

The rise and fall of an arbitrary tradition: an experiment with wild meerkats

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Humans often follow the choices of others, even when profitable alternatives exist, leading to the maintenance of arbitrary traditions. Arbitrary traditions have also been shown to persist in captive groups of other animals, but it is unclear whether they do so in the wild where there are ample opportunities for exploring alternatives. We conducted the first experiment examining the maintenance of arbitrary traditions in wild mammal groups. We trained ‘demonstrators’ in seven meerkat groups to obtain rewards from one out of the two distinctive landmarks. Two control groups had no trained demonstrators. Naive individuals initially ignored the landmarks, but were more likely to approach them and obtain rewards following encounters with demonstrators. Individuals in control groups were less likely to obtain rewards. While control groups showed no landmark preference, experimental groups initially preferred the landmark chosen by demonstrators, even though an equally rewarding alternative was nearby, leading to the establishment of local traditions. However, individuals that learned that one landmark was profitable began to explore the other rather than conforming to the majority behaviour, so traditions collapsed over time. This suggests that where conformist tendencies are lacking, the maintenance of traditions in natural populations depends on the relative influence of social and individual learning.

Keywords: culture; meerkats; social learning; *Suricata suricatta*; traditions

1. INTRODUCTION

The social transmission of information between individuals is common across human and animal societies (Boyd & Richerson 1985; Galef & Giraldeau 2001; Laland & Hoppitt 2003). One important consequence is that individual’s choosing between different options often copy the choices of others, even if the options provide equivalent benefits (Boyd & Richerson 1985; Giraldeau *et al.* 2002). For example, across a range of species, individuals prefer to eat foods that other conspecifics have eaten, even if other equally palatable and nutritious options are available (Nicol 1995; Galef & Giraldeau 2001; Galef 2003; Addressi *et al.* 2005; Lupfer-Johnson & Ross 2007). Similarly, individuals often prefer to follow routes used by others, even if equivalent or shorter routes are available (Laland & Williams 1998; Reader *et al.* 2003, 2008). This tendency to replicate the behaviour of others may lead to the establishment and persistence of behavioural patterns or traditions that are shared by members of a group (Fragaszy & Perry 2003).

If traditions are sufficiently long-lived, they may modify the selective pressures acting on populations and thereby influence genetic evolution (Boyd & Richerson 1985; Laland *et al.* 2000). Such effects are thought to be a major driving force in human evolution, where behavioural traditions are often highly durable, and have been implicated in the origins of peculiar human dietary adaptations, cognitive mechanisms and prosociality (Boyd & Richerson 1985; Richerson & Boyd 2005). By contrast, traditions in

other species are generally thought to be more ephemeral, and their potential to affect population gene frequencies more limited (Boyd & Richerson 1985; vocal dialects in song birds and cetaceans may be important exceptions (Grant & Grant 1996; Whitehead 1998; Beltman *et al.* 2004)). If we are to improve our knowledge of the role of social transmission in evolution and the relations between the traditions of humans and other animals, it is important to determine the factors that affect whether traditions persist or collapse.

Laboratory studies have shown that traditions may spread through groups of animals under controlled conditions (Galef & Allen 1995; Laland & Williams 1998; Whiten & Mesoudi 2008). However, the degree to which the results of captive studies reflect the processes at work in natural populations is unclear. The spatial restriction of animals, their enforced proximity to other individuals and the presence of abundant food may all increase the frequency and precision of social learning, as well as the chance that arbitrary or maladaptive traditions may persist (Laland *et al.* 1993). In addition, the social dynamics of captive groups may differ from those shown in the wild, which may affect the patterns of information transmission through groups (Coussi-Korbel & Fragaszy 1995). Moreover, existing studies typically consider contexts where there may be potentially severe costs for deviating from the social norm. For example, preferences for foods eaten by conspecifics may persist because sampling unknown foods carries the risk of consuming toxins (Galef 1993). Similarly, socially learned preferences for foraging routes in ants and fishes may be maintained because learning alternative routes would involve leaving the safety of the group (Day *et al.* 2001). It is far less clear

