

Social-learning abilities of wild vervet monkeys in a two-step task artificial fruit experiment

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Social learning is the basis for the formation of traditions in both human and nonhuman animals. Field observations and experiments provide evidence for the existence of traditions in animals but they do not address the underlying social-learning mechanisms. We used an established laboratory experimental paradigm, the artificial fruit design, to test for copying of a sequence of actions and local enhancement in six groups of wild vervet monkeys, *Chlorocebus aethiops*. We introduced a two-step task where models had to remove a bar to untie a rope that blocked a single door of a box. The models were high-ranking individuals that monopolized the box early on and discovered by trial and error how to open it. We obtained successful models in three groups, while the other three groups acted as controls. After 20 successful demonstrations, we tested subjects with a box that had a rope in the same position but the rope was not functional. Under these conditions, sequential copying of the two-step opening did not occur. Only individuals that were exposed to models were likely to touch the bar if door opening was not immediately successful, providing evidence for local enhancement. When we presented the boxes with the functional rope, we found no effect of having been exposed to a model on the probability that subjects solved the task. We conclude that the social-learning abilities of wild vervet monkeys are relatively limited and discuss potential problems concerning the technical difficulty of the task.

Keywords

artificial fruit, *Chlorocebus aethiops*, field experiment, local enhancement, manipulation task solving, social learning, tradition, vervet monkey

Efficient social learning plays an essential role in human life as it provides the basis for traditions and culture (Plotkin 2007). Thus, studying the roots of culture in other animals has been a key research topic for decades (Whiten 2009). Field studies on social learning have inferred its presence by providing evidence that nonhuman animals may have traditions. Three different approaches are prominent in the literature. First, researchers have noted naturally occurring novel individual behaviours and documented the spread of the behaviour in their study groups or study populations, such as potato washing in Japanese macaques, *Macaca fuscata* (Itani & Nishimura 1973), the opening of milk bottles by blue tits, *Cyanistes caeruleus* (Hinde & Fisher 1951) or song dialects in white-crowned sparrows, *Zonotrichia leucophrys* (Marler & Tamura 1964). Second, novel behaviours were experimentally introduced and their spread/persistence documented. Classic examples are the exchange of entire fish subpopulations and the subsequent recording of the formation and persistence of new spawning migrations (Helfman & Schultz 1984; Warner 1988) as well as the spread of novel food-finding behaviour in birds (Lefebvre 1986; Langen 1996). Recent studies in

the wild on meerkats, *Suricata suricatta* (Thornton & Malapert 2009) and marmosets, *Callithrix jacchus* (Pesendorfer et al. 2009) have tested whether initially useful specific techniques may persist once the experimenter allows alternative solutions to the problem. In the third approach, the existence of traditions has been inferred by identifying behaviours that are common in one population but absent in others while the differences do not seem to be based on differences in ecology. Examples include a variety of tool use behaviours such as nut cracking, termite fishing or sponge use in chimpanzees, *Pan troglodytes*, or the use of sticks in orang-utans, *Pongo pygmaeus* (Whiten et al. 1999; van Schaik et al. 2003).

While the field studies cited above provide strong support for the existence of social learning in wild animals, they do not allow conclusions to be drawn on what aspects of behaviour are learned socially and what aspects are learned individually. For example, an animal may learn socially only that an object or a location is interesting, but then it has to find out for itself how to gain benefits. Socially acquiring information about an object is called stimulus enhancement, while socially acquiring information about a location is called local enhancement (Hoppitt & Laland 2008). These supposedly simple social-learning mechanisms are contrasted with more cognitively demanding mechanisms such as the ability to learn socially a sequence of actions (sequence imitation) or the ability to learn socially a novel behaviour through imitation of the correct

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movements (production imitation; Hoppitt & Laland 2008). The realization that there are many forms of social-learning mechanisms and that observations cannot tell them apart (Heyes 1993) caused the development of sophisticated laboratory experiments, where key variables could be controlled by scientists. These laboratory experiments demonstrated that a variety of vertebrate species might be able to learn socially through production imitation (Laland & Plotkin 1990; Bonnie et al. 2006; Horner et al. 2006; Dindo et al. 2008). However, demonstrating that captive animals are able to learn socially in sophisticated ways does not necessarily imply that wild animals of the same species regularly use social learning to solve problems, or that they regularly imitate. The experiments in captivity were designed such that the experimental individuals were close to the demonstrator and not distracted by potential alternatives. In the field, animals may be more spread out, have alternative food sources and may need to look out for predators. In a study that tested social-learning mechanisms directly in captivity and in the field, kea, *Nestor notabilis*, failed to imitate in a task where imitation learning had been previously demonstrated in the laboratory (Gajdon et al. 2004). There is thus a clear need for more experimental field studies on the diversity of potential social-learning mechanisms.

