	−1.68	0.61	
Age category			
Adult	0	0	
Juvenile	3.21	0.96	
Pup	0.93	0.64	

Analysis as in Table A5 but with binary response term indicating whether an individual ever scratched the top box. Estimated variance component for group identity, fitted as a random term = 1.04, SE = 1.00.

Table A7
GLM on factors affecting preferential adoption of the Flap technique

		df	*P*
Full model			
Task (Flap, Stairs)	42.13	1	<0.001
Age category (adult, juvenile, pup)	2.52	2	0.116
Sex	2.17	1	0.161
Minimal model	Coefficient estimate	SE	
Constant	−1.15	0.28	
Task			
Flap	0	0	
Stairs	−2.13	0.35	

Owing to the small numbers of individuals in each group that obtained food, data within Stairs and Flap groups were pooled. Data were fitted to a binomial distribution with logit-function, with the number of times individuals obtained food using the Stairs as the numerator and the total number of times food was obtained using either technique (Stairs + Flap) as the denominator. The analysis was conducted on data from the 18 individuals that obtained food from the Box.

Table A8
GLMM on factors affecting the probability that individuals in experimental groups would obtain food using the demonstrator's technique

	Wald statistic (χ^2)	*df*	*P*
Full model			
Ever scrounged (no, yes)	11.36	1	<0.001
Demonstrator's technique (Flap, Stairs)	2.57	1	0.109
Ever saw success (no, yes)	1.65	1	0.199
Proportion of time alone with Box	0.14	1	0.709
Sex	1.45	1	0.229
Age (adult, juvenile, pup)	0.64	2	0.725
Minimal model	Coefficient estimate	SE	
Constant	−3.05	0.76	
Ever scrounged			
No	0	0	
Yes	2.74	0.81	

Data were fitted to a binomial distribution with logit-link function and binary response terms (1 or 0) indicating whether an individual ever obtained food using the demonstrator's technique. The analysis was conducted on data from the 78 untrained individuals in experimental groups that interacted with the Box during the experiment, with group identity included as a random term (estimated variance component = 1.12, SE = 1.42).

Table A9
GLMM on factors affecting the probability that individuals in experimental groups that never scrounged from group members performing the Stairs technique would learn the Stairs technique

	Wald statistic (χ^2)	*df*	*P*
Full model			
Ever observed Stairs (no, yes)	7.03	1	0.010
Proportion of time alone with Box	4.64	1	0.035
Task (Flap, Stairs)	0.02	1	0.890
Sex	0.90	1	0.345
Age (adult, juvenile, pup)	0.14	2	0.934
Minimal model	Coefficient estimate	SE	
Constant	−2.24	0.50	
Ever observed Stairs			
No	0	0	
Yes	2.12	0.80	
Proportion of time alone with Box	28.39	13.19	

Data were fitted to a binomial distribution with logit-link function and binary response terms (1 or 0) indicating whether an individual ever obtained food using the Stairs technique. The analysis was conducted on data from the 68 untrained individuals in experimental groups that interacted with the Box during the experiment, but never scrounged from an informed individual performing the Stairs technique. Group identity was fitted as a random term (estimated variance component = 0.0, SE = 0.0).