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whether traditions will persist in situations where there are ample opportunities for individual learning at low cost. Such persistent traditions are common in humans, where conformist social learning often leads to the maintenance of arbitrary trends and fashions (Richerson & Boyd 2005), and have been reported in captive chimpanzees (*Pan troglodytes*) where individuals may persist in demonstrating the prevalent behaviour in the group, even if they discover an equally profitable alternative (Whiten *et al.* 2005; Bonnie *et al.* 2007).

Field studies are essential to determine the extent to which arbitrary traditions can persist in natural animal populations in contexts where alternatives are easily discoverable. Observational studies indicate that such traditions may be relatively common among primates. For example, reports suggest that different populations of monkeys and apes exhibit idiosyncratic arrays of gestures, social interactions and object manipulation that lack obvious immediate benefits, and may be considered local social conventions (Whiten *et al.* 1999; Perry *et al.* 2003; van Schaik *et al.* 2003; Leca *et al.* 2007). These studies are often cited as evidence that the cultural behaviours of primates are more akin to humans than those in other species, where traditions are typically found in limited contexts and where there are clear fitness benefits from adopting the choices of others (Whiten 2005; Whiten & van Schaik 2007). However, the capacity of other species to maintain traditions in contexts with low-cost opportunities for individual learning has seldom been considered in natural populations. Moreover, without experiments, it is very difficult to obtain direct evidence that social learning is responsible for behavioural differences between groups of wild primates.

To date, very few studies have used experiments to test the spread of socially learned information in the wild (a recent review by Whiten & Mesoudi (2008) lists only three such studies, noting that two of them found little or no evidence of social transmission). Here, we use an experimental approach to examine the establishment and persistence of a simple tradition in a population of individually recognizable, habituated wild meerkats (*Suricata suricatta*). Meerkats are cooperatively breeding mongooses living in the semi-arid regions of southern Africa in groups comprising a dominant breeding pair and a variable number of helpers of both sexes that assist in rearing young (Brotherton *et al.* 2001). When foraging, they move as a dispersed group, searching individually for invertebrate and small vertebrate prey (Doolan & Macdonald 1996). They exhibit teaching of prey-handling skills (Thornton & McAuliffe 2006) and social learning of food preferences (Thornton 2008a) in the wild, and pups are thought to employ social cues in their development of preferences for particular foraging microhabitats (Thornton & Hodge 2009).

Animals such as meerkats that forage in heterogeneous habitats often choose to forage in locations indicated by the presence of conspecifics (Galef & Giraldeau 2001; Thornton & Hodge 2009). If such locations are associated with distinctive landmark cues, individuals may develop preferences for foraging at such landmarks, even though other locations may be equally productive and could be discovered through individual exploration (Giraldeau *et al.* 2002). Such preferences could lead to the establishment of local traditions within groups (Midford *et al.* 2000).

Our experiment mimicked such a situation. We trained individual demonstrators in seven groups to show a preference for one of two distinctively shaped and coloured landmarks that indicated the presence of water and buried food. We then presented both landmarks when other group members were present, to examine whether naive individuals would adopt the preference of demonstrators, despite the fact that the alternative landmark was nearby and equally rewarding. A further two groups served as controls, where we presented landmarks but had no trained demonstrators. We predicted that naive individuals in experimental groups would initially ignore the landmarks, but would learn to obtain rewards from them following interaction with demonstrators, and would prefer the landmark indicated by demonstrators. Individuals in control groups were expected to be less likely to obtain rewards from the landmarks. To investigate the persistence of preferences for particular landmarks, we conducted repeated experimental sessions over a period of weeks, and used these to examine the consistency of individuals' choices. As individuals learned that they could obtain rewards from the landmarks, they too could serve as models for other group members. We therefore examined whether, during the course of the experiment, individuals were more likely to make the same choice in consecutive encounters with the landmarks if another individual was present at the landmarks in the previous encounter. We analysed our results using multifactorial models, including data on the characteristics of the individuals involved, such as age, sex and dominance status, which may influence transmission dynamics. To our knowledge, this is the first two-option social diffusion experiment to be conducted on a population of wild mammals.

