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SOCIAL LEARNING AND TRADITIONS IN WILD VERVET MONKEYS

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Pour Callou

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General Abstract

Social learning is the basis for allowing the transmission of specific behaviours inside a social unit, i.e. the formation of traditions. Early field studies suggested the existence of traditions in non-human animals, while more recent laboratory experiments have demonstrated social learning abilities in a variety of species. I established a unique bridge between these perspectives by conducting three different social learning experiments on six groups of wild vervet monkeys (*Chlorocebus aethiops*) at the Loskop Dam Nature Reserve, in South Africa. Using this approach, I investigated what mechanisms wild vervets use when they learn a task socially. Furthermore, theoreticians pointed out that social learning is only driven by positive selection under certain conditions. Therefore, I investigated how important the identity of a model is for the occurrence of social learning and I tried to understand why some individuals are more copied than others from a functional perspective. Finally, by analysing the stability over time of the socially acquired behaviours, I could ask whether traits acquired through social learning may turn into arbitrary traditions.

First, I presented laboratory-style 'artificial fruit' boxes that had two doors on opposite, differently coloured ends. A dominant individual invariably monopolized the box during an initial demonstration phase, in which one door was blocked. This created consistent demonstrations of one of the two possible solutions in each of six study groups. Three groups had female models and three had male models. Following demonstrations I found a significantly higher participation rate ('stimulus enhancement') by other group members and significant evidence for manipulation of the same door ('local enhancement') in groups with female models compared to groups with male models. These differences appeared to be due to selective attention of bystanders to female model behaviour, while male and female models attracted similar numbers of bystanders and showed similar levels of aggression towards those bystanders. The results demonstrate the eminent role of dominant females as a source for directed social learning in a species with female philopatry.

In this same first experiment, I analysed the proper solving of the task. During their first trial, I observed which individuals managed to open artificial fruit thus accessing the reward. This time I did not find an effect of the model sex but I found that the two groups in contact with humans were more successful than the others. This result suggests some enhanced manipulation skills due to contact with humans or their facilities.

The second experiment involved a more complex artificial fruit to test for sequence imitation, where two steps were necessary to open the door: remove a bar on the top of the box which releases a rope that was blocking the door and then pull the door. Vervets largely failed to show more complex social learning abilities in this experimental setup. However monkeys in group with models touched the bar significantly more often during their first manipulation than control individuals did. This latter result implies again the use of 'local enhancement' as social learning mechanism in wild vervets.

Finally, I conducted a food cleaning experiment that was inspired by a classic study that documented the spread of sweet potato washing in a semi-natural population of Japanese macaques. I offered the monkeys grapes covered with sand and noted if and how they cleaned the food before eating. Each group was subjected to 15 trials. Vervets either did not clean the grapes or either rubbed with their hands, rubbed on substrates, or opened the fruit with their teeth or hands to eat the inside only. I found strong variance between individuals of the same group as well as between groups with respect to the techniques used. Matrilines rather than entire groups appeared to be the key unit for social transmission, where conformity of feeding techniques could be documented.

Taken together, the findings imply that in species with complex social structures, migration does not necessarily lead to an exchange of socially acquired information within populations, causing much localized traditions.

General Introduction

The core of evolutionary biology research is focused on evolution of genetically determined traits. Less well studied is the 'second inheritance system' (Whiten 2005), within which behavioural innovations are transmitted culturally, through social learning. However, recent years have seen an explosion of discoveries about such phenomena in fish, birds and mammals. The study of animal social learning and culture has seen enormous scientific progress in the last 10-15 years, driven by a mixture of factors including the fruits of long-term field studies (Whiten & van Schaik 2007), new approaches to captive and experimental research (Whiten & Mesoudi 2008) and computational modelling (Richerson & Boyd 2005).

Such cultural transmission is an important phenomenon to understand as it represents a 'second inheritance system' (Whiten 2005) that evolved on the back of genetic evolution and now forms a parallel evolutionary stream (Mesoudi et al. 2006). Cultural and genetic evolution share fundamental characteristics such as information transmission, mutation, selection and adaptation (Mesoudi et al. 2006). They differ in other respects, principally in terms of substrate (brain versus DNA), and the speed with which adaptation to environment and evolutionary change can occur (relatively rapidly, through copying others, in the case of culture). We now know an enormous amount about genetic or 'biological' evolution, but relatively little about the cultural stream.

My research focuses on animal social learning and traditions. 'Social learning' is 'the learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products' (Heyes 1994). 'Traditions' as defined by Fragaszy and Perry (2003) are 'a distinctive behaviour pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning'. 'Culture' is most difficult to define but biologists have defined culture as 'group-typical behavioural patterns, shared by community members, that rely upon socially learned and

transmitted information' (Laland & Janik 2006). These definitions are well schematized in Figure 1 (Whiten & van Schaik 2007).

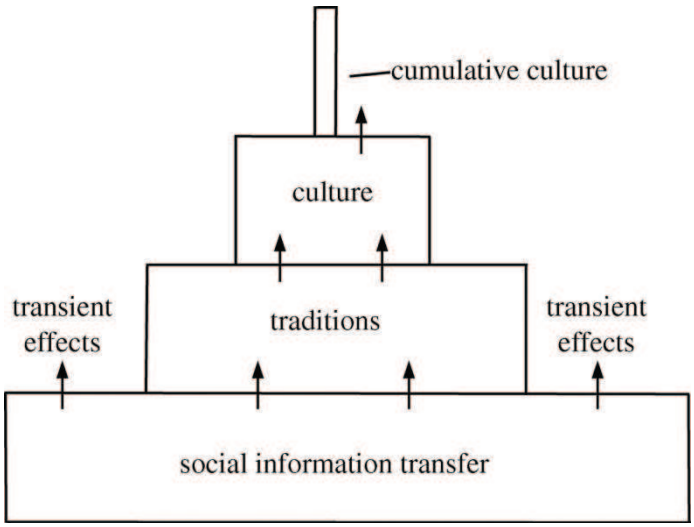

Figure 1. Culture pyramid. Social information transfer (foundation layer) is widespread in vertebrates and occurs also in invertebrates (see text for references). However, only a subset of such transfer eventuates in sustained traditions (layer two), because effects of social learning are often transitory only (e.g. using public information to judge profitable foraging patches). The occurrence of traditions may also be more restricted taxonomically than use of social information per se. More rarely still, cultures exist that are defined by the existence in the same species of multiple traditions forming unique local complexes (layer three). Cumulative culture (layer 4) occurs when more complex traditions arise by elaboration on earlier ones, generating the richness of human cultures yet minimally evidenced in other species. Relative sizes of each layer are notional. Arrows indicate the reliance of each layer on pre-existing lower layers. After Whiten and van Schaik (2007)

The data obtained by long-term field studies on wild chimpanzees (Goodall 1986; McGrew 1992) allowed obtaining tables of putative chimpanzee traditions varying across the communities. Researchers identified 39 putative behavioural traditions across Africa, and showed that individuals can be assigned to their locality on the basis of their cultural profile, as can people (Whiten et al. 1999, 2001). This apparent cultural complexity contrasts to earlier suggestions of animal traditions, which

typically reported only a single such behaviour pattern, as for example dialects in birdsong (Marler & Tamura 1964).

Scientists studying other animals have built on this work and reported multiple cultural variations through similar observational approaches. Notably, van Schaik et al (2003) used precisely the same analytical method to reveal 24 cultural variants among orang-utans, more recently updated to over 30 (van Schaik 2009). Others have described multiple traditions in organisms as diverse as whales and dolphins (Rendell & Whitehead 2001), capuchin monkeys (Panger et al. 2002; Perry et al. 2003), Japanese macaques (Leca et al. 2007) and bowerbirds (Madden 2008). Accordingly there is a new realization that cultural processes may be more widespread in animal populations than previously appreciated. Other studies have documented individual or smaller sets of cultural variations in a wider range of taxa including mammals, birds and fish (Fragaszy & Perry 2003; Danchin et al. 2004; Whiten & van Schaik 2007; Laland & Galef 2008).

However, it is difficult to be sure, under wild conditions and without experiments, that such apparent traditions are truly socially learned. Critical reviews (e.g. Laland & Janik 2006) have argued, for example, that some of the variation may be due to undetected environmental factors. Field experiments have the power to resolve this. For example by experimentally providing artificial foraging tasks and control conditions, but until recently such studies are lacking due to the practical difficulties of such experiments with animals, especially primates, in the field. Instead, a series of 'diffusion experiments' has been initiated in captivity, in which different behavioural techniques to deal with the same foraging problem have been experimentally induced in different groups, and their spread and maintenance as traditions documented. (in chimpanzees: Whiten et al. 2005, 2007; in capuchins: Dindo et al. 2008, 2009). Only very recently have some captive social learning experiments been successfully translated into the field with meerkats (Thornton & Malapert 2009) and primates (Gruber et al. 2009; Pesendorfer et al. 2009).

The lack of knowledge about social mechanisms used by wild animals has to be filled with experiments that adapt established laboratory designs to field conditions. Laboratory experiments have demonstrated the ability of many species to imitate (Laland & Plotkin 1990; Bonnie et al. 2006, Horner et al. 2006, Dindo et al. 2008). However, testing for social learning mechanisms in wild groups is very important as captivity might provide an environment that improves the animals' ability to copy precise movements of others due to physical proximity, due to having plenty of time to look what others are doing, and due to the enhanced security because of the lack of predators. As a consequence, imitation might be rare in the field context, and socially learned information might rely on more simple mechanisms such as 'stimulus enhancement' or 'local enhancement' (Hoppitt & Laland 2008).

Another gap in the social learning studies is knowledge about the spreading pattern of socially acquired information in a natural group. For primates that live in stable social groups with hierarchical structures and certain levels of kin relationships (Smuts et al. 1987), it has been argued that some individual are predisposed to be models for other group members, independently on the efficiency of their behaviour in a given situation (de Waal 2001). With understanding who learns from whom one would be able to test the 'social model hypothesis'- also known as bonding and identification-based observational learning (BIOL), which predicts that primates living in structured social groups are most likely to learn from social models such as knowledgeable, older, high ranking members of the same group and species (de Waal 2001). In addition, the hypothesis suggests that social learning in this taxonomic group is linked to conformity. Young and subordinate individuals want to behave like old and dominant individuals do. Therefore, individuals may sometimes copy the behaviour of models whose behaviour is unsuitable for the current situation, and fail to copy the behaviour of other group members even in situations where that would be favourable (de Waal 2001). Currently, there are no experimental demonstrations in primatology that an individual's

identity (that is, its relatedness to other group members and/or its social status) affects the likelihood that others will copy its behaviour.

Building on this open-field of social learning experiments on wild animal I designed three methods to test vervet monkeys. I chose vervet monkeys as my study species due to previous personal observations during my master on wild vervets in the Loskop Dam Nature Reserve, in South Africa (van de Waal, unpublished master thesis). During my master field season, first of all I realized that these animals were ideal to conduct experiments as I assisted the experiments of Fruteau et al. (2009) and thus saw that vervets are not neophobic and very willing to participate in set-ups involving food. Secondly my master study was on the grooming patterns of adult females of two groups during the birth season. I observed much different behaviours in these two groups belonging to the same genetic population and in very similar ecology, which raised my interest to investigate the potential importance of social learning for small scale variation in behaviour in these wild primates. Furthermore, vervet groups are composed of multiple adult males and females and their offspring. Such a group composition seemed ideal to document the spread of social information within a group, in contrast to simpler social systems like an adult breeding pair and its offspring or a harem system. Also, in Loskop groups typically consisted of about 20 individuals, which was a good compromise between my interest in social complexity and the need to identify members in all study groups individually. To have a decent sample size for my experiments, I decided to work on six groups. All groups were located along the tourist road of the reserve with the lake of Loskop Dam on the southern side and hills on the north (Fig. 2). With the help of many master students and assistants, I was able to habituate four more groups to observers' presence.

