

Wild vervet monkey infants acquire the food-processing variants of their mothers

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In the ability and motivation to copy others, social learning has been shown to provide a mechanism for the inheritance of behavioural traditions. Major questions remain about the circumstances and models that shape such social learning. Here, we demonstrate that behavioural food-processing variants among wild vervet monkey, *Chlorocebus aethiops*, mothers are matched by their infants in their first manipulative approaches to a new foraging problem. In our field experiment, grapes covered with sand were provisioned within groups of wild vervet monkeys that included experienced adults and 17 naïve infants. Monkeys dealt with the dirty food in four different ways. All infants first adopted their mother's way of handling the grapes, rather than those of other mothers or other monkeys eating nearby. Mothers who handled grapes in different ways had infants who were more likely to explore different approaches to handle the sandy grapes. Rarer cases of co-feeding siblings further suggest that copying may occur on the matriline level. Our findings suggest a capacity for detailed copying by infants of their mothers' and matriline members' food-processing techniques when encountering new foods, underlining the significance of familial models in such primate social groups.

How much of their behavioural repertoires do animals learn from others? To what extent does such social learning provide a 'second inheritance system' (Whiten, 2005) allowing faster adaptation than genetic change? Such questions have attracted increasing attention in the life sciences (Kendal, Galef, & van Schaik, 2010; Mesoudi, 2011; Nielsen, Subiaul, Galef, Zentall, & Whiten, 2012; Whiten, Hinde, Stringer, & Laland, 2011) and related disciplines (Pagel, 2012; Ramsey, 2013; Sterelny, 2012) with animal social-learning research spanning a diverse range of vertebrate and invertebrate groups (Allen, Weinrich, Hoppitt, & Rendell, 2013; Franklin & Franks, 2013; Franks & Marshall, 2013; Slagsvold, Kleiven, Eriksen, & Johannessen, 2013; Wright, Wilkinson, & Moss, 2012). Observations in the wild have revealed numerous putative traditions in natural populations of primates, cetaceans and other taxa (Allen et al., 2013; Hopper & Whiten, 2012; Hoppitt & Laland, 2013).

Cultural diffusion experiments, in which alternative behaviour patterns such as foraging techniques are initially seeded in only single individuals in different groups, have demonstrated the

spread of new traditions through social learning in primates (e.g. chimpanzees, *Pan troglodytes*: Whiten, Horner, & de Waal, 2005; Whiten et al., 2007; capuchins, *Cebus apella*: Dindo, Thierry, & Whiten, 2008; Dindo, de Waal, & Whiten, 2009; vervets, *Chlorocebus aethiops*: van de Waal, Claidière, & Whiten, 2013; van de Waal & Whiten, 2012). However, such studies have been largely restricted to captive populations, as have a small corpus of such experiments with other mammals (e.g. rats, *Rattus norvegicus*: Galef & Allen, 1995; Laland & Plotkin, 1992), birds (e.g. blackbirds, *Turdus merula*: Curio, Ulrich, & Vieth, 1978; cowbirds, *Molothrus ater*: Freeberg, King, & West, 2001) and fish (e.g. guppies, *Poecilia reticulata*: Laland & Williams, 1997); for a review see Whiten and Mesoudi (2008). One of the principal remaining challenges is to complete similar experimental tests of social learning and cultural transmission in wild animals, typically a more challenging enterprise (Slagsvold & Wiebe, 2011; Thornton & Clutton-Brock, 2011). Field experiments remain rare, but already cover taxa ranging from fish to birds and suricates (Helfman & Schultz, 1984; Langen, 1996; Lefebvre, 1986; Thornton & Malapert, 2009; Warner, 1988; for a review see Reader & Biro, 2010). Such experiments on primates have only recently been completed, demonstrating social learning in the wild (ring-tailed lemurs, *Lemur catta*: Kendal, Custance, et al., 2010; Schnoell & Fichtel, 2012; vervets: van de Waal, Borgeaud, & Whiten, 2013; van de Waal & Bshary, 2011; van de Waal, Krützen,

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Hula, Goudet, & Bshary, 2012; van de Waal, Renevey, Favre, & Bshary, 2010). Since these studies seeded alternative behaviour patterns and monitored their spread in groups, the social learning they have identified is 'horizontal', between individuals belonging to a single generation, who may or may not be closely related.