2. MATERIAL AND METHODS

(a) *Study site and population*

We conducted experiments on nine groups of 7–19 meerkats living in semi-desert along the dry Kuruman River in the South African Kalahari (Russell *et al.* 2002) between December 2007 and May 2008. Groups were located by radio tracking collared individuals and all animals were identifiable through unique dye marks on their fur. All individuals were habituated to close observation (< 1 m) and had been monitored since birth, so their ages were known precisely (within 2 days). During the course of our experiments, several individuals made the transition from pups (< 3 months) to juveniles (3–6 months) or from subadults (6–12 months) to adults (more than 12 months; age categories as per Brotherton *et al.* 2001). To avoid analyses where one individual could be in multiple age classes, we therefore categorized meerkats as young (< 180 days) or old (more than 330 days). Young animals were still growing and had poorly developed foraging skills, while old individuals were at or approaching full body size and were competent foragers (Thornton 2008b,c). There were no individuals between the age of 180 and 330 days present at the time of the study.

(b) *Materials*

'Landmarks' consisted of eight distinctively coloured plastic geometric shapes of equal area (210 cm²). Landmarks were arranged into pairs with high contrast colour and luminance that are easily distinguishable by meerkats (Bernau 1969): blue (U) and red-and-white striped (Z), green circle and white

Table 1. Experimental protocol

experimental groups	landmarks		demonstrators ^a
	positive	neutral	
AZ			DM, SF
W			DM
CD			DF, SM
E			SM
D			DM, SM
ZZ			DM
KU			SF
control groups	neutral	neutral	
F			
L			

^aD, dominant; S, subordinate; M, male; F, female.

triangle, black rectangle and yellow star, purple moon and yellow-and-black striped (Y). Each landmark contained a water dispenser with the nozzle protruding from the surface of the landmark, such that meerkats could obtain water by licking the nozzle. During experiments, landmarks were affixed to a plastic tray measuring 39 × 32 cm. Trays were covered in sand, with small pieces of hardboiled egg hidden under the sand as rewards. The edges of the tray were camouflaged using cardboard covered in sand so that when they were placed on the ground, the landmark but not the tray was clearly visible.

(c) Experimental protocol

We assigned seven experimental groups with trained demonstrators. Two groups served as controls, with no demonstrators. One of the pairs of landmarks was randomly allocated to each group. Among the experimental groups, there were two groups allocated to each of the three pairs of landmarks, and one group for the fourth. The two control groups were randomly allocated to one pair of landmarks each (table 1).

(i) Training

In the experimental groups, one of the landmarks in the pair was designated as 'positive' and the other as 'neutral'. Where there were two groups allocated to the same pair of landmarks, the positive landmark differed between groups. In each experimental group, we trained one or two adult individuals as demonstrators. We had planned to have one dominant and one subordinate demonstrator in each group,

but this was not possible due to natural deaths and emigrations, so demonstrator number and dominance status varied between groups (table 1). 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. No other meerkats saw the landmarks during this time. We began training by using crumbs of hardboiled egg to lure individuals to a tray with the positive landmark on it. We rewarded individuals by placing crumbs of egg on top of the sand and squeezing the water dispenser inside the landmark so that they could drink the water that dribbled out. Once individuals were reliably approaching the landmarks, we began to hide egg under the sand. Finally, when demonstrators were consistently approaching the positive landmark, unearthing the hidden food and/or drinking from the bottle, we conducted presentations where both the positive and neutral stimulus were placed 1.5 m apart from each other in the demonstrator's line of view. Both landmarks contained water dispensers and were on trays with buried egg. To reinforce the positive stimulus, we squirted the neutral landmark with a water pistol if the demonstrator approached it. Squirting caused individuals to move away from the landmark, but did not cause discernable fear responses. Training ceased when demonstrators consistently ate or drank at the positive landmark and ignored the neutral landmark. Demonstrators retained their preference throughout the group phase, and were reinforced by squirting on the rare occasions where they approached the neutral landmark.