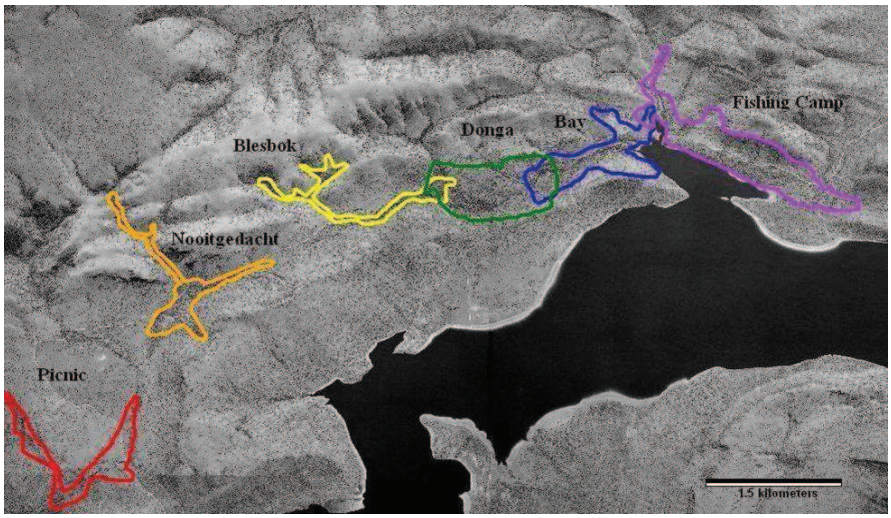

Figure 2. The home ranges of the six groups of vervets during summer 2007-2008 (Borgeaud et al., in prep)

The first experiment I conducted used a classical laboratory design called the 'artificial fruit' (Whiten et al. 1996), a baited box with multiple openings to access the reward. My artificial fruit was a 'simple' version adapted to vervets. I did the experiments on six groups of vervets and had models that were either a dominant female or a dominant male. In the field, 'artificial fruit' boxes were presented that had two doors (one sliding, one pulling) on opposite, differently coloured ends. One option was blocked during the demonstration phase, creating consistent demonstrations by the monopolizing individual of one possible solution. Three groups had a dominant female as model and three groups had a dominant male as model. In vervet monkeys females are the philopatric sex, while males migrate at sexual maturity (Dunbar & Thelma 2001). Therefore, I could investigate a more refined aspect of the 'social model hypothesis' also called BIOL (De Waal 2001), namely that members of the philopatric sex might elicit more social learning than members of the migrating sex. I then predicted that female models would be more likely to attract group members to the task and more likely to induce social learning than male models. In contrast, if

dominance per se is the key factor to induce social learning, I predicted that groups with male models would learn as well as groups with female models. In this experiment, any effect of the sex of the model on the likelihood of social learning could not be explained by differences in relevant knowledge as models of both sexes were as successful in their demonstration, but two alternative explanations could remain. First, members of one sex could be more aggressive, keeping group members away and therefore precluding efficient social learning. Second, group members might pay selectively more attention to the actions of models of one sex, therefore being more likely to learn from members of this sex. I predicted that if tolerance is the key to successful social learning, models of the less aggressive sex would elicit a greater number of bystanders. Likewise, I predicted that if the effect of the sex of the model is caused by selective attention, models of the sex that elicits more successful social learning would receive more attention during the task.

Furthermore I analyzed the success of opening the artificial fruit during the first manipulation. As neither the efficiency of the model demonstration or its sex induced more successful opening at first trial, we added the factor of group in contact with humans and their facilities or not. This last point allowed me to test the hypothesis that a humanized environment might enhance vervet manipulative skills, based on the hypothesis that captivity seems to enhance capacities beyond standard natural abilities, known as 'enculturation effect' (Whiten and van Schaik 2007).

The second experiment involved a more 'complex' version of the artificial fruit, where two steps were necessary to reach a reward (Whiten 1998), in my design: first remove a bar on the top of the box to release a rope blocking the door, then pull the door. This more complex set-up allows testing for the ability to copy a sequence of behaviour and try to analyse which mechanism is responsible for social learning in wild vervets. In this experiment, only three models successfully demonstrated the task. The three other groups were used as control to test if monkeys were

attracted to the aluminium bar. During the experimental phase, the box looked as if it was blocked by the rope, but actually the rope was not tight under the box. Therefore individuals could access the reward by just pulling the door open without removing the bar. My prediction was that if vervets are capable of copying a sequence of actions, the individuals that had been exposed to a model should touch or remove the bar before trying to open the door, while individuals from groups without models should not do so.

Finally the third experiment was a food cleaning experiment inspired by the famous putative tradition of sweet potato washing in Japanese macaques (Itani & Nishimura 1973). In a group of semi-free ranging macaques living on a Japanese island, one juvenile female started washing sweet potatoes in the sea, a cleaning behaviour which would remove the dirt from the peel as well as add a salty taste to the food. The spreading of this cleaning technique in the social unit has been documented in details until it became an arbitrary feeding tradition in this study group. In my experimental design, the vervets were offered grapes covered with sand and I noted if and how they cleaned the food before eating as well as who was eating at the same time. Each group was subjected to 15 trials. I hypothesized that different techniques to clean the grapes should appear in our different groups through social learning. If these behaviours stay constant in the social unit they should evolve in arbitrary traditions based on conformity.

With these three experiments I hope to draw a general picture on social learning and traditions in wild vervet monkeys. The two-door artificial fruit should give me the opportunity to test the possibility to train a model to demonstrate one option to group members as well as give us first insight if simple social learning mechanisms occur and under which conditions. Building on this knowledge, the more complex task that involves copying a sequence of actions should bring more detailed information on the social learning mechanism as well as the manipulation skills of our study species. Finally, the repeated food cleaning experiments

should enable me to test if without trained models social learning may lead to between-group variation in feeding techniques as well as to within-group conformity potentially leading to the formation of arbitrary traditions.

References

Bonnie KE, Horner V, Whiten A & de Waal FBM 2006 Spread of arbitrary customs among chimpanzees: a controlled experiment. Proceedings of the Royal Society B, **274**, 367-372.

Borgeaud C, van de Waal E & Bshary R (in preparation) Group size correlates with home range size, distance travelled per hour, vigilance and activity budget, a study on six groups of vervet monkeys (*Cecopithecus aethiops*).

Danchin E, Giraldeau L-A, Valone TJ & Wagner RH 2004 Public information: from nosy neighbours to cultural evolution. *Science* **305**, 487-491.

Dindo M, Thierry B & Whiten A 2008 Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proceedings of the Royal Society of London 'B'* **275**, 187-193.

Dindo M, de Waal FBM & Whiten A 2009 In-group conformity sustains different foraging traditions in capuchin monkeys (*Cebus apella*). *PLoS One* **4**, e7858.

Dunbar RIM & Thelma E 2001 *Guenons, macaques, and baboons*. In : The new encyclopedia of mammals (ed. D. MacDonald), pp. 356-375. Oxford, UK: Oxford University Press.

Fragaszy DM & Perry S (eds.) 2003 *The biology of traditions: models and evidence*. Cambridge: Cambridge University Press.

Fruteau C, Voelkl B, van Damme E & Noe R 2009 Supply and demand determine the market value of food providers in wild vervet monkeys. *Proceedings of the National Academy of Sciences of the United States of America - Biological Sciences* **106**, 12007-12012.

Goodall J 1986 *The chimpanzees of Gombe: patterns of behaviour*. Boston, MA: Harvard University Press.

Gruber T, Muller MN, Strimling P, Wrangham R & Zuberbühler K 2009 Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Current Biology* **19-21**, 1806-1810.

Heyes CM 1994 Social learning in animals: Categories and mechanisms. *Biological Reviews* **69**, 207-231.

Hoppitt W & Laland KN 2008. Social processes influencing learning in animals: a review of the evidence. *Advances in the Study of Behavior* **38**, 105-165.

Horner V, Whiten A, Flynn E & de Waal FBM 2006 Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences of the United States of America - Biological Sciences* **103**, 13878-13883.

Itani J & Nishimura A 1973 In *Precultural behaviour*, ed. Menzel EW, Jr (Karger, Basel, Switzerland), pp. 26-50.

Laland KN & Plotkin HC 1990 Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Animal Learning & Behavior* **18**, 246-251

Laland KN & Janik V 2006 The animal cultures debate. *Trends in Ecology & Evolution* **21***,* 542-547.

Laland KN & Galef BG Jr. (eds.) 2008 *The question of animal culture*. Cambridge, MA: Harvard University Press.

Leca J-B, Gunst N & Huffman MA 2007 Japanese macaque cultures: Inter- and intra-troop behavioural variability of stone handling patterns across 10 troops. *Behaviour* **144**, 251-281.

Madden JR 2008 Do bowerbirds exhibit cultures? *Animal Cognition* **11**, 1-12.

Marler P. & Tamura M 1964 Song 'dialects' in three populations of white-crowned sparrows. *Science*, **146**, 1483-1486.

McGrew WC 1992 *Chimpanzee material culture: implications for human evolution.* Cambridge: Cambridge University Press.

Mesoudi A, Whiten A & Laland KN 2006 Towards a unified science of cultural evolution. *Behavioral and Brain Science* **29**, 329-383.

Panger M, Perry S, Rose L, Gros-Luis J, Vogel E, Mackinnon KC & Baker M 2002 Cross-site differences in foraging behavior of white-faced capuchins (*Cebus capuchinus*). *American Journal of Physical Anthropolology* **119**, 52-56.

Perry S, Baker M, Fedigan L, Gros-Luis J, Jack K, Mackinnon KC, Manson J, Panger M, Pyle K & Rose LM 2003 Social conventions in white-face capuchins monkeys: evidence for behavioral traditions in a neotropical primate. *Current Anthropol*ogy **44**, 241-268.

Pesendorfer MB, Gunhold T, Schiel N, Souto A, Huber L & Range F 2009 The Maintenance of Traditions in Marmosets: Individual Habit, Not Social Conformity? A Field Experiment. *PLoS ONE* **4**, e4472, doi:10.1371/journal.pone.0004472.

Rendell L & Whitehead H 2001 Cultures in whales and dolphins. *Behavioral and Brain Sciences* **24**, 309-382.

Richerson P & Boyd R 2005 *Not by Genes Alone.* Chicago University Press.

van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS & Merrill M 2003 Orangutan cultures and the evolution of material culture. *Science* **299**, 102-105.

van Schaik 2009 Geographic variation in the behavior of wild great apes: Is it really cultural? In Laland KN & Galef BG (Eds.) *The Question of Animal Culture*. Harvard University Press pp. 70-98.

Smuts BB, Cheney DL, Seyfarth RM, Wrangham RW & Struhsaker TT (eds) 1987 *Primate societies*. Chicago, IL: Chicago University Press.

Thornton A & Malapert A 2009 Experimental evidence for social transmission of food acquisition techniques in wild meerkats. *Animal Behaviour* 78, 255-264.

de Waal FBM 2001 *The ape and the sushi master: cultural reflections of a primatologist*. New York : Basic Books.

van de Waal E 2006 How to negotiate without language: Grooming markets in vervet monkeys. *Unpublished master thesis*.

Whiten A, Custance DM, Gomez J-C, Teixidor P & Bard KA 1996 Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology* **110**, 3-14.

Whiten A 1998 Imitation of the sequential structure of actions by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology* **112**, 270-281.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW & Boesch C 1999 Cultures in chimpanzees. *Nature* **399**, 682-685.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW & Boesch C 2001 Charting Cultural Variation in Chimpanzees. *Behaviour* **138**, 1481-1516.

Whiten A 2005 The second inheritance system of chimpanzees and humans. *Nature* **437**, 52-55.

Whiten A, Horner V & de Waal FBM. 2005 Conformity to cultural norms of tool use in Chimpanzees. Nature **437**, 737-740.

Whiten A & van Schaik CP 2007 The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society 'B'* **362,** 603-620.

Whiten A, Spiteri A, Horner V, Bonnie KE, Lambeth SP, Schapiro SJ & de Waal FBM 2007 Transmission of multiple traditions within and between chimpanzee groups. *Current Biology* **17**, 1038-1043.

Whiten A & Mesoudi A 2008 Establishing an experimental science of culture: animal social diffusion experiments. *Philosophical Transactions of the Royal Society 'B'* **363**, 3477-3488.

Chapter 1) 'Simple' artificial fruit

Part 1.A

Selective attention to philopatric models causes directed social learning in wild vervet monkeys

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Abstract

Human behaviour is often based on social learning, a mechanism that has been documented also in a variety of other vertebrates. However, social learning as a means of problem-solving may be optimal only under specific conditions, and both theoretical work and laboratory experiments highlight the importance of a potential model's identity. Here we present the results from a social learning experiment on six wild vervet monkey groups, where models were either a dominant female or a dominant male. We presented 'artificial fruit' boxes that had doors on opposite, differently coloured ends for access to food. One option was blocked during the demonstration phase, creating consistent demonstrations of one possible solution. Following demonstrations we found a significantly higher

participation rate and same-door manipulation in groups with female models compared to groups with male models. These differences appeared to be owing to selective attention of bystanders to female model behaviour rather than owing to female tolerance. Our results demonstrate the favoured role of dominant females as a source for 'directed' social learning in a species with female philopatry. Our findings imply that migration does not necessarily lead to an exchange of socially acquired information within populations, potentially causing highly localized traditions.