Recently, van de Waal et al. (2010) provided the first direct evidence for social-learning mechanisms in wild primates using a standard experimental design in laboratory studies on primates: a baited box, called 'artificial fruit' (Whiten et al. 1996). In a 'two-door' experiment on vervet monkeys, *Chlorocebus aethiops*, trained models demonstrated the opening of either a pull or a slide door situated at colour-marked opposite ends of the box. During the experiment, subjects could open the box with either door. Van de Waal et al. (2010) found evidence that vervets used the same door as the model but only if the model was a female rather than a male. In addition, subjects were more likely to participate and thus manipulate the box if the model was a female. Thus, vervet monkeys appeared to pay selective attention to the philopatric sex (Cheney & Seyfarth 1983). In any case, the study provided evidence for both stimulus enhancement (increased participation) and local enhancement (touching the same door as the model) when models were females. Also, a few individuals successfully opened the box on the first trial (van de Waal & Bshary, in press). Thus, the technical difficulty of the task was considerable but solvable.

In this study, we extended the 'two-door' artificial fruit experiment carried out by van de Waal et al. (2010), in which the artificial fruit could be opened in a single step, by presenting a two-step artificial fruit task to wild vervet monkeys. The first step consisted of removing an aluminium bar held by two rings on top of the box because the bar held a rope that blocked a single door (Fig. 1). The second step consisted of opening the door by pulling on a knob. As in the previous artificial fruit experiment (van de Waal et al. 2010), a high-ranking individual soon monopolized the box in each group. Three individuals learned to solve the task through trial and error and became models, while three groups where dominants failed to learn to solve the task were used as control groups.

We used this experimental approach to ask three questions. First, as shown by van de Waal et al. (2010), we asked whether the identity of the model would affect the occurrence of social learning. As it turned out, we had one adult female, one juvenile female and one fully grown yet still resident male as models. Thus, sample sizes are small for each age/sex class and we simply describe how these variables may affect social learning. Second, we asked whether subjects copied sequential actions when they tried to open the box. This mechanism has been documented in chimpanzees (Whiten 1998). If vervet monkeys have this ability, we predicted that subjects in groups with a model would touch (and potentially remove) the bar before touching the door, while control animals should touch the knob immediately owing to their previous



Figure 1. Vervet 'Kira' interacting with the two-step task.

experience with the 'two-door' artificial fruit (van de Waal et al. 2010). In a first round of trials, the rope was in place but not functional, so that the door could be opened without prior removal of the bar. We had hoped that our models would differ in the way they removed the bar (such as pulling or pushing it out), so that we could have tested not only for imitation of a sequence of actions but also for the imitation of arbitrary movements (production imitation, Hoppitt & Laland 2008). However, all models pulled the stick and switched sides from where they pulled, excluding analyses on production imitation. In a second round of trials, the removal of the bar was mandatory for successful opening of the door. We anticipated that success would be low, as the one-step artificial fruit experiment had already yielded relatively low success rates (van de Waal & Bshary, in press). Thus, we asked whether model presence would increase individual success at opening the two-step box, irrespective of the underlying mechanism.

METHODS

Study Site and Population

Experiments were conducted between 2007 and 2009 on six neighbouring groups of habituated wild vervet monkeys at Loskop Dam Nature Reserve, South Africa. The reserve, situated 250 km northeast of Johannesburg, covers 25 000 ha. Vervet monkeys live in stable family groups, which during our experiments varied from 13 to 21 individuals. Groups are typically composed of an alpha male, a few subordinate males and several matriline (females and their offspring). Females remain in their natal group all their life, while males migrate to another group when they are sexually mature, usually at around 4 years of age (Struhsaker 1967; Cheney & Seyfarth 1983). Our six study groups, Picnic, Nooitgedacht, Blesbokvlakte, Donga, Bay and Fishing Camp (named after sites on the Park map), live in contiguous home ranges along a tourist road that allows easy access to each group. Group compositions are summarized in Table 1.