(ii) Group phase

Once demonstrators were fully trained, we began group presentations. These were conducted during 60–90 min sessions when the group was foraging in the morning or afternoon. We conducted a total of 9–17 sessions at each group, with sessions spaced at least one day apart (mean days between sessions = 6.5 ± 0.5). The two landmarks were placed 1.5 m apart from each other in the path of foraging group members. Both landmarks contained water dispensers and were affixed to trays with buried egg. We conducted repeated presentations throughout the session as the group moved, alternating the two landmarks between left and right to control for any side biases and cleaning them with antiseptic wipes to remove potential odour cues. Whenever an individual passed within 2 m of the landmarks (hereafter termed an 'encounter' with the landmarks), we noted its identity, whether it approached a landmark and whether it ate or drank. An 'approach' was defined as orienting towards a landmark and moving to within 5 cm of it. We replenished the hidden egg as required to ensure that food rewards were always available. To determine the responses of naive individuals, we attempted to ensure that all individuals' first encounter with the landmarks occurred when there was no demonstrator present nearby. In subsequent presentations, any individual (including demonstrators) could approach the landmarks. Whenever an individual was eating or drinking at the landmarks, we made note of all other meerkats within 2 m and noted whether the animal at the landmarks was joined by another group member. 'Joining' is defined as orienting and moving to within 20 cm of a meerkat at the landmarks. During each presentation session, we endeavoured to ensure that all individuals passed within 2 m of the landmarks at least once.

(d) Statistical analyses

Data were analysed in GENSTAT v. 8.1 (Rothamstead Experimental Station, Harpenden, UK). Multifactorial analyses were conducted using generalized linear mixed models (GLMM), with group and 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 non-significant terms were obtained by adding each term individually to the minimal model. We inspected the residuals from all models to ensure homogeneity of variance, normality of error and linearity, applying log transformations where necessary. Kolmogorov–Smirnov tests were used to confirm that residuals were normally distributed.

Details of specific models are given below.

(i) Initial responses to landmarks

We compared individuals' responses to the landmarks before and after joining another group member at the landmarks using GLMMs. 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 approached the landmarks or obtained rewards from them. We conducted separate analyses using individuals in experimental groups that joined demonstrators and individuals across all groups that joined any other meerkat at the landmarks. We fitted encounter (before or after joining another group member at the landmarks) as an explanatory factor, along with individual age category (young or old), sex, dominance status, landmark pair and, where relevant, treatment (experimental or control group) and whether or not the meerkat encountered at the landmarks was a trained demonstrator. Group and individual identities were included as random terms.

(ii) Obtaining rewards

We used a χ^2 test to compare the proportion of individuals in control and experimental groups that ever obtained food or water from the landmarks when alone throughout the duration of the experiment. We also conducted a GLMM with a logit link function and binary response terms (1 or 0) indicating whether or not an individual ever obtained rewards from the landmarks. As the total number of sessions varied between groups, we included number of sessions as an explanatory variable, along with treatment (experimental or control group), individual characteristics (age, sex and dominance status) and landmark pair. Group identity was included as a random term. The analysis used data from all 109 individuals (not including trained demonstrators) in the nine groups.

