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

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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.

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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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)

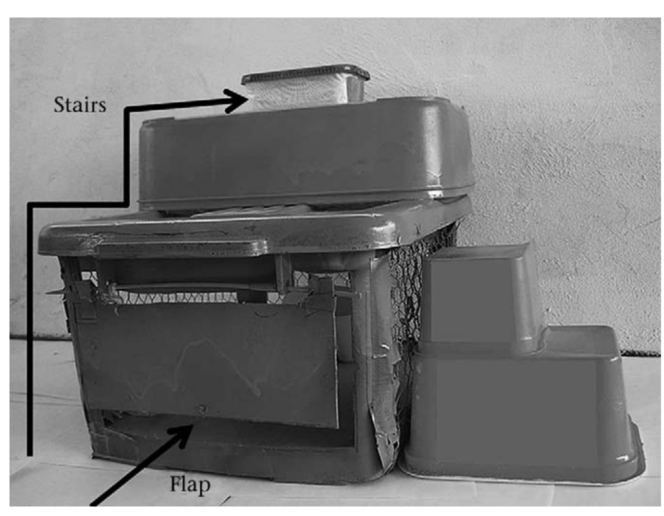

Figure 1. The 'Box'. The 'Stairs' technique involved climbing up the Box and breaking a paper lid to obtain hidden food; the 'Flap' technique involved going through a flap to obtain food inside the Box.