All groups had been exposed to the presence of human researchers for at least 2 years before they were tested. All individuals were recognized by their faces and a recognition file with portrait pictures and specific individual features (scars, etc) was constructed for each group. Two of the six groups were in regular contact with tourists, who typically visit the Park on weekends: the 'Fishing Camp group' and the 'Picnic group'. The latter and the 'Donga group' had previously been used for experiments (Fruteau et al. 2009). All six groups had previously been tested on the 'two-door' artificial fruit experiment (van de Waal et al. 2010). This previous artificial fruit experiment habituated the monkeys to the

Table 1
The composition of the study groups

Group	Adult male	Adult female	Juvenile	Infant	Total	Model
Donga	3	6	1	4	14	Lul=JF
Bay	4	6	6	5	21	Kir=AF
Fishing Camp	2	4	15	0	21	Sc=JM
Blesbokvlakte	2	3	8	0	13	–
Picnic	2	3	6	2	13	–
Nooitgedacht	2	3	9	1	15	–

Males are scored as adults once they migrated, while females are scored as adults once they had given birth. Group members that did not fulfil these criteria were scored as juveniles if they were at least 1 year old, and as infants if they were younger. In the model column the name code of the model is given and its age–sex class (JF = juvenile female, AF = adult female, JM = juvenile male).

manipulation of knobs on the Plexiglas door through either pulling or sliding. In all six groups, these ‘two-door’ one-step trials were finished before the two-step artificial fruit trials started (time between the ‘two-door’ one-step experiment (van de Waal et al. 2010) and the two-step experiment presented here: Fishing Camp = 1 day; Nooitgedacht = 7 days; Blesbokvlakte = 14 days; Bay = 35 days; Donga = 146 days; Picnic = 152 days).

Experimental Design

We used a new version of the established laboratory design, the ‘artificial fruit’ (Whiten et al. 1996; Whiten 1998), to test for the presence of social learning. Our artificial fruits were wooden boxes (10 × 10 cm and 20 cm high) painted in blue with one Plexiglas pull door blocked by a rope attached to the top of the box by an aluminium bar (Fig. 1). Each box contained one-eighth of an apple. The door could be opened by removing the bar, which would release the rope, enabling the door to be opened by pulling a knob (see Supplementary Material). The rope was blocked under the box during the demonstration phase, obliging the model to remove the bar to get access to the reward.

As we worked with wild groups, we could not choose a model and train it in isolation from the other group members. Therefore, we started by simply offering a baited open box to the group, which was soon monopolized by a dominant individual or, if the dominant did not solve the task, other high-ranking individuals in the group. We offered the set-up on at least 6 mornings in each group to give the monopolizing individual time to solve the task by individual learning based on trial and error. In half of the groups, a model learned to open the box consistently, while the other groups were used as controls.

In subsequent trials, we made sure that successful models were in sight and that they observed the experimenter setting up the box, so that they would continue with demonstrations and prevent other group members from gaining personal experience. We conducted one session per day consisting of eight demonstration trials to keep the models motivated. Human experimenters sat about 5 m away from the box during trials, waited for the model to eat the piece of fruit, and then walked up to the box to bait it again. The demonstration phase continued until the model had performed 20 successive successful trials, which consisted of removing the bar without touching the blocked door and then opening the door. The three models needed between four and 12 sessions spread over 4–57 days to complete the demonstration. The status of the model varied between each group. In Bay group, the model was the dominant female; in Fishing Camp group the model was the fully grown son of the alpha female; and in Donga group the model was the young daughter of the dominant female. The former two individuals were also models in the ‘two-door’ artificial fruit experiment (van de Waal et al. 2010), while the latter model replaced the dominant male of the

group who gave up after several unsuccessful attempts to open the box.