Introduction

Efficient social learning plays an essential role in human life as it provides the basis for traditions and culture (Plotkin 2007). As a consequence, studying the roots of culture in other animals has been a key research topic for decades (Whiten 2009). Theoretical studies on social learning rules suggest that individuals should be selective when deciding both when to learn socially and who to choose as a model (Boyd & Richerson 1985; de Waal 2001; Henrich & Gil-White 2001; Giraldeau et al. 2002; Laland 2004; Mesoudi 2008). A few empirical studies have identified rules for choosing models (Nicol & Pope 1999; Schwab et al. 2008), revealing typically that successful individuals are likely to induce social learning. For example, laboratory experiments demonstrated that nine-spined sticklebacks preferably copied foraging patches of larger individuals (Duffy et al. 2009). However, sticklebacks are also able to compare their own foraging success with the success of others and choose foraging locations accordingly (Kendal et al. 2009). This latter result implies that these fish are flexible with respect to the question 'who is a good model?' and are thus able to choose the best option in each situation.

For primates, living in stable social groups with hierarchical structures and certain levels of kin relationships (Smuts et al. 1987), it has been argued that certain individual are predisposed to be models for other group members, independent of their suitability in a given situation (de

Waal 2001). The 'social model hypothesis'- also known as bonding and identification-based observational learning (BIOL)- predicts that primates living in structured social groups are most likely to learn from social models such as knowledgeable, older, high ranking members of the same group and species (de Waal 2001). In addition, the hypothesis predicts that social learning in this taxonomic group is linked to conformity. Young and subordinate individuals want to behave like old and dominant individuals do. Therefore, individuals may copy the behaviour of models even if their behaviour is unsuitable for the current situation, and fail to copy the behaviour of other group members even when that would be favourable (de Waal 2001). The hypothesis could explain why the use of humans as models often yields negative results for social learning in non-human primates, despite the models' perfect knowledge for the tasks in question (Call & Tomasello 1996). In contrast, the use of female conspecifics as models has allowed the demonstration of the development of arbitrary traditions in captive chimpanzees (Whiten et al. 2005). Nevertheless, there are no demonstrations that an individual's identity (that is, its relatedness to other group members and/or its social status) affects the likelihood that others will copy its behaviour.

In this paper we report tests of the social model hypothesis in a field experiment on six vervet monkey groups. We used a standard experimental design in laboratory studies on primates: a baited box, called an 'artificial fruit' (Whiten et al. 1996). These artificial fruits can be opened in two different ways, but one option is blocked during the demonstration phase so that models consistently open the box in one way (figure 1). During the experiment, subjects could potentially open the box in both ways. Therefore, a significant repetition of the models' behaviour demonstrates social learning. We had three groups where the dominant female acted as model and three groups where a dominant male acted as model. In vervet monkeys, females are the philopatric sex, while males migrate at sexual maturity (Dunbar & Thelma 2001). Therefore, we could investigate a more refined aspect of the social model hypothesis, namely that members of the philopatric sex might elicit more social learning than

members of the migrating sex. In that case, we predicted that female models would be more likely to attract group members to the task and more likely to induce social learning than male models. In contrast, if dominance per se is a key factor to induce social learning, we predicted that groups with male models would learn as well as groups with female models.

In our experiment, any effect of the sex of the model on the likelihood of social learning could not be explained by differences in relevant knowledge, but two alternative explanations would remain. First, members of one sex could be more aggressive, keeping group members away and therefore precluding efficient social learning. Second, group members might pay selectively more attention to the actions of models of one sex, therefore being more likely to learn from members of this sex. To distinguish between these alternatives, we noted the number of bystanders during the demonstrations, whether they looked at the model during the moment of box opening and the number of aggressive actions initiated by the model during the demonstrations. We predicted that if tolerance is the key to successful social learning, models of the less aggressive sex would elicit a greater number of bystanders. Likewise, we predicted that if the effect of the sex of the model is caused by selective attention, models of the sex that elicits more successful social learning would receive more attention during the task.

Material and methods

a) Study site and population

Experiments were conducted between 2006 and 2008 on six neighbouring groups of habituated wild vervet monkeys (Chlorocebus aethiops) 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 varied from 13 to 23 individuals during our experiments. Groups are typically composed of an

alpha male, a few subordinate males and several matrilines (i.e. 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. 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 1 year 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: the Fishing Camp group and the Picnic group. The latter and the Donga group had been used for experiments before (Fruteau et al. 2009).

b) Experimental design

We used an established laboratory design, the artificial fruit (Whiten et al. 1996), to test for the presence of social learning. Our artificial fruits were wooden boxes with two Plexiglas doors on opposite ends (figure 1), with one-eighth of an apple inside. One door could be opened by pulling a knob (electronic supplementary material, movie S1), while the other door could be opened by sliding it to the left side holding a knob (electronic supplementary material, movie S2). One door was locked during the demonstration phase. Observers could potentially identify the door that the model used because the knobs were placed at different locations on the respective doors and because the two sides of the box differed in colour: one half was wooden while the other half was black.

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 invariably soon monopolized by a dominant individual. In subsequent trials we made sure

that this dominant was in proximity to the box so that it would continue to prevent other group members from gaining personal experience. During the initial demonstration phase, a model learned to open the box in one particular way because the alternative method was prevented. This led to consistent behavioural demonstrations of how to open the box in the presence of the subjects. The demonstration phase continued until the dominant had performed 25 successive successful trials, which consisted of approaching, manipulating and opening the correct door without prior touching of the blocked door.We conducted one session consisting of eight demonstration trials per day to keep the models motivated. Human experimenters sat about 5 m away from the box during trials, waited for the dominant to eat the piece of fruit, and then walked up to the box to bait it again. Our six models needed between 5 and 15 sessions spread over 11–63 days to complete the demonstration.

Monopolizing individuals were female for three models (Bay, Blesbokvlakte and Picnic groups) and male for three models: twice the alpha male (Donga and Nooitgedacht groups) and once the fully grown son of the alpha female (Fishing Camp group). We assigned one pull door (Picnic) and one slide door (Bay) task to female models and to male models, respectively (Nooitgedacht = pull, Donga = slide). A coin toss determined that the third female model (Blesbokvlakte) be confronted with a pull-door task, and then we assigned the slide door to the third male model (Fishing Camp) in order to have an even number of models on each type of door.

c) Data collection

During the experiments we used two means to prevent the model from monopolizing the box, so that other group members could access it as well: we either offered four dispersed boxes simultaneously or we targeted isolated individuals and placed the box close to them. Now the boxes could be opened from both sides (in two different ways). We noted who participated and whether participants manipulated the same door as the

model. All trials were filmed with a digital video camera. The data could be coded unambiguously: an individual participated if it touched the box, and location of first manipulation could be identified because of the colour coding of the two halves.

To investigate how male or female models affect the behaviour of other group members, we collected information on the number of bystanders, the frequency with which models behaved aggressively towards bystanders and whether bystanders looked at the models during the opening of the artificial fruit. We defined bystanders as individuals within 5 m of the artificial fruit. Data on the number of bystanders were collected each time the model opened the box.

d) Data analyses

For the analyses on social learning, we calculated participation rate as the percentage of individuals that touched a box once during the experimental phase. Of all the individuals that touched the box we counted the number of individuals per group that touched the same door as the model. 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 if the individual was tolerated by the model during the demonstrations. Such early experiences might have modified behaviour independently of the models' demonstrations. Also, individuals younger than one year were not counted for group size as they never participated in the experiments.

To investigate how male or female models affect the behaviour of other group members during demonstrations, we calculated for each trial the ratio of bystanders divided by group size. These values were then used to compare the six study groups with respect to attendance of demonstrations. We also compared the total number of different bystanders between groups with male or female models. To complete this last analysis, we checked the number of different bystanders in each group that attended

the demonstrations at least once. We also calculated one value per day for the frequency of aggression shown by the models. We divided the number of the models' aggressive acts by the mean number of bystanders and by the total duration of one demonstration session (as aggression was noted for the entire duration of an experimental session rather than just when a box was baited). Finally, we calculated for each bystander the frequency of looking at the model during the opening of the box. We analysed the data once for all group members and once excluding the offspring of dominant female models to test the potential effect of matriline membership.

e) ***Statistical analyses***

We conducted both χ^2 tests that treated each experimental individual as an independent data point and generalized linear binomial models (using the LME4 package under the R CRAN 2009 interface; Bates & Sarkar 2007) with group identity as a nested variable to control for potential dependencies between members of the same group. The similarity of the results indicates the robustness of our conclusions. We conducted two-level nested design ANOVA using SPSS 16.0 for all the non-binomial datasets.

Results

a) Female models promote more social learning than male models do

Individuals without any prior experience were more likely to participate in the experimental phase if the model was a female rather than a male (χ^2 tests: n = 64 potential participants, $\chi^2 = 15$, d.f. = 1, $p < 0.001$; figure 2). This difference persisted in a nested generalized linear binomial model controlling for potential group effects (GLM model using Laplace: n = 64, $z = 23.846$, $p < 0.001$).

Individuals manipulated the same side as the model significantly more often than expected by chance ($\chi 2$ test: n = 35, x2 = 4.1, d.f. = 1, $p < 0.05$). Separate analyses for male and female models revealed that individuals manipulated the same side if a female was the model (χ^2 test: n = 23, x2 = 8.5, d.f. = 1, $p < 0.01$), while side choice was not significantly different from random with male models (χ^2 test: n = 12, x2 = 0.1, d.f. = 1, ns). The difference between males and females was significant (χ^2 test: n = 35, $\chi^2 = 4.4$, d.f. = 1, $p < 0.05$; figure 3). The effect of model sex persisted in a nested generalized linear binomial model controlling for potential group effects (GLM model using Laplace: n = 35, z = 22.358, p = 0.018). The key results remained when we removed all data on members of the female models' matrilines to exclude the potentially confounding effects of mother–offspring relationships on our dataset. In these control analyses, we still found that females elicited higher levels of participation than males (χ^2 test: n = 63, $\chi^2 = 11.6$, d.f. = 1, $p < 0.001$) and that individuals more often manipulated the same side that the female model had used than expected by chance (χ^2 test: n = 34, x2 = 4.5, d.f. = 1, $p < 0.05$).

b) Causes of differences in social learning depending on the sex of the model

There was no significant difference of attendance in groups with female or male models (two-level nested-design ANOVA: n = 36, F = 0.288, p = 0.619; figure 4a). This lack of significant difference persisted when we checked how many group members were at least once a bystander (GLM model using Laplace: n = 104, z = 0.707, p = 0.489). In addition, male and female models did not differ significantly with respect to the frequency of aggressive acts towards nearby individuals during the experiments (two-level nested-design ANOVA: n = 31, F = 1.029, p = 0.365; figure 4b). In contrast, we found that individuals within 5 m of the box were more likely to look at female models at the moment of box opening than at male models (two-level nested-design ANOVA: n = 32, F = 9.935, p = 0.008; figure 4c). Excluding the offspring of dominant female models to control for effects of matriline membership did not alter the

results (attendance per trial—two-level nested-design ANOVA: $n = 36$, $F = 0.003$, $p = 0.962$; n different individuals attending—GLM model using Laplace: $n = 97$, $z = 0.055$, $p = 0.956$; frequency of aggressive acts—two-level nested-design ANOVA: $n = 31$, $F = 0.025$, $p = 0.882$; look at model—two-level nested-design ANOVA: $n = 30$, $F = 22.090$, $p < 0.001$).

Discussion

The aim of our experiment was to test whether wild vervet monkeys learn preferentially from male or female models, and if so what causes such differential social learning. In addressing these questions, we also tested whether wild vervet monkeys learn socially at all in a task that allowed the demonstration of social learning in other primate species under laboratory conditions.

a) Bystanders pay more attention to female models than to male models

The most important conclusion from our experiment is that in vervet monkeys bystanders seem to use only core members of the social group as role models for the spread of novel foraging behaviours under natural conditions. Theoreticians have pointed out that individuals should be selective about who they observe when gathering information and speculated about optimal social learning rules (Boyd & Richerson 1985; de Waal 2001; Henrich & Gil-White 2001; Giraldeau et al. 2002; Laland 2004; Mesoudi 2008). The hypothesis that individuals should copy successful group members has repeatedly received experimental support (Nicol & Pope 1999; Duffy et al. 2009; Kendal et al. 2009). In contrast to these laboratory studies, wild vervet monkeys appeared to ignore success per se: male models induced less stimulus enhancement (participation in the experiment) than female models did, and they did not induce local enhancement in other group members despite being successful at the task of opening the box and being successful in general as indicated by their dominance.