(iii) Choices of landmarks

We used binomial tests to examine whether individuals' choices of landmarks before and after joining demonstrators differed from chance. We also conducted a GLMM with binary response terms (1 or 0) indicating whether or not untrained individuals across all groups chose the same landmark as the individual they last joined at the landmarks throughout the duration of the experiment. Group and

individual identities were random terms in the model, and explanatory variables were: session number (log transformed), time since encountering the group member at the landmarks (s), landmark pair, treatment (experimental or control group), characteristics of the choosing individual (age, sex and dominance) and characteristics of the group member encountered at the landmarks (age, sex, dominance and whether it was a trained demonstrator). The analysis used data from 61 individuals across the nine groups that ate or drank at the landmarks within 30 min of joining another group member at the landmarks (4–12 individuals per group; mean = 7.4 ± 1.0 in experimental groups and 4.5 ± 0.5 in control groups). Cases where longer periods had elapsed were excluded as results could be confounded by individuals forgetting about cues encountered in the previous encounter.

Over the short-term, individuals' choices from one encounter with the landmarks to the next could vary depending on whether they have recently joined other meerkats at the landmarks. We examined the factors affecting meerkats' landmark choices over consecutive encounters using a GLMM on the probability that individuals would choose the same landmark that they chose in their previous encounter. We fitted a binomial response term indicating whether the choice of landmarks was the same or different (1 or 0) to the choice the previous time they encountered the landmarks alone. The first encounter from each session was excluded. Session number, time since last encounter, landmark pair, treatment and individual characteristics were fitted as explanatory terms, along with whether or not another meerkat was present at the landmarks on the previous encounter. Group and individual identities were fitted as random terms. The analysis used the same 61 individuals as above.

(iv) Probability of being joined

We investigated the factors affecting the probability that an individual eating or drinking at the landmarks would be joined by another group member using a GLMM with a binary response term (1 or 0) indicating whether or not the animal at the landmarks was joined. The model used 2458 different encounters by 97 individuals (including demonstrators) in all nine groups. Group and individual identity were included as random terms and session number, treatment and characteristics of the individual at the landmarks (age, sex, dominance status and whether it was a trained demonstrator) were fitted as explanatory variables.

(v) Degeneration of traditions

We examined whether initial biases towards positive stimuli degenerated over time using a GLMM, where the number of times during a session that each individual ate/drank at the positive landmark was fitted as the numerator in a binomial response term, with the total number of times the individual ate/drank as the denominator. In control groups, one of the two landmarks was randomly assigned as positive for the analysis. As the total number of sessions varied between groups, we considered only the first nine sessions in each group. We fitted treatment (experimental or control group) as an explanatory variable, along with session number, landmark pair and individual characteristics. Group and individual identity were included as random terms.

3. RESULTS

(a) *Initial responses to landmarks*

Naive individuals initially tended to ignore the landmarks when alone, but were significantly more likely to approach them and obtain food after joining another meerkat at the landmarks. For 100 out of 109 individuals across all nine groups, the first time they came within 2 m of the landmarks was when there were no other meerkats present (in the other nine instances, a demonstrator ran to the landmarks when the naive individual first came across them). Of these 100 individuals, 84 did not approach the landmarks. Of the 16 individuals that did approach the landmarks, only two obtained food or water. By contrast, 96 out of these 100 individuals approached the landmarks the first time they encountered another meerkat at the landmarks (McNemar's test of individuals approaching alone versus with another meerkat: $\chi^2 = 78.01$; $p < 0.0001$), and 44 obtained food (McNemar's test; $\chi^2 = 40.02$; $p < 0.0001$). Among the 84 individuals that did not approach the landmarks on their first encounter, there were 25 who joined a demonstrator that was feeding at the positive landmark on their second encounter, and who subsequently encountered the landmarks alone again later (on their third encounter). These individuals were significantly more likely to approach the landmarks and obtain rewards from them after joining the demonstrator than before (GLMMs: approaching: $\chi^2 = 5.45$, $p = 0.020$; obtaining rewards: $\chi^2 = 5.01$, $p = 0.025$). No other explanatory variable had a significant effect in these analyses. Once formerly naive individuals began approaching the landmarks, they became potential models for other group members. If we consider the 77 individuals in seven groups that encountered the landmarks alone, then when any other individual (trained demonstrator or not) was at the landmarks and then alone again, individuals were more likely to approach and obtain rewards from the landmarks following an encounter with another individual (GLMMs: approaching: $\chi^2 = 15.96$, $p < 0.001$; obtaining rewards: $\chi^2 = 15.36$, $p < 0.001$). Young individuals (<180 days) were significantly more likely than old individuals (more than 330 days) to eat or drink at the landmarks ($\chi^2 = 8.19$, $p = 0.004$), but age had no significant effect on the probability of approaching the landmarks. There were no other significant factors in either analysis.