Once the demonstration period was accomplished, we conducted the two rounds of trials that tested for social learning. In the first round, individuals could open the boxes without removing the bar (as the rope was just hidden under the box but not attached), while in the second experiment, individuals had to remove the bar to open the door and get the reward. We used two methods to prevent models from monopolizing the boxes, so that other group members could get access to them as well. We either offered four dispersed boxes simultaneously or we targeted isolated individuals and placed a box close to them.

Data Collection

During demonstrations, we noted in each session which group members were at some point within 5 m of the box and hence at a distance where they could have easily observed the actions of the model.

For both rounds of trials (rope loose and rope blocked), we noted which individuals actively participated. During each participant’s first interaction, we recorded whether it first manipulated the bar or the door, how long it interacted with the box, and whether it touched the bar during the trial. A trial began when the participant first touched the box and ended when the individual moved away to a distance of at least 1 m. All interactions with the box were filmed with a digital video camera. The data could be coded unambiguously: an individual participated if it touched the box, the location of the first manipulation could be identified because of the part touched (bar or door), and success was coded as the individual having the piece of food in its hand, thus having opened the door in the process.

Data Analyses

For the social-learning analyses, we calculated whether individual propensity to touch the bar or the door first was affected by the presence/absence of a model in the group. We then asked how many individuals touched the bar at least once during their first manipulation and whether this was affected by the presence/absence of a model in the group. We recorded the length of the first manipulation to control for the possibility that the probability that an individual would touch the bar was correlated with length of the interaction. We also counted how many participating monkeys with and without a model actually got the reward and ate the piece of apple. During the second experimental phase, once the rope was blocked, we counted how many vervets with and without a model touched the bar during their first manipulation and how many of those removed the bar at least once. For the statistical analyses, we excluded group members that had gained access to the box during the demonstration phase, either before the model consistently monopolized the box or because they were tolerated during the demonstrations. Such early experiences might have modified behaviour independently of the models’ demonstrations. Also, we excluded individuals that were less than 1 year old from our analyses involving group sizes, as these individuals never participated in the experiments.

All the statistical analyses we conducted were nonparametric statistical tests using SPSS 16.0 (SPSS Inc., Chicago, IL, U.S.A.).

Ethical Note

Our experiments were approved by ABERRU boards of UNISA as well as Park Boards of the Mpumalanga Province, South Africa. Our set-up involved some feeding competition. However, as we were interested in individuals’ first manipulation we did not repeat the

experiments often and kept the amount of food relatively small (one-eighth of an apple) in the learning phase to make sure that the models were motivated, while we needed only one observation per subject during each experimental phase.

RESULTS

Effect of Models on Participation

Regarding all subjects, the presence or absence of a model did not significantly affect the likelihood that individuals actively participated in the experiment by touching the box (active participants with models: 12 of 44 subjects; active participants without models: 16 of 34 subjects; chi-square test: $\chi^2_1 = 3.263, P = 0.071$). In the groups with a model, all 12 active participants had been within 5 m of the box at least once during demonstration; however, so had 30 of the 32 nonparticipating subjects. We found a strongly significant effect of the subjects' performance in the previous 'two-door' experiment: 27 of the 28 active participants had successfully opened the 'two-door' artificial fruit during our previous experiment, while 42 of the 50 individuals that did not touch the box had failed to open the 'two-door' artificial fruit (chi-square test: $\chi^2_1 = 41.936, P < 0.0001$). The one new active participant was a juvenile of the Picnic group that had been too young (<1 year) during the one-step artificial fruit experiment.

Numbers actively participating varied greatly between groups: three of 18 individuals in the Bay group with the dominant female as the model; nine of 17 individuals in the Fishing Camp group with the fully grown son of the alpha female as the model; and none of the nine individuals in the Donga group with the juvenile female of the dominant matriline as the model. As each model was idiosyncratic with respect to its age/sex class, we could not test quantitatively how age/sex class of a model might influence social learning.

For the second experimental phase, when the rope was attached and the bar needed to be removed to get the reward, 11 monkeys from groups with a model actively participated, whereas six monkeys from control groups manipulated the box. There was no significant difference in the distribution of individuals from control groups actively participating in the second task and the individuals from the model groups (chi-square test: $\chi^2_1 = 6.08, P = 0.435$).