The social learning rule demonstrated by the vervets may have evolved because females, as members of the philopatric sex, might have both more detailed knowledge about the distribution of food resources in their territory and closer ties with most other group members (Smuts et al. 1987; Dunbar 1988). If this was the case, they may often be better than immigrants as sources for social learning, at least in the context of foraging. Based on our findings we hypothesize that in species in which members of one sex form the core of stable groups, the migration of members of the other sex leads to proper exchange of genetic adaptations but much less to the exchange of socially acquired adaptive information. Our hypothesis leads to the testable prediction that naturally occurring traditions based on social learning may not only be readily identified in comparisons between populations (Whiten et al. 1999; van Schaik et al. 2003) but also in comparisons between sympatric or even neighbouring groups. Such idiosyncratic group traditions should then be expressed primarily by members of the philopatric sex and the offspring.

b) Female models elicit social learning because of selective attention by group members

We had two hypotheses that could have explained why female models elicit more social learning in group members than male models do. The data do not support the idea that male models are more aggressive towards bystanders than female models are. Therefore, the hypothesis that variation in the models' tolerance may either allow or hinder social learning in bystanders is not supported. In contrast, we found clear evidence in favour of the hypothesis that group members pay selective attention to female models. Experiments on common marmosets demonstrate that animals are often limited with respect to the duration for which they can direct their attention to a specific observation task (Range & Huber 2007): individuals paid longer attention to models of the opposite sex. In ravens, individuals show more attention towards affiliated group members (Scheid et al. 2007), a rule that explains our results also. This is because though the differences between male and female models persisted

when we removed all offspring of the female models from the analyses, most other group members will still be both more related to and more familiar with female models than with male models. Our results are in line with a comparative study on keas, dogs and humans that supports the notion that selective attention according to identity of models and situation should be incorporated in studies on social learning to better understand variation in results (Range et al. 2008).

c) Methodological considerations

One important notion is that while we had planned to obtain equal numbers of male and female models for our six groups, we naturally obtained three males and two females by chance and only had to specifically attract the dominant female of the Blesbokvlakte group to replace a juvenile as model. Ideally, the models would have been preselected by us based on random choice. Thus, we cannot exclude the possibility that some unknown variable that correlates with model sex may have influenced our results. Our treatment groups did not vary systematically with respect to levels of habituation, access to human facilities, group size, number of males in the group or territory size. As we did not find any effect of group identity within each model sex class, we can conclude that these variables cannot explain our results. Thus, the sex of the model indeed seems to be the key variable for the observed differences between groups.

d) Experimental evidence for social learning in wild primates

To our knowledge, our study provides the first experimental evidence that wild primates learn socially from a model. Such evidence is paramount in laboratory studies on primates and other vertebrate taxa (Laland & Plotkin 1990; Gajdon et al. 2004; Whiten et al. 2005; Dindo et al. 2008). Under field conditions, experimental evidence for social learning has been provided only for other vertebrate taxa (Helfman & Schultz 1984; Lefebvre 1986; Warner 1988; Langen 1996; Thornton & Malapert 2008).

For primates, indirect evidence exists based on the documentation of naturally occurring diffusion of novel behaviours within a group (Itani & Nishimura 1973) or on the identification of major behavioural differences between populations that do not seem to be well explained by any ecological differences between sites (Whiten et al. 1999; van Schaik et al. 2003). Therefore, there is a clear need for more experimental field studies on learning mechanisms.

Our results provide evidence for both stimulus enhancement and local enhancement. Female models attracted more group members to the task than male models did, and monkeys with female models apparently not only learned that an object may be of interest but also where to manipulate the object. Evidence for more complex social learning mechanisms like production imitation (Hoppitt & Laland 2008) are still lacking for field studies. In fact wild keas failed in a social learning task where captive ones had succeeded (Gajdon et al. 2004). Another important future direction would be to offer artificial fruits for an extended period of time and monitor similarities between members of the same group. The persistence of different opening methods in different groups would demonstrate the establishment of arbitrary traditions for which until now there has been no clear-cut evidence from the small number of field experiments (Thornton & Malapert 2008; Pesendorfer et al. 2009).

Conclusions

It has been noted that the fact that the overwhelming majority of social learning studies have been completed in captivity limits the validity of the field as a whole (Whiten & Mesoudi 2008). Our study joins a very few others (Helfman & Schultz 1984; Lefebvre 1986; Warner 1988; Langen 1996; Thornton & Malapert 2008; Pesendorfer et al. 2009) in demonstrating that it is possible to conduct field experiments in order to bridge the gap of knowledge on decision rules for social learning and the establishment of traditions in wild animals. With more studies of this kind,

we will be able to establish the conditions under which animals may learn socially, what mechanisms they use and what circumstances lead to the formation of traditions. With such new evidence, we will soon be able to properly reflect on what specific aspects of our cultural transmission capacities are shared with other species.

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References

Bates, D. & Sarkar, D. 2007 lme4: linear mixed-effects models using S4 classes. R package version 0.9975-12. http://CRAN.R-project.org/.

Boyd, R. & Richerson, P. J. 1985 Culture and the evolutionary process. Chicago, IL: University of Chicago Press.

Call, J. & Tomasello, M. 1996 The effect of humans on the cognitive development of apes. In Reaching into thought: the minds of the great apes (eds A. E. Russon, K. A. Bard & S. T. Parker), pp. 371-403. Cambridge, UK: Cambridge University Press.

de Waal, F. B. M. 2001 The ape and the sushi master: cultural reflections of a primatologist. New York, NY: Basic Books.

Dindo, M., Thierry, B. & Whiten, A. 2008 Social diffusion of novel foraging methods in brown capuchin monkeys (Cebus apella). Proc. R. Soc. B. 275, 187-193. (doi:10.1098/rspb.2007.1318)

Duffy, G. A., Pike, T. W. & Laland, K. N. 2009 Sizedependent directed social learning in nine-spined sticklebacks. Anim. Behav. 78, 371-375. (doi:10.1016/j.anbehav.2009.05.015)

Dunbar, R. I. M. 1988 Primate social systems. Ithaca, NY:Cornell University Press.

Dunbar, R. I. M. & Thelma, E. 2001 Guenons, macaques, and baboons. In The new encyclopedia of mammals (ed. D. MacDonald), pp. 356-375. Oxford, UK: Oxford University Pres.

Fruteau, C., Voelkl, B., van Damme, E. & Noe, R. 2009 Supply and demand determine the market value of food providers in wild vervet

monkeys. Proc. Natl Acad. Sci. USA 106, 12007-12012. (doi:10.1073/pnas.0812280106)

Gajdon, G., Fijn, N. & Huber, L. 2004 Testing social learning in a wild mountain parrot, the Kea (Nestor notabilis).Learn. Behav. 32, 62-71.

Giraldeau, L.-A., Valone, T. J. & Templeton, J. J. 2002 Potential disadvantages of using socially acquired information. Phil. Trans. R. Soc. Lond. B. 357, 1559-1566. (doi:10.1098/rstb.2002.1065)

Helfman, G. S. & Schultz, E. T. 1984 Social transmission of behavioural traditions in a coral reef fish. Anim. Behav. 32, 379-384. (doi:10.1016/S0003-3472(84)80272-9)

Henrich, J. & Gil-White, F. J. 2001 The evolution of prestige: freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. Evol. Hum. Behav. 22, 165-196. (doi:10.1016/S1090-5138 (00)00071-4)

Hoppitt, W. & Laland, K. N. 2008 Social processes influencing learning in animals: a review of the evidence. Adv. Study Behav. 38, 105-165. (doi:10.1016/S0065- 3454(08)00003-X)

Itani, J. & Nishimura, A. 1973 The study of infrahuman culture in Japan: a review. In Precultural behaviour (ed. E. W. Menzel Jr), pp. 26-50. Basel, Switzerland: Karger.

Kendal, J. R., Rendell, L., Pike, T. W. & Laland, K. N. 2009 Nine-spined sticklebacks deploy a hill-climbing social learning strategy. Behav. Ecol. 20, 238-244. (doi:10.1093/beheco/arp016)

Laland, K. N. 2004 Social learning strategies. Learn. Behav. 32, 4-14.

Laland, K. N. & Plotkin, H. C. 1990 Social learning and social transmission of foraging information in Norway rats (Rattus norvegicus). Anim. Learn. Behav. 18, 246-251.

Langen, T. A. 1996 Social learning of a novel foraging skill by white-throated magpie-jays (Calocitta formosa, Corvidae): a field experiment. Ethology 102, 157-166.

Lefebvre, L. 1986 Cultural diffusion of a novel food-finding behaviour in urban pigeons: an experimental field test. Ethology 71, 295-304.

Mesoudi, A. 2008 An experimental simulation of the 'copy successful individuals' cultural learning strategy: adaptive landscapes, producer–scrounger dynamics and informational access costs. Evol. Hum. Behav. 29, 350-363. (doi:10.1016/j.evolhumbehav.2008.04.005)

Nicol, C. J. & Pope, S. J. 1999 The effects of demonstrator social status and prior foraging success on social learning in laying hens. Anim. Behav. 57, 163-171. (doi:10.1006/ anbe.1998.0920)

Pesendorfer, M. B., Gunhold, T., Schiel, N., Souto, A., Huber, L. & Range, F. 2009 The maintenance of traditions in marmosets: individual habit, not social conformity? A field experiment. PLoS ONE 4, e4472. (doi:10.1371/journal.pone.0004472)

Plotkin, H. 2007 The power of culture. In The Oxford handbook of evolutionary psychology (eds R. I. M. Dunbar & L. Barrett), pp. 11-19. Oxford, UK: Oxford University Press.

Range, F. & Huber, L. 2007 Attention in common marmosets: implication for social learning experiments. Anim. Behav. 73, 1033-1041. (doi:10.1016/j.anbehav.2006.07.015)

Range, F., Horn, L., Burgnyar, T., Gadjon, K. G. & Huber, L. 2008 Social attention in keas, dogs and human children. Anim. Cogn. 12, 181-192. (doi:10.1007/s10071-008-0181-0)

Scheid, C., Range, F. & Bugnyar, T. 2007 When, what and whom to watch? Quantifying attention in ravens (Corvus corax) and jackdaws (Corvus monedula). J. Comp. Psychol. 121, 380-386. (doi:10.1037/0735-7036.121.4.380)

Schwab, C., Bugnyar, T. & Kotrschal, K. 2008 Preferential learning from non-affiliated individuals in jackdaws (Corvus monedula). Behav. Proc. 79, 148-155. (doi:10.1016/j.beproc.2008.07.002)

Smuts, B. B., Cheney, D. L., Seyfarth, R. M., Wrangham, R. W. & Struhsaker, T. T. (eds) 1987 Primate societies. Chicago, IL: Chicago University Press.

Thornton, A. & Malapert, A. 2008 The rise and fall of an arbitrary tradition: an experiment with wild meerkats. Proc. R. Soc. B 276, 1269-1276. (doi:10.1098/rspb. 2008.1794)

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. 2003 Orangutan cultures and the evolution of material culture. Science 299, 102-105. (doi:10.1126/science.1078004)

Warner, R. R. 1988 Traditionality of mating site preferences in a coral reef fish. Nature 335, 719-721. (doi:10.1038/335719a0)

Whiten, A. 2009 The identification and differentiation of culture in chimpanzees and other animals: from natural history to diffusion experiments. In The question of animal culture (eds K. N. Laland & B. G. Galef), pp. 99-124. Cambridge, MA: Harvard University Press.

Whiten, A. & Mesoudi, A. 2008 Establishing an experimental science of culture: animal social diffusion experiments. Phil. Trans. R. Soc. B. 363, 3477-3488. (doi:10.1098/rstb.008.0134)

Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P. & Bard, K. A. 1996 Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). J. Comp. Psychol. 110, 3-14. (doi:10.1037/0735-7036.110.1.3)

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R.W. & Boesch, C. 1999 Cultures in chimpanzees. Nature 399, 682-685. (doi:10.1038/21415)

Whiten, A., Horner, V. & deWaal, F. B. M. 2005 Conformity to cultural norms of tool use in Chimpanzees. Nature 437, 737-740. (doi: 10.1038/nature04047)

Table 1. The composition of the study groups. Males are scored as adults once they have migrated, while females are scored as adults once they have given birth. Group members that did not fulfil these criteria were scored as juveniles if they were at least one year old, and as infants if they were younger.

Group	Adult male	Adult female	Juvenile	Infant	Total
Bay	4	5	7	0	16
Picnic	2	4	6	3	15
Blesbokvlakte	2	3	5	3	13
Donga	4	6	6	4	20
Nooitgedacht	3	5	6	3	21
Fishing Camp	3	5	12	3	23

Figure 1. (A) A vervet monkey manipulating the pull door, marked with wooden colour, and (B) a vervet monkey manipulating the slide door, marked with black colour.