(b) *Obtaining rewards*

Throughout the duration of the experiment, 65 out of 82 untrained meerkats in experimental groups (79.3%) obtained food or water from the landmarks, compared with only 14 out of 27 (53.8%) of individuals in control groups (χ^2 test: $\chi^2 = 7.65$, $p = 0.006$). GLMM analysis revealed that individuals were more likely to obtain food or water if they were in an experimental group ($\chi^2 = 4.56$, $p = 0.033$) and were young ($\chi^2 = 11.36$, $p < 0.001$). There was no significant effect of sex, dominance status, landmark pair or the total number of sessions ($p > 0.220$).

(c) *Choices of landmarks*

Among the 14 individuals in experimental groups that approached the landmarks on their first encounter (with no other meerkat present), there was no significant preference for the positive landmark (8 out of 14 individuals; two-tailed Binomial test: $p = 0.791$).

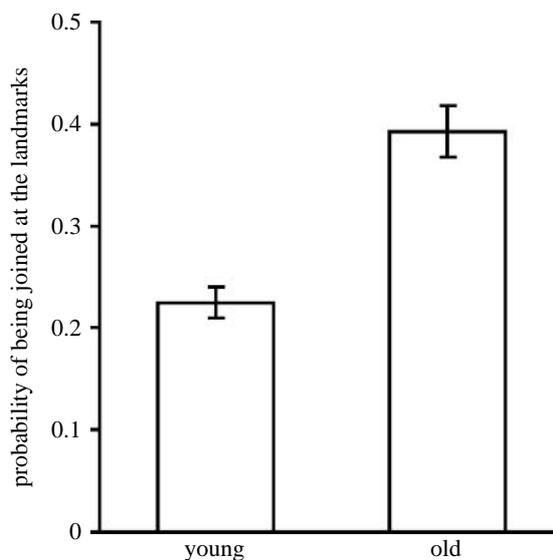


Figure 1. Old individuals were significantly more likely than young animals to be joined by another group member when they were at the landmarks (GLMM: $\chi^2 = 37.15$, $p < 0.001$).

By contrast, among the 30 individuals that ate at the landmarks after joining a demonstrator, 25 chose the positive landmark (Binomial test: $p < 0.0001$). The same pattern holds true if we consider the first approaches by naive individuals after joining any individual (demonstrators or formerly naive individuals that have joined a demonstrator), with 49 out of 61 individuals choosing the positive landmark (Binomial test: $p < 0.0001$). However, the tendency to choose the same landmark as the individual most recently encountered at the landmarks declined over the course of session days (GLMM: $\chi^2 = 4.82$, $p = 0.028$). There was no significant effect of the time (in seconds) elapsed since the last encounter with another individual at the landmarks, the landmark pair or characteristics of the individuals involved in this analysis. Similarly, in a GLMM examining consistency in choices from one encounter with the landmarks to the next, individuals were less likely to choose the same landmark in consecutive encounters as the experiment went on ($\chi^2 = 7.89$, $p = 0.005$), controlling for a significant effect of the time (in seconds) elapsed since the previous encounter ($\chi^2 = 10.80$, $p = 0.001$). Individuals were significantly more likely to choose the same landmark again if there was another meerkat at the landmarks in their previous encounter ($\chi^2 = 10.11$, $p = 0.002$). No other explanatory variables had a significant effect in the analysis.