However, it is likely that one of the most common pathways of social learning in the wild is the 'vertical' one from caretaker to offspring, which is not addressed by the kinds of diffusion experiments noted above. In cooperatively breeding species, such vertical transmission may also involve helpers (Müller & Cant, 2010; Raihani & Ridley, 2008; Thornton, 2008), but in other cases, mothers typically appear to play a primary role. For example, in white-tailed ptarmigans, *Lagopus leucura*, mothers use calls to indicate high-quality food sources to offspring, and the latter maintain a preference for these food sources after maternal 'teaching' has stopped (Clarke, 2010). In primates, detailed studies have revealed predicted dietary correlations between mother–infant pairs in wild orang-utans, *Pongo pygmaeus* (Jaeggi et al., 2010) and correlations in termite-fishing techniques (notably depth of probe insertion) between mother and daughter chimpanzees (Lonsdorf, Eberly, & Pusey, 2004). Field experiments on vervet monkey infants suggest that they copy the feeding preferences of their mother, although a potential role of additional group members who generally share the same preference could not be excluded (van de Waal, Borgeaud, et al., 2013). In this study we examined familial matching not in wild vervets' food choices, but in the more complex domain of food-processing techniques

Our experimental method was based on the famous sweet potato washing studies of Japanese macaques, *Macaca fuscata* (Kawai, 1965). In a previous study, we offered grapes made dirty with sand to groups of vervets and recorded the emergence of four different approaches to cleaning that showed significant similarities within, rather than between, matriline (van de Waal et al., 2012). In this study we focused more specifically on the closest relationship, that between mother and infant, analysing the responses of 17 infants who were naïve to the experimental protocol. Based on earlier observations, our hypothesis was that infants would first join the experiment when their mother was feeding and match their mother's manipulative approach, even if other group members were eating simultaneously and possibly exhibiting alternative methods.

METHODS

Study Animals and Experimental Procedure

Experiments were conducted between 2007 and 2010 on six neighbouring groups of habituated wild vervet monkeys at Loskop Dam Nature Reserve, Mpumalanga Province, South Africa. We provided each group with a plastic box containing grapes covered with sand (100 g of sand for 2 kg of grapes that were shaken together in the closed plastic box to ensure that all grapes were sandy) in quantities that varied depending on group size and composition such that even subordinates could eventually get access to the food, typically after dominant individuals had finished eating. For each group we conducted 15 experimental sessions spaced over 9–15 months, and a final session after a 1-year gap. We used focal sampling to record how each of the 104 individuals in these groups processed 10 grapes in each session. All sessions were videotaped, and later used to complete data sets on individuals for whom we had not directly observed 10 grapes being processed. To examine the behaviour of only naïve infants we conducted experiments separated by a minimum of 4 months. This meant that infants could not observe experimental sessions before 3 months of age when they start to take solid food.

We distinguished four highly discriminable approaches to cleaning: (1) Rub-hands (rubbing the grape in the hands), (2) Rub-substrate (rubbing the grapes on a substrate including the ground, branches, stones, plastic box), (3) Open-mouth (opening the grape with the teeth and eating the inside without the peel), and (4) Open-hands (opening the grape with the hands and eating the inside without the peel). Some monkeys ate the grapes directly with the sand, called 'No cleaning' (van de Waal et al., 2012). Because of the latter it seems inappropriate to call all the different behaviours 'techniques' and instead we describe them simply as 'approaches'.

Data Coding, Analyses and Statistics

We analysed the feeding approaches of 17 infants aged 4–8 months of age from four different groups (Bay, Blesbokvlakte, Donga and Picnic groups), who were observed during their first encounters with sandy food. Two observers in the field recorded how these infants dealt with their first 10 sandy grapes. As the different approaches used different body part or substrates, they could be coded unambiguously. From video, the methods used by the mother and any neighbours (any monkey feeding at the box at the same time) during this same period were coded. We first compared the approach applied by the infant to its first grape with that used by the mother directly beforehand. Next, considering the first 10 grapes eaten, we created an index of similarity between each infant's approaches and its mother's by awarding one point for each grape processed using the same approach by both parties. We compared the mother–infant similarity score with the mean index of infant similarity to other members of the group eating in the same period. We divided the other group members into two categories: matriline members (siblings) and others (nonmatriline members, unrelated).