A

B

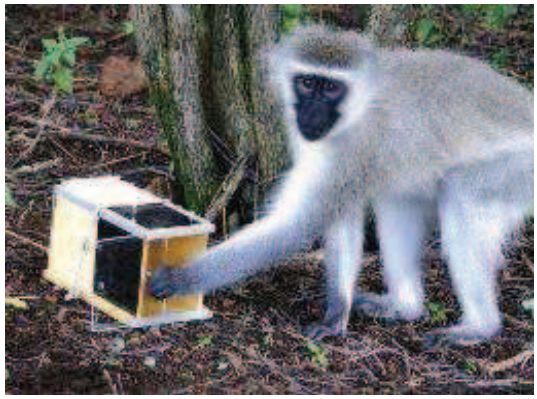


Figure 2. Percentage of individuals belonging to six different groups (Bay, Picnic and Blesbokvlakte with female models; Donga, Nooitgedacht and Fishing Camp with male models) that participated in the experiment. Numbers in white represent sample sizes for each group.

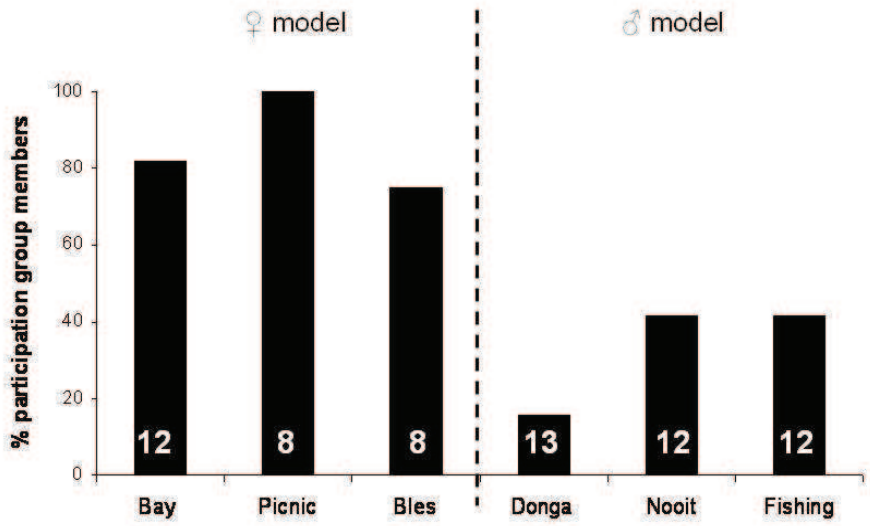


Figure 3. Number of individuals in six different groups that manipulated the box either on the same side as the model (black parts) or on the opposite side (white parts).

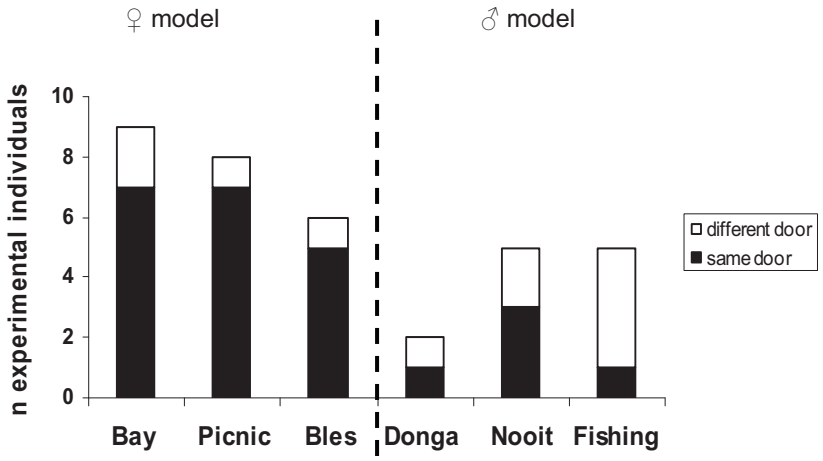
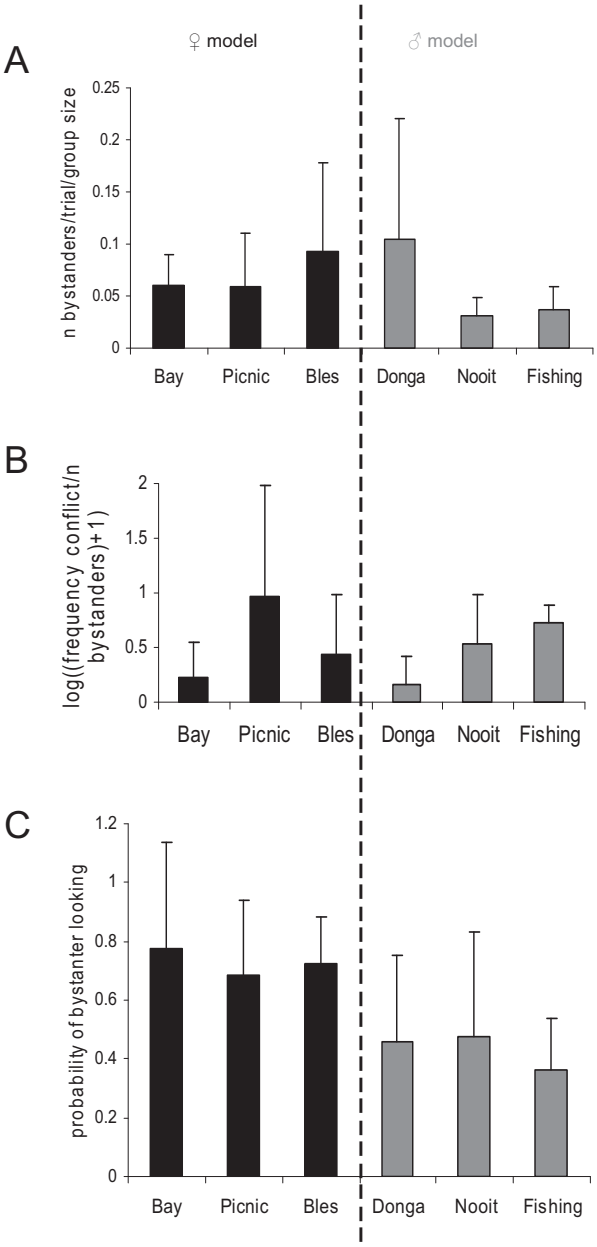


Figure 4. (A) Number of individuals within 5 m of the box (bystanders) per trial corrected for group size in six different groups. (B) The log-transformed frequency of aggression performed by the model towards bystanders per experimental session, and (C) the mean probability for each bystander that it looks at the model at the moment of box opening. For all three results, means ((A) per trial, (B) per experimental session, (C) of individual bystander means) and s.d. are shown. Results for groups with female models (Bay, Picnic and Blesbokvlakte) are shown in black bars, while results for groups with male models (Donga, Nooitgedacht and Fishing Camp) are shown in grey bars.


A
♀ model
♂ model
n bystanders/trial/group size
0.25
0.2
0.15
0.1
0.05
0
Bay
Picnic
Bles
Donga
Nooit
Fishing
B
log((frequency conflict/n bystanders)+1)
2
1.5
1
0.5
0
Bay
Picnic
Bles
Donga
Nooit
Fishing
C
probability of bystanter looking
1.2
1
0.8
0.6
0.4
0.2
0
Bay
Picnic
Bles
Donga
Nooit
Fishing

Part 1.B.

Contact with human facilities appears to enhance technical skills in wild vervet monkeys (*Chlorocebus aethiops*)

Article to be resubmitted to *Folia Primatologica,* with most of the reviewers' comments incorporated in this version

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Abstract

Technical abilities of primates are typically tested in the laboratory. It has been argued that close contact between animals and humans may lead to an increase in skills due to an 'enculturation' of subjects. Here, we provide evidence that exposure to human facilities may improve wild vervet monkeys' technical skills in a social learning task using the 'artificial fruit' approach. Two of our six study groups had access to human facilities within their territories. Only members of these two groups were likely to successfully open the artificial fruit during their first attempt. Success appeared to be independent of individual sex or the type of task. Our results highlight the possibility that human enculturation may allow captive monkeys to acquire more technical skills than their wild counterparts, and we suggest that this possibility should be tested in further field experiments.

Introduction

The 'technical intelligence hypothesis' (Byrne 1997) proposes that the evolution of technical skills in primates (and possibly also in birds, see Huber & Gajdon 2006) might have selected for an increase in relative brain size. Laboratory studies show evidence for a variety of technical skills present in both primates and birds, including tool use (Whiten et al. 2005; Bonnie et al. 2006; Bentley-Condit and Smith 2010) and opening of artificial fruits – boxes that contain food which can be opened in various ways (capuchin monkeys: Custance et al. 1999; Dindo et al. 2008; chimpanzees: Whiten et al. 1996; Whiten 1998; gorillas: Stoinski et al. 2001; marmosets: Caldwell and Whiten 2004; orang-utans: Stoinski and Whiten 2003). Artificial fruits were invented to test for social learning rather than for technical skills. Nevertheless, the subjects' ability to open the artificial fruit in the same way as a model previously demonstrated was part of the evidence for social learning. Of all the species tested on artificial fruits, only marmosets failed at opening the box after demonstration. Thus, the results suggest that most primates are able to open such boxes, at least after having been exposed to demonstrations by conspecifics. However, there is a lack of experiments on wild animals to test whether captive conditions may affect the ability to open artificial fruits. Even in the only study conducted in the wild that used artificial fruits to test for social learning the subjects were orang-utans that had been raised in captivity except one individual offspring of a rehabilitant (Custance et al. 2001). Therefore, the results might have been influenced by the subjects' previous experience in captivity. In another field study, Pesendorfer et al. (2009) found that wild marmoset monkeys learned to open artificial fruits through individual learning but without specifying whether individuals solved the task immediately or only after repeated exposure.

Comparisons between results obtained in captivity and results obtained under natural conditions are important because it is known that captivity can induce the development of capacities beyond standard natural abilities, known as 'enculturation effect' (Whiten and van Schaik 2007).

Enculturation is commonly observed when great ape infants are raised like human children, which may lead to unusually elaborate comprehension of human language in great apes (Savage-Rumbaugh and Levin 1994). Captivity may also cause an increase in socially guided exploration opportunities, which could bring about enhanced cognitive performance (Gardner and Gardner 1989; Tomasello and Call 2004). For example, captive capuchin monkeys that have contact with a larger set of objects and more "leisure" time to manipulate them exhibit an even broader range of object manipulation and tool use behaviours than their wild congeners (Beck 1980; Gibson 1990; Visalberghi 1990; Fragaszy et al. 2004). Further experiments have shown that human-reared capuchins behaved better in relation to social learning of tool use than individuals that were mother-reared (Fredman and Whiten 2008), . Together, these experiments suggest that the cognitive abilities of adult primates may depend on experimentally induced variation in environmental conditions during development. However the consequences of this 'enculturation' issue are controversial (Tomasello et al. 1993; Bering 2004; Tomasello and Call 2004) and the discussion has hitherto centred on evidence that apes reared in intimate interaction with humans appear to have heightened powers of social cognition that include imitation. Alternative possibilities include that the enhanced abilities of enculturated apes are due to them being less neophobic towards objects in general or that 'enculturation' enhances just attention towards humans. Also the human-raised monkeys had more extensive experience with different objects and tools than their wild counterparts. During their lives they may have learned about the properties of these objects (Call and Tomasello 1996), rendering it easier for them to socially learn new ways to utilize them.

However, the absence of documentation of certain skills in the wild does not necessarily imply that the primates are incapable of solving the same tasks as captive monkeys. In contrast to laboratory-based studies, field experiments on primates are rare and we are not aware of any study that has used the same experimental design in both laboratory and wild animals of the same species. Outside primates, keas failed to imitate in a

task where imitation had been previously demonstrated in the laboratory (Gajdon et al. 2004). There is thus a clear need for more experimental field studies for a proper appreciation of the animals' cognitive skills, both in the context of social learning and in the context of technical skills.

Here we investigated the possibility that exposure to human facilities enhances technical skills in an experiment using six groups of wild vervet monkeys. We subjected the six groups to a social learning task, using the artificial fruit design (van de Waal et al. 2010). Initially, a dominant individual monopolised the baited box where one of two doors was locked. Following individual learning, this led to consistent behaviour when opening the box. In a previous study on the same population, van de Waal et al. (2010) found that other group members were more likely to participate and manipulate the same door when the model was female, rather than male. In the current study, we analyse which of three variables predict the successful opening of the box during the first trial. First, female models may be more likely to facilitate successful opening than male models. Second, as one door had a knob for pulling and the other door a knob for sliding, the type of task may cause variation in success. Finally, if enculturation affects technical skills, then contact with human facilities might affect individual success when opening artificial fruit boxes. We took advantage of the fact that two of the six groups had regular access to human facilities (a picnic site and fishermen's houses).