Effect of Models on Probability of Copying

Most individuals touched the door first (nine with models, 16 without models), while only a few individuals in groups with a model ($N = 3$) and no individuals in control groups touched the bar first. Thus, we found a nonsignificant tendency for individuals with a model to be more likely to copy the model's sequence of actions (exact Fisher's test: $N = 28, P = 0.067$; Fig. 2a). Participants in groups with a model were significantly more likely to touch the bar during their first interaction than participants in groups without models (exact Fisher's test: $N = 28, P = 0.001$; Fig. 2b). This result was apparently not caused by these individuals spending longer interaction with the box, as we did not find that unsuccessful individuals in groups with models were more persistent than individuals in groups without models (Mann–Whitney U test: $Z = -0.152, N_1 = N_2 = 10, P = 0.912$; Fig. 2c). Exposure to a model did not significantly affect the probability that individuals managed to open the box and gain the reward (exact Fisher's test: $N = 28, P = 0.401$; Fig. 2d).

Effect of Models on Probability of Opening the Box

We found no difference in the number of individuals from groups with or without models that touched the bar during the first manipulation (exact Fisher's test: $N = 17, P = 0.62$; Fig. 3a). In

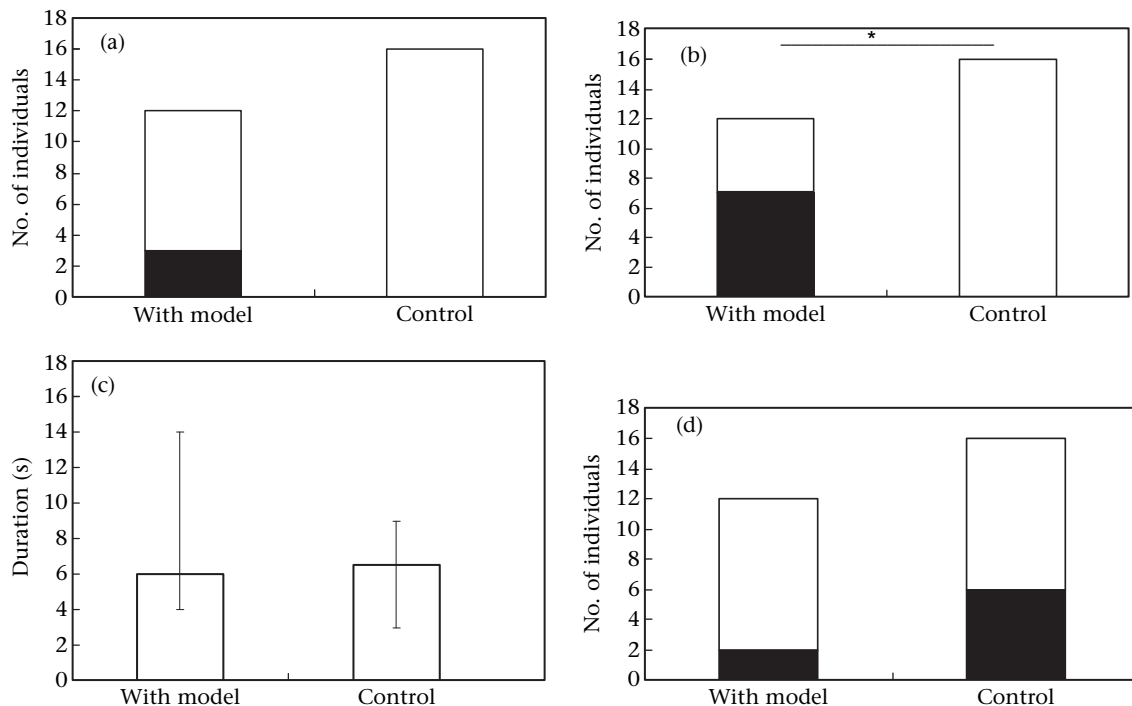


Figure 2. (a) Number of individuals in groups with a model or control that touched the bar (black) or the door (white) first during their first manipulation. (b) Number of individuals in groups with a model or control that touched the bar at least once (black) or never touched it (white) during their first manipulation. * $P < 0.05$. (c) Duration (median and quartiles) of the first manipulation in groups with a model or control. (d) Number of individuals in groups with a model or control that did (black) or did not (white) get access to the reward during their first manipulation.