To test the probability of observed similarities in behavioural profiles between mothers and their infants arising by chance, we carried out two randomization tests. The test statistic in both was the mean Euclidean distance between the behavioural profiles of mother and infant across all mother/infant pairs (with profiles represented as four-element vectors and the Euclidean distance being the square root of the summed squared differences at each position in the vectors). In the first test we randomized mother/infant pairings, so in each randomization each mother was paired with a randomly selected infant (sampled without replacement from the 17 available). In the second test we randomly assigned approach occurrences to each infant, by permuting the 17×4 matrix of approach usage counts (infant \times approach) while preserving the row and column sums (i.e. each infant still consumed exactly 10 grapes and each approach was used the same number of times as in the observed data). In each test we ran 100 000 randomization trials, giving a precision of 0.00001, and used the proportion of trials in which the average distance between mother/infant pairs was less (i.e. the profiles were more similar) than the observed value as the test *P* value. These tests were run in R (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>), using the 'vegan' package for matrix permutations.

We compared the number of different approaches used by the mother and by the infant for the 10 grapes, as well as the variation in approach between the first grape and all 10, through Spearman rank correlations across infant–mother pairs. These statistical analyses employed nonparametric tests using IBM SPSS Statistics 21.0 (SPSS Inc., Chicago, IL, U.S.A.).

Ethical Note

Our set-up involved some feeding competition, which has the potential to increase rates of aggressive encounters. However,

while aggression is known to induce social stress, our experimental set-up involved feeding in enough quantities for all group members to gain access. The consumption of high-quality food should have reduced stress related to energetic needs and hence partly compensated for any effects of social stress. Our experiments were approved by ABERRU boards of UNISA as well as the Park Boards of the Mpumalanga Province, South Africa.

RESULTS

Four different approaches were used by infants: Rub-hands, Rub-substrate, Open-mouth and No cleaning. Of the 17 infants studied, 16 ate their first sandy grape using the same approach as their mother had used immediately beforehand (see the [Supplementary video](#) for an example). The mother of one infant (Ivy) had disappeared, but this infant ate with her older sister, India. Since India was already a mother, and the infant slept with her and was groomed by her at maternal levels, we treated India as Ivy's 'mother-substitute' (results remain robust if this pair is excluded; statistics not shown here). Ivy first ate using the approach of this sister. Accordingly, 17/17 infants first used the approach used by their mother or mother-substitute. In their first approaches, 10 mother–infant pairs used Rub-hands, one Rub-substrate and six No cleaning. Grouping these data as 11 mother–infant pairs cleaning versus six No cleaning, we found a significant link between maternal and infant approaches to food cleaning (Fisher's exact test: $N = 17$, 11:0 versus 0:6, $P < 0.0001$).

Another way to quantify similarity between mother and offspring is to focus on those mothers that showed variation in approach techniques in the 10-grape data set and ask how likely it would be that the infants matched the approach the mother was using just before each infant ate its first grape. Nine mothers showed variation, and the way these mothers approached their grape immediately before their infants' first grape represented on average 66.7% of mothers' approach techniques during the 10 observations. The observed 100% matching by the infant (9/9) was thus significantly higher than expected based on mothers' repertoires (binomial test: $N = 9$, expectation = 0.67, observed = 1, $P = 0.027$).

Comparing observed infant and maternal behavioural profiles across the first 10 grapes infants dealt with (Fig. 1) to the permuted data sets revealed a significantly higher similarity between

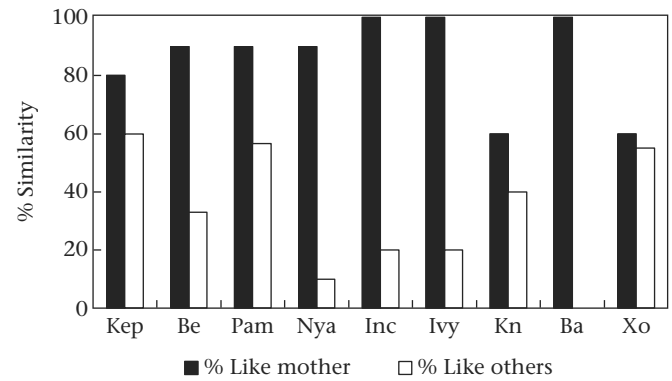


Figure 2. Percentage similarity between approaches used by infants (name code: 2 letters = male, 3 letters = female) and their mother versus other group members. The latter data were only available for this subset of infants.

mothers and infants (smaller average mother/infant distance) than expected by either randomization test (for both tests $P < 0.00001$). This means the probability of obtaining the observed levels of similarity between mother/infant behavioural profiles by chance is vanishingly small either if infants are randomly paired with mothers or instances of each type of approach are randomly distributed across infants.