Material and Methods

a) Study site and population

Experiments were conducted between 2006 and 2008 on six neighbouring groups of habituated wild vervet monkeys (*Chlorocebus aethiops*) at Loskop Dam Nature Reserve, South Africa. The reserve, situated 250km north-east of Johannesburg, covers 25,000 ha. Vervet monkeys live in stable family groups which, during our experiments, varied

in size from 13 to 23 individuals. Groups were composed of multiple males and several matrilines (females and their offspring), and adults of both sexes could be ranked in separate linear hierarchies (van de Waal et al. 2010). Females remain in their natal group throughout their life while males disperse to non-natal groups when they are sexually mature, usually at around 4 years of age. 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. Exact group compositions can be found in Table 1 in van de Waal et al. (2010).

All groups had been habituated to the presence of human researchers for at least one year before they were tested and could be approached at less than 5m. All individuals could be recognized based on a combination of age, sex and face characteristics. Of the six groups, two were in regular contact with humans and their facilities (Fishing camp and Picnic groups). These human structures consisted on barbecue places, toilettes and dust bins in the two sites as well as three fisherman huts in the Fishing camp home range that could be rented by fishermen. Both sites were frequently occupied by humans mainly during week-ends and holidays period, also maintenance workers of the reserve would regularly clean and check them. These human structures were only a small part of much larger home ranges of these two groups of vervet monkeys meaning that contacts with humans and their structures were not constant and spread in time. We have no quantified information about the time these monkeys spent around humans or their facilities neither of the type of contact. Nevertheless, at both sites we observed humans feeding the monkeys, monkeys entering dustbins, monkeys pushing windows to enter toilettes, and monkeys stealing food from humans. The ‘Picnic group’ and the ‘Donga group’ had been exposed to foraging experiments before (Fruteau et al. 2009) but these experiments did not involve any technical problem solving by the monkeys.

b) Experimental design

We used an established laboratory design, the 'artificial fruit' (Whiten et al. 1996). Our 'artificial fruits' were wooden boxes with two Plexiglas doors, on opposite ends (Fig. 1), with 1/8 of an apple inside. One door could be opened by pulling a knob while the other door could be opened by sliding it to the left side holding a knob (movies can be found following the link http://rspb.royalsocietypublishing.org/content/suppl/2010/03/16/rspb.2009.2260.DC1.html). One door was locked during the demonstration phase for the social learning experiment (van de Waal et al. 2010). Observers could potentially identify the door that the model used because the knobs were placed at different locations on the respective doors and because the two sides of the box differed in colour: half of the box with one door was wooden while the other half was black. The aspects important for the social learning task are described elsewhere (van de Waal et al. 2010).

Monopolizing individuals became models, in three groups they were the alpha female (Bay, Blesbokvlakte and Picnic groups) and in the three other groups they were dominant males: twice the alpha male (Donga and Nooitgedacht groups) and once the fully grown son of the alpha female (Fishing Camp group). We assigned one pull door (Picnic) and one slide door (Bay) task to female models and to male models, respectively (Nooitgedacht = pull, Donga = slide). A coin toss determined that the third female model (Blesbokvlakte) be confronted with a pull-door task, and then we assigned the slide door to the third male model (Fishing Camp) in order to have an even number of models on each type of door. In conclusion, the two groups that are in regular contact with humans differed with respect to the sex of the model and the type of door the model opened during demonstrations.

c) Data collection and analyses

We noted for each group member whether it managed to open the box during its first trial and via the door it touched first. An individual could make several contacts and movements with that door; however, if the subject switched to the other door or if it left we scored 'failure'. The length of the first manipulation, consisting of the duration from the first contact with a door until switching door or leaving, was also recorded for each participant. An individual's first trial could take place at any time when the experimental set-up was available (total n of individuals participating= 53, from which total after demonstrations=35, and total before/during demonstration=18). Individuals were said to have opened the door successfully if they accessed the food inside the box via the door they first touched. While this criterion may appear very restrictive, only three additional individuals that failed according to our criterion solved the task at some later moment. Therefore, the success at the first trial was a good estimator of a vervet's manipulative skills. The models in each group were excluded from the analysis because we introduced several intermediate levels of complexity (door half closed, held up by a stick, etc) to make sure that they would open the box successfully. Individuals younger than one year never participated in the experiments. As van de Waal et al. (2010) found no differences of participation due to age or sex of participants we excluded these variables from the current analyses. We investigated three variables: sex of the model (male or female), type of door that individuals tried to open (pull door or slide door), and access to human resources (yes or no).

d) Statistical analyses

We conducted generalised linear binomial models (using the lme4 Package (Bates and Sarkar 2007) under the R CRAN 2009 interface) with group identity as a nested variable to control for potential dependencies between members of the same group. We analysed separately whether the sex of the model, the type of door manipulated, and access to human

facilities affected the probability that individuals opened the box during their first attempt. We also conducted a non-parametric statistical test using SPSS 16.0.

Results

Overall, success rate in opening the boxes during the first trial was relatively low: only 17(of which 10 during demonstrations, 7 after demonstrations) of 53 individuals (32.1 %) successfully accessed the food within the box. Neither the sex of the model (nested GLM model using Laplace: n=53, z=-0.034, p=0.973, Fig. 2) nor the type of door (nested GLM model using Laplace: n=53, z=0.224, p=0.823, Fig. 2) significantly influenced the probability of success. In contrast, individuals belonging to groups that had regular contact to human facilities were significantly more likely to succeed than individuals belonging to groups without such exposure (nested GLM model using Laplace: n=53, z=3.831, p<0,001, Fig. 2). This result was apparently not due to a longer first manipulation length as we did not find that successful individuals were more persistent than unsuccessful individuals (Mann-Witney U-test, n=53, Z=-0.385, p=0.700, Fig.3)

Discussion

We asked whether the sex of a model, the type of door manipulated, and/or a monkey's pre-exposure to human artefacts influenced the probability that wild vervet monkeys would successfully open an artificial fruit box during their first attempt. According to earlier results, social learning from female models with respect to participation and local enhancement does not seem to prepare subjects for successful opening of the box (van de Waal et al. 2010). Thus, the monkeys did not seem to make detailed observations of fine tuned movements that would enable them to copy the movement patterns. Also, we did not find any

evidence that either of the two necessary door-opening techniques was easier for the monkeys to perform as success rates were equally low independently of the door manipulated. As the duration of the first manipulation did not differ between successful and unsuccessful individuals, the hypothesis that higher success rates of opening at first trial might be due to reduced neophobia of monkeys that are in contact with humans and human facilities is not supported by our data. In contrast, our results favour the idea that exposure to humans and human facilities allowed our subjects to gain the necessary knowledge and experience that enabled them to perform better in our experiment than unexposed conspecifics did. Low manipulation skills of wild primates have previously been documented in studies on marmosets (Hasley et al. 2006) and on baboons (Laidre 2008). A possible explanation for these observations is that wild primates have less time for the exploration of novel objects, due to trade-offs with other important tasks like predator avoidance and/or competition over resources. While sample size is small (6 groups) and hence similar studies should be conducted at other sites, our results corroborate the point made by others (Gajdon et al. 2004; Whiten and Mesoudi 2008) that results obtained in captivity should be interpreted with care and ideally be repeated on wild individuals that are naive with respect to human influences to test whether similar results can be obtained.

While field experiments are relatively rare, there is accumulating evidence that it is feasible to address questions about cognitive mechanisms in the wild. Examples involve fishes (Helfman and Schultz 1984; Warner 1988), birds (Lefebvre 1986; Langen 1996; Gajdon et al. 2004, Raihani and Ridley 2008), and mammals including primates (Pesendorfer et al. 2009, Thornton and Malapert 2009, van de Waal et al. 2010). With respect to the results of the current study it would be interesting to conduct the same experiment on captive vervet monkeys. If captive vervets are generally successful in opening the boxes during their first attempt with or without prior demonstrations, the results would support the hypothesis that exposure to human structures provides an environment that is likely to enculturate primates in a way that makes them more apt at solving technical

problems. The ability to solve technical problems may also enable primates to perform better at other cognitive processes, and hence may facilitate imitation or other relatively sophisticated social learning mechanisms (Fredman and Whiten 2008). Such potential cross-links between cognitive domains deserve more attention in future studies.

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References

Bates D, Sarkar D. (2007). lme4: linear mixed-effects models using S4 classes. R package version 0.9975-12. http://CRAN.R-project.org/.

Beck BB (1980). *Animal tool behaviour: the use and manufacture of tools by animals*. Garland STPM Press, New York.

Bentley-Condit VK and Smith EO (2010). Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour* 147: 185-32A.

Bering J (2004). A critical review of the "enculturation hypothesis": the effects of human rearing on great ape social cognition. *Animal Cognition* 7: 201-212.

Bonnie KE, Horner V, Whiten A, de Waal FBM (2006). Spread of arbitrary customs among chimpanzees: a controlled experiment. *Proceedings of the Royal Society 'B'* 274: 367-372.

Byrne RW (1997). The technical intelligence hypothesis: an additional evolutionary stimulus to intelligence? In *Machiavellian intelligence II: extensions and evaluations* (Whiten A, Byrne RW, eds.), pp. 289-311, Cambridge University Press, Cambridge.

Caldwell CA, Whiten A (2004). Testing for social learning and imitation in common marmosets, *Callithrix jachus*, using an "artificial fruit". *Animal Cognition* 7: 77-85.

Call J, Tomasello M (1996). The effects of humans on the cognitive development of apes. In: *Reaching into thought: The minds of the great apes*. (Russon AE, Bard KA, Parker ST, eds), pp 371-403. Cambridge University Press, Cambridge.

Custance DM, Whiten A, Fredman T (1999). Social learning of artificial fruit processing in enculturated capuchin monkeys. *Journal of Comparative Psychology* 113: 13-23.

Custance DM, Whiten A, Sambrook T, Galdikas B (2001). Testing for social learning in the "artificial fruit" processing of wildborn orangutans (*Pongo pygmaeus*), Tanjung Puting, Indonesia. *Animal Cognition* 4: 305-313.

Dindo M, Thierry B, Whiten A. (2008). Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proceedings of the Royal Society 'B'* 275: 187-193.

Fredman T, Whiten A (2008). Observational learning from tool using models by human-reared and mother-reared capuchins monkeys (*Cebus apella*). *Animal Cognition* 11: 295-309.

Fragaszy DM, Izar P, Visalberghi E, Ottoni EB, de Oliveria MG (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology* 64: 359-366.

Fruteau C, Voelkl B, van Damme E, Noe R (2009). Supply and demand determine the market value of food providers in wild vervet monkeys. *PNAS* 106: 12007-12012.

Gajdon G, Fijn N, Huber L (2004). Testing social learning in a wild mountain parrot, the Kea (*Nestor notabilis*). *Learning & Behavior* 32: 62-71.

Gardner BT, Gardner RA (1989). Prelinguistic development of children and chimpanzees. *Human Evolution* 4: 433-460.

Gibson KR (1990). Tool use, imitation, and deception in a captive cebus monkey. In *"Language" and intelligence in monkeys and apes:*

comparative and developmental perspectives (Parker ST, Gibson KR, eds), pp 205-218. Cambridge University Press, Cambridge.

Halsey LG, Bezerra BM, Souto AS (2006) Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task? *Animal Cognition* 9: 229-233.

Helfman GS, Schultz ET (1984). Social transmission of behavioural traditions in a coral reef fish. *Animal Behaviour* 32: 379-384.

Huber L, Gajdon BT (2006). Technical intelligence in animals: the kea model. *Animal Cognition* 9: 295-305.

Laidre ME (2008). Spontaneous performance of wild baboons on three novel food-access puzzles. *Animal Cognition* 11: 223-230.

Langen TA (1996). Social learning of a novel foraging skill by white-throated magpie-jays (*Calocitta formosa, Corvidae*): a field experiment. *Ethology* 102: 157-166.

Lefebvre L (1986). Cultural diffusion of a novel food-finding behaviour in urban pigeons: an experimental field test. *Ethology* 71: 295-304.

Pesendorfer MB, Gunhold T, Schiel N, Souto A, Huber L, Range F (2009). The Maintenance of Traditions in Marmosets: Individual Habit, Not Social Conformity? A Field Experiment. *PLoS ONE* 4(2): e4472. Doi:10.1371/journal.pone.0004472.

Raihani NJ, Ridley AR (2008). Experimental evidence for teaching in wild pied babblers. *Animal Behaviour* 75: 3-11.

Savage-Rumbaugh ES, Levin R (1994). *Kanzi: the ape at the brink of the human mind*. New York, NY: Wiley.

Stoinski TS, Whiten A (2003). Social learning by orangutans in a simulated food-processing task. *Journal of Comparative Psychology* 117: 272-282.

Stoinski TS, Wrate JL, Ure N, Whiten A (2001). Imitative learning by captive western lowland gorillas (*Gorilla gorilla gorilla*) in a simulated food-processing task. *Journal of Comparative Psychology* 115: 272-281.