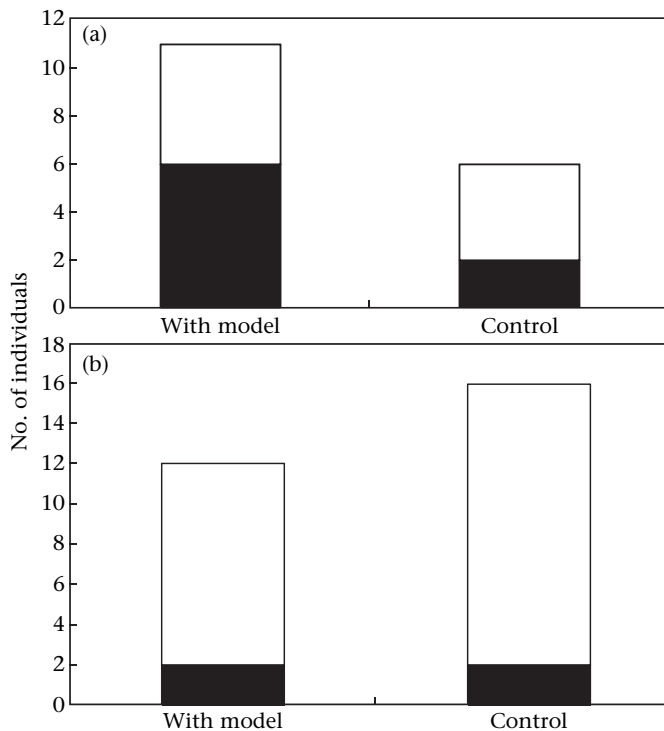


Figure 3. (a) Number of individuals in groups with a model or control that touched the bar at least once (black) or never touched it (white) during the second experimental phase when the rope was attached and the bar needed to be removed to get access to the reward. (b) Number of individuals in groups with a model or control that successfully removed the bar at least once (black) or never removed it (white) during all trials.

addition, only two individuals with models and two individuals without models succeeded in solving the two-step task, yielding no significant differences between individuals in groups with or without models (exact Fisher test: $N = 28$, $P = 1$; Fig. 3b). Of the few individuals ($N = 15$) that touched the box during demonstrations, none managed to open the box.

DISCUSSION

We presented a two-step design artificial fruit to wild vervet monkeys with or without knowledgeable models, to ask whether they learn socially about the task. We also wanted to know whether vervets would show evidence for copying a sequence of actions, in which case we predicted that they would complete the two steps in the right order when exposed to a model. Finally, we asked whether exposure to a model increases the probability that individuals would solve the entire two-step task and hence get access to the reward inside the artificial fruit.

Our results provided evidence for local enhancement learning, that is, copying the location of the actions of the model (Hoppitt & Laland 2008), as subjects with a model were more likely to touch the bar at some point during their manipulation of the box than subjects without a model. This result was not caused by different durations of manipulations. These results confirm those from the previous experiment by van de Waal et al. (2010) on a ‘two-door’ artificial fruit where subjects copied the choice of door from female models.

As we had three models that differed in age/sex class, we cannot evaluate the potential importance of these variables for the occurrence and precise mechanisms of social learning in this task. Several authors have pointed out that the identity of a model should play a major role in an individual’s decision to learn socially or not (Boyd & Richerson 1985; de Waal 2001; Laland 2004), and

van de Waal et al. (2010) demonstrated that wild vervets are more likely to learn socially from philopatric female models than from migrating male models. Thus, additional experiments yielding a larger number of models would be necessary to address the importance of model identity in the two-step task. However, our results yield no conclusive evidence that vervet monkeys copy socially a sequence of actions. As the sample size was small and we found a tendency for models to induce the copying of a sequence, a future study with a larger sample size should be conducted to provide a more definitive answer.

