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Report

Imitation and Traditions in Wild Banded Mongooses

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Summary

Evidence has accumulated in recent years indicating that traditions are not a unique feature of human societies but may be common in primates and some other mammals [1–8]. However, most documented cases remain contentious because observational studies of free-living animals suffer from interpretive weaknesses [9, 10], whereas social diffusion experiments performed in captivity (e.g., [6–8]) may not reflect conditions found in nature [2, 10]. Here we use experiments under natural conditions to demonstrate that wild banded mongooses (*Mungos mungo*) pass preferences for one of two possible foraging techniques on to the next generation through contextual imitation. Notably, both techniques coexisted within the same groups and were transmitted concurrently between adults and pups, which form close one-to-one associations during the period of pup dependency. This experimental demonstration of a foraging tradition in wild mammals provides critical evidence to support previous accounts of traditions in nonhuman animals based on distribution patterns of natural behaviors [1–4]. Moreover, our data provide the first experimental demonstration of imitation in wild mammals and, contrary to common assumption [9, 11], show that social learning need not lead to an increased behavioral homogeneity within groups.

Results and Discussion

Human traditions are ubiquitous and play a central role in our societies, but it remains unclear to what extent this phenomenon is unique to humans or shared with nonhuman animals. Behavioral traditions, defined as enduring behavioral practices that are shared by several individuals of a species and transmitted through social learning [12], have been studied widely in nonhuman animals via two main approaches. Observational studies (using an ethnographic method or method of exclusion) show a rich picture of differences in behavioral repertoires between populations of primates and cetaceans that cannot easily be explained by genetic or ecological factors [1–4], and a recent experiment shows that such population-specific behavior is maintained when a novel task is presented [13]. Yet these studies do not provide direct evidence that social learning is involved in the transmission of behavioral variants between individuals [9, 10, 14]. In addition, carefully controlled experiments with captive primates show evidence for faithful cultural transmission of behavioral variants over multiple transmission steps [6–8, 15]. However, experimental evidence for traditions in wild mammals is lacking to date, and it is therefore unclear whether cultural transmission mechanisms identified in captive studies actually play a role in shaping behavioral differences between individuals and populations in nature, evidence that is crucial for claims of traditions in wild animals. Likewise, imitation of foraging strategies has been demonstrated in captive mammals and birds [16, 17] (although see [18] for an alternative interpretation), but evidence from wild populations is lacking.

Our experiment bridges the gap between population-level studies of wild animals based on observational data and experimental studies conducted in captivity by transferring the powerful two-action method commonly used with captive animals [17] to a population of wild mammals. In this approach, individuals observe a conspecific accessing a food reward via one of two possible techniques, and it is then tested whether the observers match the witnessed technique. We collected data on five groups of wild but habituated and individually marked banded mongooses in Queen Elizabeth National Park, Uganda. In total, 127 individuals contributed to at least one of the analyses presented. In each group, some individuals observed one foraging technique and others the second technique. In addition to increased ecological validity, this experiment thus includes replication at the level of the group that is often missing in captive studies, which are typically restricted to single social groups. Furthermore, the within-groups design allowed us to exclude even subtle ecological differences as explanations for variation in the technique preferred.

Banded mongooses are small (<2 kg) carnivores that live in male-biased groups of 5–40 individuals [19]. They are particularly interesting for studies of social learning because dependent pups form exclusive one-to-one associations with providers (known as “escorts”), who are typically young nonbreeding adult males [20, 21]. Pups spend most of the time during foraging immediately next to their escorts and aggressively monopolize access to them [22]. Mean relatedness between an escort and its associated pup (r = 0.28 ± 0.04, n = 40) is only marginally higher than the relatedness between the escort and other pups in the same litter (r = 0.20 ± 0.05) [23]. This system is therefore ideally suited to study information transfer in discrete pup-adult dyads.

Banded mongooses feed on a wide range of prey species, some of which require extractive foraging. Prey items with a hard shell, such as bird eggs or rhinoceros beetles, are cracked either with the mouth while holding them in place with the front paws (the biting technique) or by hurling them against a hard surface such as a stone or the stem of a tree (the smashing technique) [24]. We took advantage of this natural behavior to design a novel food item, a modified Kinder egg plastic container (Figure 1) containing a mix of rice and fish, which could be opened via either of the two described techniques (see Supplemental Experimental Procedures available online for details and Movie S1 and Movie S2 for example video clips).

The artificial food item was first presented to adults in the absence of pups to determine their preferences for the two opening techniques. We found that adults differ markedly in

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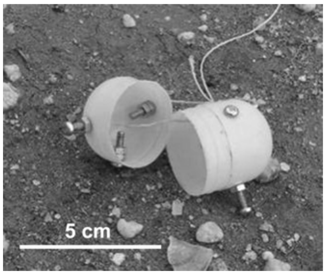

Figure 1. Artificial Food Item

The modified Kinder egg plastic container could be opened via either the smashing or the biting technique.