Thornton A, Malapert A (2009). The rise and fall of an arbitrary tradition: an experiment with wild meerkats. *Proceedings of the Royal Society 'B'* 276: 1269-1276.

Tomasello M, Call, J (2004). The role of humans in the cognitive development of apes revisited. *Animal Cognition* 7: 213-215.

Tomasello M, Kruger AE, Ratner H (1993). Cultural learning. *Behavioral & Brain Sciences* 16: 595-552.

Visalberghi E (1990). Tool use in *Cebus*. *Folia Primatologica* 54: 146-154.

van de Waal E, Renevey N, Favre CM, Bshary R (2010). Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society of London 'B'* in press.

Warner, RR (1988). Traditionality of mating site preferences in a coral reef fish. *Nature* 335: 719-721.

Whiten A (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology* 112: 270-281.

Whiten A, van Schaik CP (2007). The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society 'B'* 362: 603-620.

Whiten A, Mesoudi A (2008). Establishing an experimental science of culture: animal social diffusion experiments. *Philosophical Transactions of the Royal Society 'B'* 363: 3477-3488.

Whiten A, Custance DM, Gomez JC, Teixidor P, Bard KA (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psycholology* 110: 3-14.

Whiten A, Horner V, de Waal FBM (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature* 437: 737-740.

Figure 1. The baited box can be opened in two ways
(A) Vervet 'Uranus' manipulating the pull door, marked with wooden color. (B) Vervet 'Naja' manipulating the slide door, marked with black color.

A

B

Figure 2. Monkeys with contact to human structures are successful manipulators
The number of individuals in six groups that either managed to open the pull door (black bars) or the slide door (grey bars) or did not manage to open (white bars) the box on their first attempt. The graph is split vertically in two groups depending on the sex of the model. On the top of each histogram bar is written the type of door assigned to the group model (pull or slide). Grey boxes: groups with access to human structures (Picnic, Fishing).

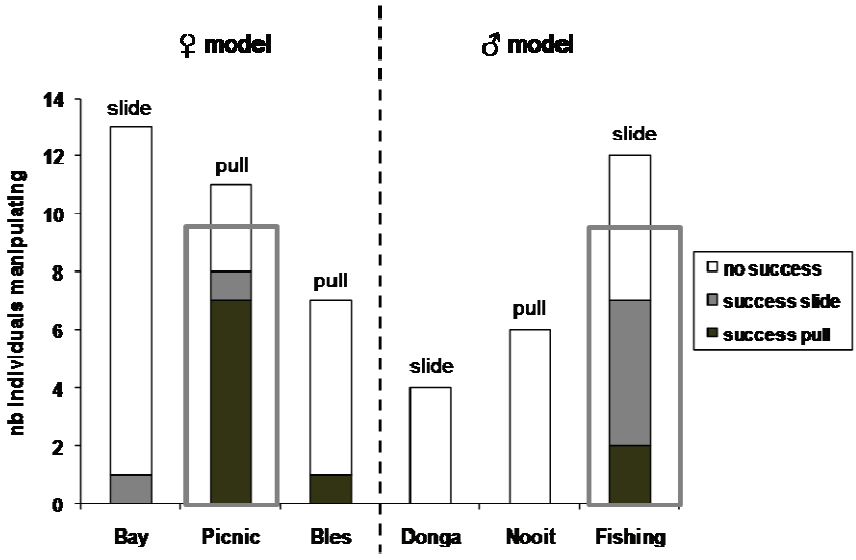
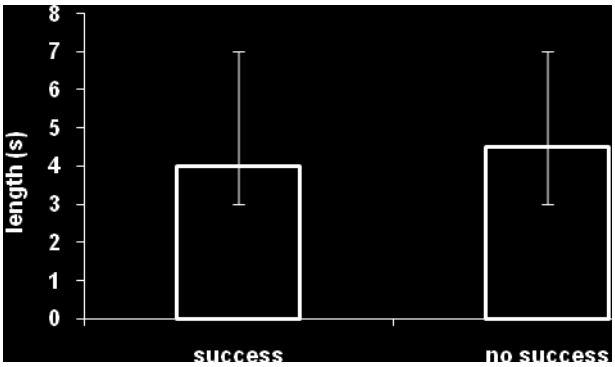


Figure 3. Manipulation time is not linked to the successful opening of a door
Duration of the first manipulation for successful manipulators ('success') and unsuccessful manipulators ('no success'). Median and interquartiles using one value per individual are shown.



Chapter 2) 'Complex' artificial fruit

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

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Abstract

Social learning is the basis for the formation of traditions in both human and non-human animals. Field observations and experiments provide evidence for the existence of traditions in animals but they do not address the underlying social learning mechanisms. Here, 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. Extending a previous experiment, where a model demonstrated how to open one of two doors of a box containing a reward, we introduced a two-step design where models had to remove a bar to untie a rope that blocked a single door. The models were high ranking individuals that monopolised 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 where the rope was not functional. Under these conditions, sequential copying of the two-step opening did not occur. However 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.

Introduction

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 non human 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, like potato washing in Japanese macaques (Itani & Nishimura 1973), the opening of milk bottles by blue tits (Hinde & Fisher 1951) or song dialects in white-crowned sparrows (Marler & Tamura 1964). Second, novel behaviours were experimentally introduced and their spread / persistence documented. Classic examples are the exchange of entire fish sub-populations 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 (Thornton & Malapert 2009) and marmosets (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 in chimpanzees and orang-utans by identifying differences in behaviour between populations

that do not seem to be based on differences in ecology (Whiten et al. 1999; van Schaik et al. 2003).

In general, the many field studies on social learning were not designed to test which exact social learning mechanism enabled the spread of information. Until now, studies on social learning mechanisms have been conducted almost exclusively in the laboratory. These laboratory experiments focussed on production imitation as the supposedly most complex social learning mechanism and indeed demonstrated that a variety of vertebrate species may be able to learn socially through production imitation (Laland & Plotkin 1990; Bonnie et al. 2006, Horner et al. 2006, Dindo et al. 2008). However, the demonstration that animals are able to learn socially in captivity does not necessarily imply that wild animals of the same species regularly use social learning to solve problems. 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, keas 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 their 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 (interacting with 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 for local enhancement (touching the same door as the model) when models were females (for definitions see Hoppitt & Laland 2008). Despite the occurrence of social learning, individuals were unlikely to successfully open the box on the first trial (van de Waal & Bshary submitted), indicating that the technical difficulty of the task was considerable.

Here we extended the experiment by van de Waal et al. (2010) by presenting a two-step artificial fruit task to the same six groups of wild vervet monkeys. The first steps 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 monopolised the box in each group. However, only three individuals managed to open the box by trial and error, while we could use the other three groups as controls.

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 will simply describe how these variables may affect social learning. Second, we asked whether individuals copied sequential actions to successfully 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 due to their previous experience with the simple artificial fruit (van de Waal et al. 2010). During the experiment the rope was in place but not functional so that the door could be opened

without prior removal of the bar. We had hoped to be able to test for the imitation of arbitrary movements as well (production imitation, Hoppitt & Laland 2008). This would have been possible if the three models had differed in the way they removed the bar, like pushing or pulling. However, all three models pulled the bar out of the holding rings, preventing us from addressing this possibility. Finally, we asked whether model presence would increase individual success at opening the two-step box. Succeeding in these technical tasks is not simple for vervet monkeys as the majority of subjects failed in the previous experiment (van de Waal & Bshary submitted). Therefore, we conducted a second experiment where the removal of the bar was mandatory for successful opening of the door.

Material & Methods

a) Study site and population

Experiments were conducted between 2007 and 2009 on six neighbouring groups of habituated wild vervet monkeys (*Chlorocebus aethiops*) at Loskop Dam Nature Reserve, South Africa. The reserve, situated 250km north-east 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 two 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: 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 manipulation of knobs on Plexiglas door through either pulling or sliding.

b) 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 x 10 x 20 cm) painted in blue with one Plexiglas pull door blocked by a rope attached to the top of the box by a aluminium bar (Fig.1). Each box contained 1/8 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 (video 1). The rope was blocked under the box during the demonstration phase obliging the model to remove the bar to access the reward.

As we worked with wild groups we could not choose a model and train it in isolation of 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. In only half of the groups, a model learned to open the box consistently.

In subsequent trials we made sure that this successful model was in proximity of the box so that it would continue to 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 5m 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 4 and 12 sessions spread over 4 to 57 days to complete the demonstration. The identity 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, while the latter model replaced the dominant male of the group who gave up after several unsuccessful attempts to open the box.

c) Data collection

During the experiments we used two methods to prevent the model from monopolising the box, so that other group members could access it as well. We either offered four dispersed boxes simultaneously or we targeted isolated individuals and placed the box close to them. In the first experiment 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 access the reward. For both experiments, we noted who 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 one meter. 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, location of 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 opening successfully the door in the process.

d) 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 the percentage of participating monkeys with and without model that 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 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 one year old from our analyses involving group sizes as these individuals never participated in the experiments.

e) Statistical analyses

We conducted non parametric statistical tests using SPSS 16.0.

Results

a) Do previous demonstrations of a model increase the participation of group members?

In the first experiment on the ability to copy a sequence of actions, individuals from groups with models were not more likely to participate in the experiment than individuals from groups without model (individuals with models: 12 out of 44 participating, individuals without models: 16 out of 34 participating; χ^2 test, χ^2 =3.263, df=1, p=0.071). Actually, 27 of the 28 participants of this experiment had been successful at opening the two-door artificial fruit in a previous experiment, while only 8 of 50 individuals that did not participate had managed to open the two-door artificial fruit. The one new participant at the complex artificial fruit was a juvenile of the Picnic group that had been less than a year old during the simple artificial fruit experiment.

3 out of 18 individuals in the Bay group with the dominant female as model participated, while 9 out of 17 individuals in the Fishing Camp group with the fully grown son of the alpha female as model participated, and 0 out of 9 individuals in the Donga group with the juvenile female of the dominant matriline as model participated. Due to this great variation in participation, 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 access the reward, 11 monkeys from groups with model participated, whereas 6 monkeys from control groups manipulated the box (χ^2 test, χ^2 =6.08, df=1, p=0.435).

b) Do repeated demonstrations of a model allow copying of a sequence of actions?

For the first touch, we found that very few individuals in groups with model (n=3) and no individuals in control groups touched the bar first, most of all experimental individuals touched the door first (9 with models, 16 without models), (Exact Fischer test, n=28, p=0.067, Fig.2A). in contrast, we found that monkeys with models touched significantly more often the bar at some point during their first interaction with the box than monkeys of control groups did (Exact Fischer test, n=28, p=0.001, Fig.2B). This result was apparently not due to a longer first manipulation length as we did not find that unsuccessful individuals in groups with models were more persistent than individuals in groups without models (Mann-Witney U-test, n=20, Z=-0.152, p=0.912, Fig.2C). The exposure to a model did not significantly affect the probability that individuals managed to open the box and gain the reward (Exact Fischer test, n=28, p=0.401, Fig.2D).

c) Does a model increase the probability that subjects open the box with the rope functional?

We found no difference in the number of individuals from groups with or without models that touched the bar during the first manipulation (Exact Fischer test, n=17, p=0.62, Fig.3A). In addition, only 2 individuals with models and 2 individuals without models succeeded in solving the two-step task, yielding no significant differences between individuals in groups with or without models (Exact Fischer test, n=28, p=1, Fig.3B).

Discussion

We presented a two-step design artificial fruit to wild vervet monkeys with or without knowledgeable models to ask whether wild vervet monkeys 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 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 solve the entire two-step task and hence get access to the reward inside the artificial fruit.

Our results provided no evidence that vervet monkeys copy socially a sequence of actions. Instead, we found evidence for local enhancement learning (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 model. This result was not caused by different durations of manipulations. These data confirm results 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 for an individual's decision to learn socially or not (Boyd & Richerson 1995, 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 where more individuals are available to act as models would be necessary to address the importance of model identity in the two-step task.

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. 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 inside but also probably remembered whether they had managed to open the two door artificial fruit (van de Waal & Bshary submitted). Even if we 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 individuals that had opened the two-door artificial fruit were more 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 that monkeys in this experiment failed to copy of 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 quite 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 naive monkeys would be necessary to either confirm or extend the current results.

The key conclusion of our second experiment, in which the rope was functional, is that the task is not simple for vervet monkeys for various reasons. Several individuals failed to pull the knob to open the door, both in the two-door experiment (van de Waal & Bshary submitted) and in the current experiment. The removal of a bar that was stuck in two rings was even more difficult. First, many individuals apparently did not understand that removal of the bar was an essential requirement for the solution of the task and did not even touch it. Second, even those that did touch the bar typically failed to remove it. Limitations in technical abilities should be considered in any future experiments that test for other social learning mechanisms like 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 note 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 submitted).

