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# 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.

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 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.

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

## 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 matrilines (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