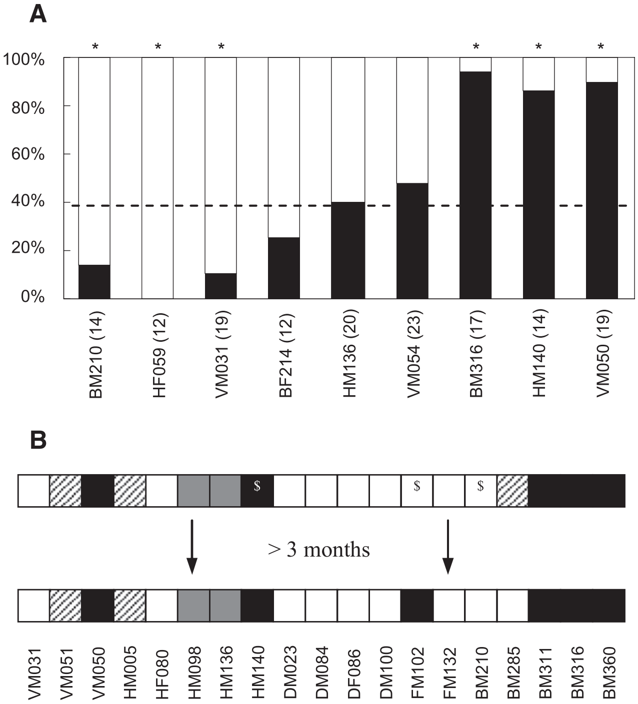

Figure 2. Adult Preferences for Opening Techniques

(A) Percentage of trials during which nine adults (chosen to illustrate population and within-group variation in opening techniques) in three groups used the smashing technique (black) or only the biting technique (white). Number of trials per individual is given in brackets. The dashed line indicates the population average for use of the smashing technique. *$p < 0.05$, significantly different from population average.

(B) Preferences of 19 adults for two seasons separated by >3 months. Black: smashing technique preferred; white: biting technique preferred; gray: no preference; hatched: no interest. $ represents one trial short of significance (see also Supplemental Experimental Procedures). ID codes given include group membership (B, D, F, H, V) and gender (M, male; F, female).

their use of the two techniques, with some individuals almost exclusively employing the biting technique, others preferring the smashing technique, and again others using both techniques about equally (preferences for nine individuals are shown in Figure 2A). Notably, both preferences occurred within the same groups. Preferences were stable over time: after a period of at least 3 months without exposure to the food item, only 2 of the 19 individuals for which sufficient data was available changed their preference (Figure 2B), significantly less than expected by chance (randomization test, $p < 0.001$).

Individual preferences therefore fulfill the longevity requirement for a behavioral tradition [12], but are they passed on from adults to pups through social learning? To test this, we assigned dependent pups to one of four categories, depending on what they observed their escorts do with the food item: in two categories, the pups repeatedly observed their escort opening the artificial food item, employing either the smashing technique ("Smash" category) or the biting technique ("Bite" category), and licking out the contents; in the remaining two categories, pups were either presented with already-open food items ("Open" category; these open items also contained the rice-and-fish mix) or did not encounter the food items at all ("None" category). Taken together, these categories allowed us to test for transmission of preferences via contextual imitation (Smash category versus Bite category)—that is, whether the mongooses learn to employ a particular technique that is already part of their behavioral repertoire in a specific context (as opposed to production imitation, in which a novel action is learned) [18, 25, 26]. They also allowed us to evaluate stimulus enhancement [26, 27] (None category versus Open, Bite, and Smash categories). A fifth, unplanned category arose because some pups associated with adults that did not show any interest in the food items, even though they clearly smelled of food. These pups observed their escort inspecting and then ignoring the food item without attempting to open it ("Ignore" category, see Movie S3 for an example video clip). For each pup, 10 trials spread over 2–4 weeks were conducted in this observation phase. All demonstrating escorts reliably used the appropriate technique (see Experimental Procedures for details).

Forty-two pups survived to the subsequent test phase, 2–4 months after the last trial of the observation phase, and were now, as independent juveniles, themselves presented with the artificial food item (10 trials per individual spread over 2–5 weeks). At this age, the mongooses have a low chance of opening the food items (see Supplemental Results for details). None of the juveniles had encountered the food item between the observation phase and the test phase, and none of them had opened one before the start of the test phase. Juveniles of the four planned categories showed equal interest in the food item (Figure 3). That is, there was no evidence for stimulus enhancement, which might be explained by general neophilia of young mongooses toward novel objects. However, juveniles of the Ignore category showed significantly less interest in the item than the individuals of the other categories (generalized linear mixed model [GLMM], $t_{37} = -3.08$, $p = 0.004$), suggesting instead an inverse social learning effect, which one might term "stimulus inhibition" (not to confuse with negative enhancement [28], which is a type of avoidance learning). Notably, both the uninterested juveniles and their escorts unhesitatingly consumed the contents of the food item if encountering an open one and sometimes even tried to steal one after it had been opened by another group member. Thus, their ignoring of the food item cannot be explained as avoidance of a food that is considered unpalatable.