(d) *Probability of being joined*

GLMM analysis revealed that old meerkats were significantly more likely to be joined at the landmarks than young individuals (figure 1). The landmark pair, treatment and other characteristics of the individual at the landmarks (sex, dominance and whether it was a trained demonstrator) had no significant effect ($p \geq 0.130$).

(e) *Degeneration of traditions*

There was no significant change in individuals' landmark choices over time in control groups, with the proportion of positive landmarks chosen remaining approximately 50 per cent throughout. By contrast, the proportion of

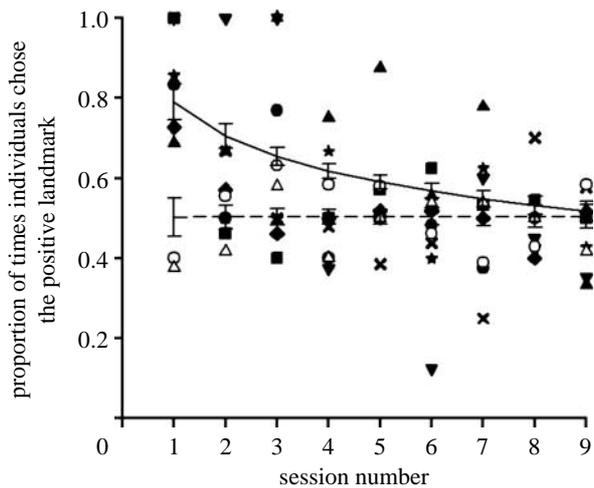


Figure 2. The proportion of times that individuals chose the positive shape declined over time in experimental groups, but remained approximately 50% in control groups (GLMM: session number \times treatment: $\chi^2 = 4.13$, $p = 0.043$). Solid symbols are means from experimental groups from raw data; empty symbols are means from control groups. The solid and dotted lines show the predicted means \pm s.e. from a GLMM for experimental and control groups, respectively. Filled circles, AZ; filled up-triangles, CD; filled down-triangles, D; filled squares, E; filled diamonds, KU; crosses, W; Stars, ZZ; open circles, F; open up-triangles, L; dashed lines, control; solid line, experiment.

positive landmarks chosen in experimental groups declined from a mean of 87 per cent on the first session day to approximately 50 per cent by the eighth day (figure 2; GLMM: session \times treatment: $\chi^2 = 4.13$, $p = 0.043$; tables S1 and S2 in electronic supplementary material). Controlling for these effects, old individuals chose a higher proportion of positive landmarks than young individuals ($\chi^2 = 10.32$, $p < 0.001$).

4. DISCUSSION

Arbitrary preferences spread and maintained through social learning are common in humans (Boyd & Richerson 1985; Richerson & Boyd 2005). Here, we show that a preference for landmarks used by knowledgeable conspecifics leads to the establishment of a simple tradition in wild meerkats. However, unlike many arbitrary human traditions whose durability can extend through generations, the traditional preference in our experiments collapsed over the course of a few days.

Most naive meerkats ignored the landmarks when they first encountered them. There was no indication that they actively avoided the landmarks or showed fearful responses towards them; merely that they were unlikely to interrupt their foraging to investigate the novel stimuli. However, encountering another meerkat at the landmarks increased the probability that individuals would approach and obtain rewards, and individuals were consequently more likely to do so the next time they came across the landmarks when alone. The presence of a conspecific at the landmarks therefore acted as a form of stimulus enhancement (Spence 1937), drawing attention to the specific characteristics of the stimulus and promoting future interaction. Individuals in control groups that lacked the example of trained demonstrators, were less likely to obtain rewards than those in experimental groups.

Individual variation was also partly explained by age, as young animals were most likely to obtain rewards, perhaps because of higher levels of explorative behaviour (Menzel 1965) or higher motivation to find food to meet the energetic requirements of growth (Reader & Laland 2001).