To investigate whether infants were specifically focusing on their mothers' approach we compared infant–mother similarities for the 10 grapes with similarities between infants and simultaneously foraging group members. We found that infant–mother similarities were significantly greater than between infants and other nonmatriline group members (Wilcoxon signed-ranks test: $Z = -3.684$, $N = 9$, $P < 0.001$; Fig. 2).

The number of approaches used by mothers (see Fig. 1) also predicted the number used by their infants (Spearman correlation: $r_s = 0.542$, $N = 17$, $P = 0.025$). Mothers that varied their cleaning methods (percentage variation in relation to first grape eaten) had infants who also varied their approaches in this way (Spearman correlation: $r_s = 0.675$, $N = 17$, $P = 0.003$).

Three infants had a total of five siblings. In these cases, the similarities between infants and siblings exactly matched the similarity between infants and mothers (80% on average, see Fig. 1). The repertoire size of approaches was numerically more similar

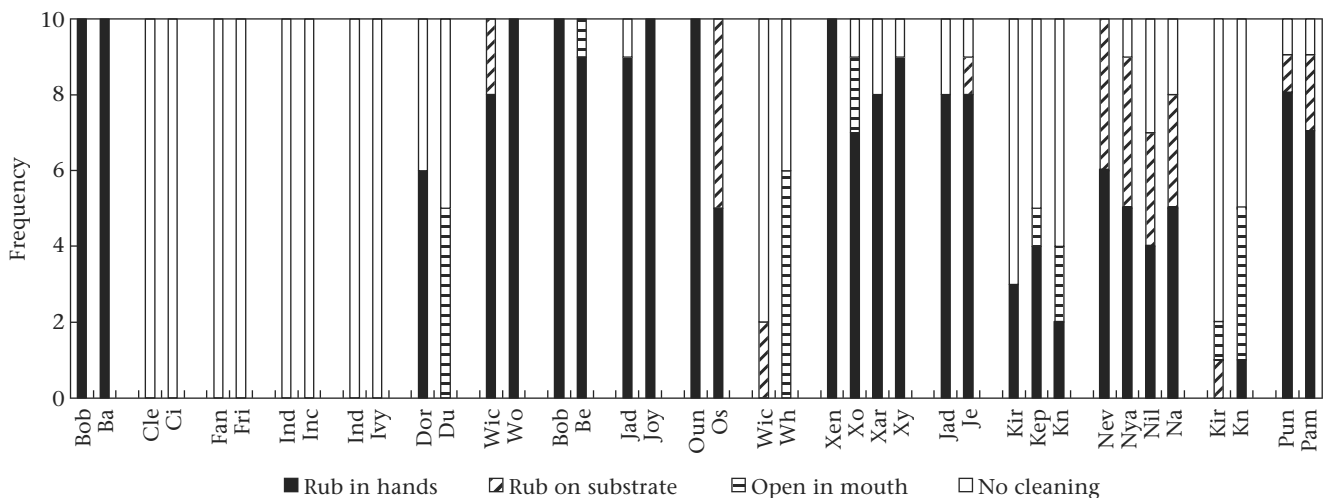


Figure 1. Use of four different approaches by mothers and their infants when the infants deal with their first 10 grapes. When siblings were eating simultaneously they are also represented after the infant. Name code: first mother, second infant (2 letters = male, 3 letters = female); siblings (matriline members have same first letter).

between infants and their siblings than between infants and their mothers (Fig. 1) but the sample is too small to assess whether this difference is statistically reliable.

DISCUSSION

We exploited knowledge gained from an earlier study showing that vervet monkeys approach the problem of eating sandy grapes in various different ways, to complete experiments investigating how naïve infants would deal with the problem. We found that the way they approached the handling of their very first grape matched the way their mother handled the grape immediately before the event. Furthermore, approach methods (rubbing in hands, rubbing on substrate, open in mouth and no cleaning) were highly correlated between infant and mother but not between infant and other simultaneously foraging group members. Finally, there was a correlation between the number of different approaches used by mother and infant.

There are two principal alternative explanations for our results: infants' behaviour may match that of their mothers because infants learn from their mothers by observation (social learning) or because of genetic inheritance of underlying manipulative dispositions. Since vervet mothers often use more than one approach, a genetic effect would be expected to yield observed values of matching that correspond to the average overlap in approaches between mother and infant. Instead, the first grape ever eaten was invariably processed exactly the way the mother processed her grape immediately before the event, consistent with social learning.