Crucially, the juveniles copied the technique they had observed as pups and continued to prefer this technique into adulthood. Juveniles of the Smash category were significantly more likely to use the smashing technique themselves than juveniles of the Bite category (GLMM, $t_8 = 3.02$, $p = 0.017$; Figure 4). This difference persisted when the individuals were

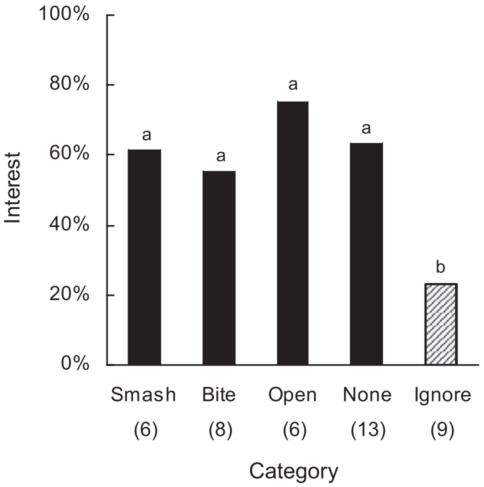

Figure 3. Juveniles' Interest in Food Items during Test Phase

Shown is the percentage of trials during which the focal animal handled the food item for at least 20 s. Hatched: unplanned category. The number of individuals per category is given in brackets. a versus b: $p < 0.01$.

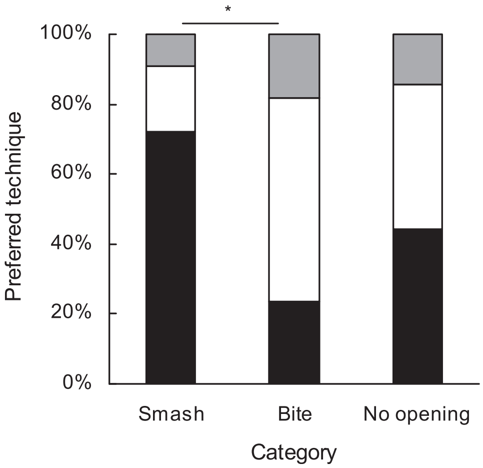

Figure 4. Juveniles' Preferences for Opening Techniques

Percentage of test trials during which the smashing technique was preferred (black), the biting technique was preferred (white), or no preference occurred (gray). The "No opening" category combines categories Open and None. *$p < 0.05$.

retested as yearlings (4–10 months after the last trial as juveniles, five surviving individuals per category; GLMM, $t_6 = 3.43$, $p = 0.014$). Individuals of the Open and None categories, on the other hand, used both techniques about equally (Figure 4). Juveniles that had not observed any opening of the food item as pups (Open and None categories) but had associated with an escort that significantly preferred the smashing technique (cf. Figure 2A) did not show such a preference (GLMM, $t_{11} = 0.014$, $p = 0.99$). Therefore, the copying effect cannot be explained by pups associating with adults that may have used one of the two techniques preferentially with natural food items. This result also rules out the alternative explanation that matching occurs because pups might preferentially associate with closer relatives or with adults of similar personality, because in these scenarios, juveniles from the Open and None categories would also be predicted to match the preferred technique of their escorts. Furthermore, when smashing, juveniles typically did so on the ground where they encountered the food item rather than on a suitable anvil (see Supplemental Results for details), indicating that they copied the smashing action rather than seeking to reconstitute a spatial arrangement of food object and anvil observed during the observation phase.

The presented data provide the first experimental evidence for a foraging tradition transmitted from one generation to the next in a wild mammal population and offer critical support for earlier claims of culturally transmitted foraging specializations derived from observational studies of large-brained primates and cetaceans [1–4]. Our data from a comparatively small-brained carnivore species further suggest that foraging traditions occur more widely than is reflected by the current focus of research (see also [29, 30] for traditions in the choice of mating sites and traveling routes in coral reef fish).

Three factors may explain why evidence for a long-term tradition was found here but not in a small number of earlier experimental studies in wild birds or mammals [31–33]. First, the tasks presented in the previous studies could easily and quickly be learned by trial and error, which probably contributed to the rapid erosion of biases introduced by social learning [33], as theoretical models predict [34]. In contrast, opening of the food item used here required substantial experience, reflected by the low success rate of the juveniles during the test phase (16%; see Supplemental Results for details). Second, our study did not require animals to learn a novel action, but rather required them to apply an action that was already part of the behavioral repertoire to a novel food object (i.e., contextual imitation). Third, our study was aimed at vertical transmission from adults to pups, rather than at horizontal transmission between adults, and young, inexperienced individuals are more likely to rely on social learning than are experienced adults [34–36].