Naive individuals showed no initial preference for either landmark. By contrast, meerkats that came across the landmarks after having joined a demonstrator at the positive landmark showed a significant preference for that landmark. As more individuals learned to approach and obtain rewards from the landmarks, they too could serve as models. During the course of the experiment, individuals were disproportionately likely to copy the choices of meerkats they recently encountered at the landmarks, but were significantly more likely to approach old individuals than young ones. This preference may arise because animals are less likely to be reliable sources of foraging information if their own skills are relatively undeveloped. Such preferences are likely to have important effects on transmission dynamics in natural populations (Coussi-Korbel & Frigaszy 1995). However, in contrast to theoretical and empirical studies suggesting that high-status individuals should be the most influential sources of information (Nicol & Pope 1999; Henrich & Gil-White 2001; Laland 2004), we found no evidence that meerkats preferentially joined dominants over subordinates. This is likely to reflect a trade-off between the potential informational benefits of joining dominants, who typically show high foraging success (Barnard 2000), and the risks being attacked by dominants (Kutsukake & Clutton-Brock 2006, 2008).

The pattern of meerkats' choices over the course of the experiment clearly illustrates the rise and fall of a simple tradition (*sensu* Frigaszy & Perry 2003). While landmark choices remained approximately 50 per cent for the duration of the experiment in control groups, preferences for the option chosen by demonstrators led to the establishment of a traditional bias towards the positive landmark in experimental groups. However, these differences were not maintained. As individuals learned about one landmark, they began to explore the other and learn that it was equally profitable, so traditions degenerated as the experiment progressed.

These results suggest that preferences for the choices of others can lead to the establishment of local arbitrary traditions in wild meerkat groups. However, rather than promoting long-term adherence to the behaviour of the majority, social learning about one landmark made formerly naive meerkats more likely to explore and learn about the other. As both options were equally rewarded and could be explored at little cost, choices became increasingly random and group-level preferences died out. We suspect that such effects, whereby a social stimulus promotes learning about one option, but thereby increases exploration and learning about similar alternatives, may be common in nature. Such effects may cause patterns of establishment and persistence of traditional behaviours in natural populations to differ from those found in captivity, where group members are closely confined and opportunities for individual learning may be limited. Indeed, where laboratory animals are given extensive opportunities for individual learning, traditions may be considerably less likely to persist (Galef & Whiskin 1997).

The maintenance of traditions in natural populations is likely to depend on both the inclination to copy the behaviour of others and motivation for individual exploration. In humans, a strong tendency to conform to the behaviour of the majority can facilitate the persistence of arbitrary traditions, even if equally profitable alternatives exist (Jacobs & Campbell 1961; Richerson & Boyd 2005). Laboratory studies of chimpanzees have found similar effects (Whiten *et al.* 2005; Bonnie *et al.* 2007) and in rats socially acquired information can override individual experience of toxic or unpalatable foods (Galef & Whiskin 2008). However, instances of non-human animals conforming to the behaviour of others, regardless of the ease and potential benefits of individual exploration, remain rare and poorly understood and have never been examined experimentally in natural populations. Such conformity, if it occurs in the wild, may be limited to contexts such as complex tool use that is difficult to learn alone or gestural conventions conferring social prestige (Perry *et al.* 2003).

This study supports the contention that, in the absence of strong conformist biases, the persistence of traditions in non-human animal populations hinges on the relative influence of social and individual learning (Galef & Whiskin 1997). While social learning causes individuals to adopt the same behaviour as others in the population, individual learning can lead to the discovery of alternatives, thereby reducing the stability of traditions. In certain cases, such as when individual exploration carries considerable risk (Kendal *et al.* 2005), social learning can provide important advantages and traditions may be maintained. However, when opportunities for individual learning are abundant, traditions will tend to die out. Arbitrary traditions may occur in nature, but they are likely to be fleeting and ephemeral.

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