More generally, several experiments have recently been conducted on both captive and wild vervet monkeys, and the emerging picture supports a potent role for social learning (van de Waal et al., 2010, 2012; van de Waal, Borgeaud, et al., 2013; van de Waal & Bshary, 2011; van de Waal, Claidière, et al., 2013; van de Waal & Whiten, 2012). That mothers may play a key role as a model for social learning was indicated by the initial grape-cleaning experiment in which similarities of approaches were evident on the level of matrilineal rather than between full adult sisters or across the entire group (van de Waal et al., 2012). Our current study has yielded results consistent with work on vervets in captivity, where it was found that they would adopt whichever of two alternative foraging techniques they witnessed; in one study the contrast involved oral versus manual opening of artificial fruits (van de Waal & Whiten, 2012) and in another it was between lifting a hatch in an artificial fruit or sliding it to left or right to extract food (van de Waal, Claidière, et al., 2013). Results of both studies showed social learning of handling techniques. These captive studies, as well as field experiments using artificial fruits (van de Waal et al., 2010) and field observations (Renevey, Bshary, & van de Waal, 2013), converge to suggest that vervet monkeys may learn socially from a range of 'role models', of which the mother is the primary one. Our recent experiments with wild vervets showed that all 27 infants tested would adopt whichever of two alternative food options their mother had learned to eat through experimental conditioning, hence precluding a genetic basis for the preference (van de Waal, Borgeaud, et al., 2013).

Our results add to a small cluster of recent findings indicating that social-learning effects can be sufficiently potent to create different 'subcultures' within the same group or community. Perhaps closest to the present study is one demonstrating consistency of techniques for grooming lice eggs from fur within matrilineal Japanese macaques, together with differences between matrilineal relationships in the techniques used (Tanaka, 1998). Going beyond matrilineal relationships, experiments have revealed consistencies in foraging techniques within subgroups of ring-tailed lemurs,

contrasting with differences between the subgroups (Kendal, Cusance, et al., 2010). Longitudinal, observational studies have shown capuchins adopting whichever of two techniques in their group they witness most as they grow up (Perry, 2009). A recent nonprimate example of socially learned intragroup differences in behaviour is the acquisition by young banded mongooses, *Mungos mungo*, of whichever of two foraging techniques is shown by an individual to which they apprentice themselves, in the same group (Müller & Cant, 2010).

These cases offer evidence for the hypothesized phenomenon of 'directed social learning' (Coussi-Korbel & Frigaszy, 1995), in which innovations diffuse not at random but through pathways shaped by the dynamics of the group's social network (Claidière, Messer, Hoppitt, & Whiten, 2013). Maternal to offspring 'vertical' transmission of the kind identified in the present study is likely to be the primary pathway in all primates, owing to the unique intimacy of the mother–infant relationship, with prolonged phases characterized by lactation, physical carrying and, later, close proximity during infants' early steps in foraging. A mother vervet monkey may present an optimal model for learning about foraging, since she has lived in the group range all her life, unlike the infant's siblings or males who migrate between groups, so her local knowledge will be superior. However, others may play a part in vertical transmission in different contexts. Our limited data on older siblings being present alongside the infants suggest that matriline membership could in fact represent an important context for social learning. Siblings are known to function as role models in cooperatively breeding species: in banded mongooses, young individuals learn socially from helpers how to crack open food items (Müller & Cant, 2010), and pied babbler, *Turdoides bicolor*, helpers 'teach' nestlings the meaning of food calls (Raihani & Ridley, 2008). However, these studies do not allow evaluation of the relative importance of the mother/parents and siblings. For vervet monkeys, a larger sample size will be needed to test this further. Confirmed cases of directed social learning from models other than the mother involve young male capuchin monkeys spending time watching adult males and learning from them in what may be a case of 'oblique' learning from nonmaternal members of the previous generation (Agostini & Visalberghi, 2005) and migrating male vervets are ready to copy the local foraging habits of new groups they enter, a form of 'horizontal' cultural transmission (van de Waal, Borgeaud, et al., 2013). As the feasibility of field experiments like those described here become recognized, we may anticipate the unravelling of what may be webs of directed social-learning effects among wild animals.

In conclusion, we have identified close matching between the ways in which infants first approach dealing with an experimentally induced foraging process and the immediately preceding style of approach displayed by their mothers. In conjunction with our other recent experiments with vervet monkeys revealing matching of manual versus oral foraging techniques (van de Waal and Whiten, 2012) and direction of manipulating artificial fruits (van de Waal, Claidière, et al., 2013), these results indicate that young monkeys may pay keener attention to details of other individuals' behaviour and their consequences, and copy these more faithfully, than previous research has suggested.

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Supplementary Material

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