We found no effect of the presence or absence of models on the likelihood that group members would participate in the experiment. Thus, we found no evidence for stimulus enhancement learning (Hoppitt & Laland 2008). The absence of such evidence is best explained by the fact that monkeys in this population had had previous experience with artificial fruits and hence probably knew that there was a high-quality food item inside, but also probably remembered whether they had managed to open the ‘two-door’ artificial fruit (van de Waal & Bshary, in press). Even if we had changed the colour and shape of the knob as well as the colour of the box, overall the size and shape of the box, as well as its content, remained the same. While we cannot assess how monkeys perceive such objects, it was evident that only individuals that had opened the ‘two-door’ artificial fruit were likely to participate in this two-step task. This result demonstrates the benefit of having prior knowledge about subjects’ previous experience when assessing performance in these and similar experiments (Martin & Bateson 1986). At the same time, the result suggests that we should not too easily dismiss the possibility that wild vervet monkeys are able to learn a sequence of acts from a model. A possible reason why monkeys in this experiment failed to copy a sequence of actions is that participating individuals first used their personal experience from the ‘two-door’ artificial fruit experiment where manipulating the knob was all that was needed for success. Only when this failed (which happened fairly frequently because the rope in front of the door demanded stronger pulling than in the previous experiment) did subjects start touching the bar, as demonstrated by the model. Thus, another experiment with a very different set-up or using naïve monkeys would be necessary either to confirm or to extend the current results.

The key conclusion of our second series of trials, in which the rope was functional, is that the task of removing a bar is more difficult for vervet monkeys than pulling open a door. Failure of several individuals to pull the door open in the first round of trials was probably a consequence of the rope warranting extra strength, as all but one subject that manipulated the box had succeeded in the previous one-step artificial fruit experiment. However, the removal of a bar that was stuck in two rings was apparently very difficult. First, many individuals apparently did not understand that they had to remove the bar to solve the task and did not even touch it. Second, even those that did touch the bar typically failed to remove it, including the three dominants that failed to become models despite repeated exposure. Limitations in technical abilities should be considered in any future experiments that test for other social-learning mechanisms such as production imitation. The standard artificial fruits used to test for production imitation involve arbitrary pushing or pulling of bars (Whiten et al. 1996). Thus, before such a test could be conducted on wild vervet monkeys, they would have to be trained first to perform such movements in other contexts. A possibility is that wild primates are less able to solve the technical aspects of the task than primates raised in captivity. Several authors have noted that captivity may lead to various degrees of ‘enculturation’ (Gardner & Gardner 1989; Tomasello & Call 2004; Whiten & van Schaik 2007). In line with this argument, we note that the four subjects that managed to solve the two-step task belonged exclusively to the two groups (Picnic and Fishing Camp) that had access to human facilities. Individuals of the

same two groups were also more likely to open the doors in the 'two-door' artificial fruit experiment than individuals of the other four groups (van de Waal & Bshary, in press).

Until recently, social-learning experiments were conducted primarily on captive subjects, with some exceptions (Helfman & Schultz 1984; Lefebvre 1986; Warner 1988; Langen 1996). This bias towards laboratory experiments raises the question how important social learning is in wild animals and whether or not wild animals use the same social-learning mechanisms as their captive counterparts (Whiten & Mesoudi 2008). Fortunately, many recent studies have illustrated that field experiments are feasible and hence offer a vital and informative additional approach to the study of social learning (Reader & Biro 2010). Interesting designs have been successfully adapted to the wild to test whether and how particular behaviours can be socially transmitted in many different taxa. For example, several scientists have manipulated individual behaviour to provide pertinent information to other group members and found evidence that subjects picked up such information. In wild guppies, *Poecilia reticulata*, individuals chose to go to foraging sites previously used by models (Reader et al. 2003), while meerkat pups accepted novel food more readily after exposure to a conspecific feeding on it (Thornton 2008). In banded mongooses, *Mungos mungo*, Müller & Cant (2010) showed that food preferences as well as foraging techniques can be persistent and learned socially through production imitation. One possible approach is the introduction of trained models into a group or a population. Following early studies on birds (Lefebvre 1986; Langen 1996), individual meerkats were trained as models that could affect the group members' choice of specific foraging patches (Thornton & Malapert 2009). Surprisingly, field experiments on social learning in primates are particularly rare. The current study, as well as the study by van de Waal et al. (2010), suggests that, at least in species with clear dominance structures, high-ranking individuals are likely to monopolize attractive food sources and associated tasks and can thus act as models for social-learning experiments.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi:10.1016/j.anbehav.2010.11.013.

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