Studies of foraging traditions are typically based on the premise that social learning results in uniform behavior within groups and in differences in behavior between groups or populations, because individuals in a group learn from each other [1, 2, 4, 9]. Our study contradicts this widespread assumption and shows that multiple traditions can coexist and be transmitted in parallel within the same group if observers copy particular role models [37] (see also [36, 38]). This finding has major implications for attempts to identify traditions based on patterns of occurrence of a behavioral variant [9, 11] and stresses the need to consider association patterns between individuals when formulating predictions [39].

Transmission of preference for the opening techniques from demonstrators to observers in our two-action task is best explained by contextual imitation. Stimulus enhancement leading to a generally increased interest in the food items cannot explain these results. Furthermore, because the mongooses were tested after a delay of several months and had no opportunity to open a food item themselves prior to the start of the test phase, we can rule out response facilitation as an alternative account to imitation [18]. Our study therefore provides the best evidence to date for contextual imitation in a wild mammal (though we cannot categorically rule out the possibility that an unmeasured proximate cue, such as the relative distribution of saliva deposited by demonstrators on the food item, may have influenced our results). Unlike studies that demonstrated imitation in captive animals [16, 40], in which observers are typically tested immediately after a large number of demonstrations with short intervals, our study provides evidence for a robust long-term effect. Finally, because the task presented was directly relevant to the mongooses' natural behavior, our data provide long-missing evidence [10] that copying of motor skills is a strategy used by animals subjected to the selection pressures of their natural environment rather than a latent capacity shown only by animals released from natural selection in captivity.

Experimental Procedures

Procedures

In both the observation and the test phase, trials started with the presentation of the food item to the focal individual and ended either when the item was opened and emptied or when the individual lost interest in it and wandered off. Trials were not started until the focal individual(s) were separated from the rest of the group by several meters to avoid possible interference through foraging competition. Potential anvils were always present within at most 10 m of the place where the object was presented, but never closer than 1 m. All food items were recovered immediately after the focal individual had abandoned them. No more than two trials per individual were conducted per day. Observation trials took place while pups formed stable associations with their escorts (at the age of 6–11 weeks) and after associations had been stable for at least 3 days. Demonstrators in the Bite category used the biting technique in 100% of the trials and never used the smashing technique; demonstrators in the Smash category used the smashing technique in 60%–100% of the trials. The food item was opened in 82% these trials. Demonstrators in the Ignore category did not show interest in the food item in at least 80% of the trials and never opened one. Pups in the Smash, Bite, and Open categories inspected the open object in 72% of the observation trials (range 30%–100%, no difference between categories; general linear model, $F_{2,\ 17} = 1.42$, $p = 0.27$) and obtained food from the open object in 36% of the trials (range 0%–90%, no difference between categories; GLM, $F_{2,\ 17} = 0.86$, $p = 0.44$).

Coding

All trials were recorded on video. The use of the smashing and the biting technique could reliably be determined from video clips. An individual was considered to be showing no interest in a particular trial if it handled the food item for less than 20 s without opening it. Juveniles were considered to have a preference for either the biting or the smashing technique within a trial if they used one technique at least twice as often as the other within the trial (number of opening attempts per trial: mean 7.9, range 4–23), yielding one data point per trial. Interobserver reliability based on 50 trials was 98% for the preferential technique used (bite, smash, no preference) and 96% for interest (yes or no).

Statistics

Adults were considered to exhibit a preference (across trials) if they used one of the two techniques significantly more often than the population average of 61% biting and 39% smashing (binomial test). The number of individuals retaining their preference after a break of several months was compared to the number expected by chance when each individual was randomly assigned to one of the observed categories (randomization with 10,000 runs; see Supplemental Experimental Procedures for details). The juveniles' interest in the food item and preference for an opening technique were compared between categories by using GLMMs with binomial error structure. Group and individual nested within group were included as random factors to account for repeated measures. For the analysis of opening techniques, trials without a clear preference (14% of trials), as well as no-interest trials, were considered null values and were thus not included in the model. An alternative approach for the analysis of opening techniques, in which each opening attempt is treated as a separate data point and in which trial number is included as an additional random factor (nested within individual), yielded the same, significant outcome. Generalized linear mixed models were performed in R 2.8.0 [41] with package MASS [42].

Supplemental Information

Supplemental Information includes Supplemental Results, Supplemental Experimental Procedures, and three movies and can be found with this article online at doi:10.1016/j.cub.2010.04.037.

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