Until recently, social learning experiments were conducted primarily on captive subjects, with some exceptions (Helfmann & Schultz 1984; Warner 1988, Lefebvre 1986; Langen 1996). This bias towards laboratory experiments raises the question as to 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, in press). 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, 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 Müller & Cant (in press) showed that food preferences as well as foraging techniques can be persistent and learned socially. 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) suggest 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. We hope that more field experiments on a variety of species will be conducted soon to broaden our knowledge of social learning and its underlying mechanisms in wild animals.

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References

Bonnie, K. E., Horner, V., Whiten, A. & de Waal, F. B. M. 2006. Spread of arbitrary customs among chimpanzees: a controlled experiment. Proceedings of the Royal Society B, **274**, 367-372.

Boyd, R. & Richerson, P. J. 1985. *Culture and the evolutionary process.* Chicago, IL: University of Chicago Press.

Cheney, D. L. & Seyfarth, R. M. 1983. Nonrandom dispersal in free-ranging vervet monkeys social and genetics consequences. American Naturalist, **122**, 392-412.

Dindo, M., Thierry, B. & Whiten, A. 2008. Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). Proceedings of the Royal Society B, **275**, 187-193.

Fruteau, C., Voelkl, B., van Damme, E. & Noe, R. 2009 Supply and demand determine the market value of food providers in wild vervet monkeys. Proceedings of the National Academy of Sciences of the United States of America - Biological Sciences, **106**, 12007-12012.

Gajdon, G., Fijn, N. & Huber, L. 2004. Testing social learning in a wild mountain parrot, the Kea (*Nestor notabilis*). Learning & Behavior, **32**, 62-71.

Gardner, B. T. & Gardner, R. A. 1989. Prelinguistic development of children and chimpanzees. Human Evolution, **4**, 433-460.

Helfman, G. S. & Schultz, E. T. 1984. Social transmission of behavioural traditions in a coral reef fish. Animal Behaviour, **32**, 379-384.

Hinde, R. A. & Fisher, J. 1951. Further observations on the opening of milk bottles by birds. British Birds, **44**, 393-396.

Hoppitt, W. & Laland, K. N. 2008. Social processes influencing learning in animals: a review of the evidence. Advances in the Study of Behavior. **38**, 105-165.

Horner, V., Whiten, A., Flynn, E. & de Waal, F. B. M. 2006. Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. Proceedings of the National Academy of Sciences of the United States of America - Biological Sciences, **103**, 13878-13883.

Itani, J., Nishimura, A .1973. The study of infrahuman culture in Japan: A review. Symposium of the IVth International Congress of Primatology. In : *Precultural Primate Behavior*. vol 1, pp 26-50. Basel: Karger.

Laland, K. N. & Plotkin, H. C. 1990. Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). Animal Learning & Behavior, **18**, 246-251.

Langen, T. A. 1996 Social learning of a novel foraging skill by white-throated magpie-jays (*Calocitta formosa, Corvidae*): a field experiment. Ethology, **102**, 157-166.

Laland, K. N. 2004. Social learning strategies. Learning & Behavavior, **32**, 4-14.

Laland KN & Janik V 2006 The animal cultures debate. *Trends in Ecology & Evolution* **21***,* 542-547.

Lefebvre, L. 1986. Cultural diffusion of a novel food-finding behaviour in urban pigeons: an experimental field test. Ethology, **71**, 295-304.

Marler, P. & Tamura, M. 1964. Song 'dialects' in three populations of white-crowned sparrows. Science, **146**, 1483-1486.

Martin, P. & Bateson, P. 1986. *Measuring behaviour, an introductory guide*. Cambridge: Cambridge University Press.

Müller, C. A., & Cant, M. A. (in press). Imitation and traditions in wild banded mongooses. Current Biology.

Pesendorfer, M. B., Gunhold, T., Schiel, N., Souto, A., Huber, L. & Range, F. 2009. The Maintenance of Traditions in Marmosets: Individual Habit, Not Social Conformity? A Field Experiment. *PLoS ONE*, 4(2): e4472. doi:10.1371/journal.pone.0004472.

Plotkin, H. 2007. The power of culture. In: *The Oxford Handbook of Evolutionary Psychology* (Ed. by R. I. M. Dunbar & L. Barrett), pp. 11-19. Oxford: Oxford University Press.

Reader, S. M. & Biro, D. (in press). Experimental identification of social learning in wild animals. Learning & Behavior.

Reader, S. M., Kendal, J. R., & Laland, K. N. (2003). Social learning of foraging sites and escape routes in wild Trinidadian guppies. Animal Behaviour, **66**, 729-739.

van Schaik C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill M. 2003. Orangutan cultures and the evolution of material culture. Science*,* **299**, 102-105.

Struhsaker, T. T. 1967 Social structure among vervet monkeys (*Cercopithecus aethiops*). Behaviour, **29**, 83-121.

Tomasello, M. & Call, J. 2004. The role of humans in the cognitive development of apes revisited. Animal Cognition, **7**, 213-215.

Thornton, A. 2008. Social learning about novel foods by young meerkats. Animal Behaviour, **76**, 227-229.

Thornton, A. & Malapert, A. 2009. The rise and fall of an arbitrary tradition: an experiment with wild meerkats. Proceedings of the Royal Society B, **276**, 1269-1276.

de Waal, F. B. M. 2001. *The ape and the sushi master: cultural reflections of a primatologist*. New York: Basic Books.

van de Waal, E., Renevey, N., Favre, C. M. & Bshary, R. 2010. Selective attention to philopatric models causes directed social learning in wild vervet monkeys. Proceedings of the Royal Society B, doi:10.1098/ rspb.2009.2260.

van de Waal E & Bshary R (submitted) Contact with human facilities appears to enhance technical skills in wild vervet monkeys (*Chlorocebus aethiops*). Folia Primatologica.

Warner, R. R. 1988. Traditionality of mating site preferences in a coral reef fish. Nature, **335**, 719-721.

Whiten, A. 1998. Imitation of the sequential structure of actions by chimpanzees (Pan troglodytes). Journal of Comparative Psychology, **112**, 270-281.

Whiten, A. 2009. The identification and differenciation of culture in chimpanzees and other animals: from natural history to diffusion experiments. In *The Question of Animal Culture*, (Ed. by K. N. Laland & B. G. Galef, Jr), pp. 99-124. Cambridge: Harvard University Press.

Whiten, A. & van Schaik, C.P. 2007. The evolution of animal 'cultures' and social intelligence. Philosophical Transactions of the Royal Society 'B', **362**, 603-620.

Whiten, A & Mesoudi, A. 2008. Establishing an experimental science of culture: animal social diffusion experiments. Philosophical Transactions of the Royal Society B, **363**, 3477-3488.

Whiten, A., Custance, D. M., Gomez, J.-C., Teixidor, P. & Bard, K. A. 1996. Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). Journal of Comparative Psychology, **110**, 3-14.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999. Cultures in chimpanzees, Nature, **399**, 682-685.

Table 1. The composition of the study groups. Males are scored as adults once they migrated, while females are scored as adults once they have given birth. Group members that did not fulfil these criteria were scored as juveniles if they were at least one year old, and as infants if they were younger.

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	-

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

Figure 2. (A) n individuals in groups with model or control that touched first the bar (black parts) or on the door (white parts) during their first manipulation. (B) n individuals in groups with model or control that touched at least once the bar (black parts) or never (white parts) during the total length of their first manipulation. (C) duration of the first manipulation in groups with model or control, median and quartiles. (D) n individuals in groups with model or control that accessed the reward (black parts) or did not access the reward (white parts) during their first manipulation.

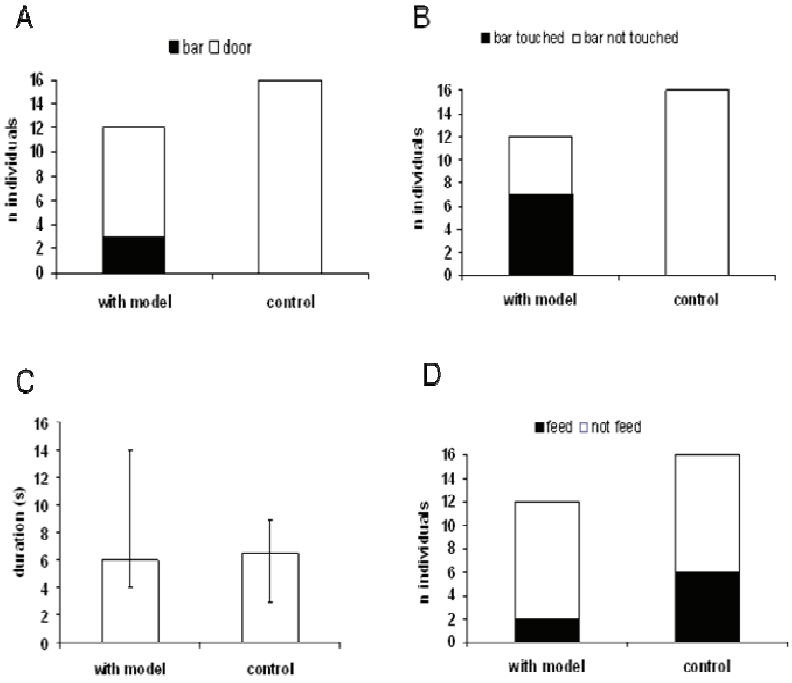
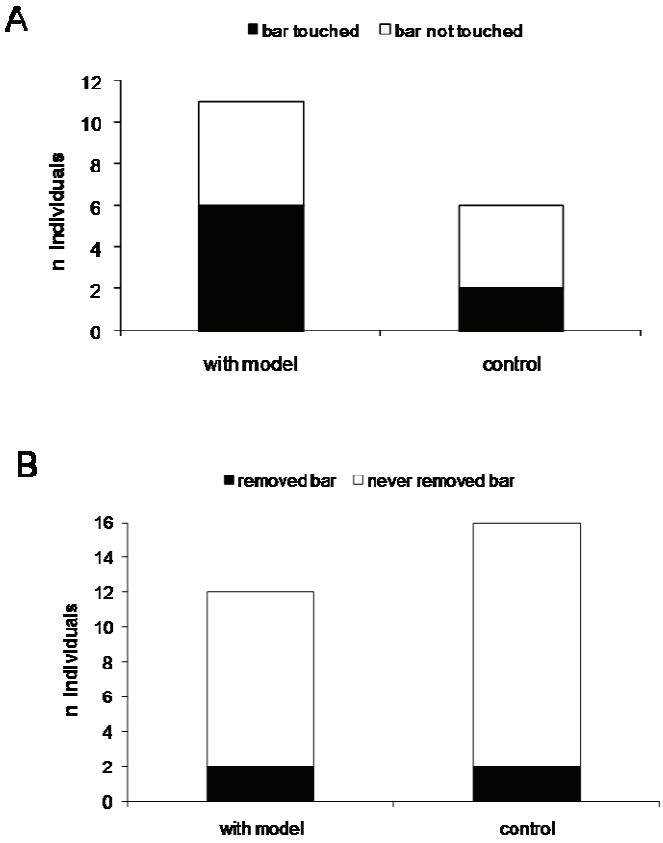


Figure 3. (A) n individuals in groups with model or control that touched at least once the bar (black parts) or never (white parts) during the second experimental phase when the rope was attached and the bar needed to be removed to access the reward. (B) n individuals in groups with model or control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



Video 1: Vervet 'Salto Costal' performing the two-steps task: first removing the bar on the top of the box, secondly opening the pull door.

Chapter 3) Food cleaning experiment

Conformity through imitation of food cleaning techniques in wild vervet monkeys

Article being commented by co-authors, before submission in *Science*.

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One sentence summary

We show experimentally that wild vervet monkeys use more similar food cleaning techniques within matrilines than within larger social units, a difference that seems to be best explained by conformity based on imitation.

Abstract

The behavioral conformity in a group provides a powerful mechanism for the formation of traditions, yet it relies on the ability to copy one another. Experimental evidence for imitation in non-human animals is restricted to captivity. We repeatedly confronted six groups of

wild vervet monkeys with grapes covered with sand and observed how they would deal with the situation. Monkeys sometimes ate grapes unclean but four different cleaning techniques also emerged. All cleaning techniques were used at more similar frequencies within matrilines and between sister matrilines while no similarity was detected on the group level. Simultaneous foraging of matrilineal members and genetic relatedness *per se* do not seem to explain our results. Thus, the observed conformity where several options are present seems based on contextual imitation.

Text

Social conformity plays an essential role in human culture as it supports the maintenance of both functional and arbitrary traditions (*1*). The importance of arbitrary traditions in animal societies is far less known, even though social learning is a topic of broad interest (*2*). Existing studies on animals typically consider contexts where there may be potentially severe costs for deviating from the social norm. For example, some foraging routes in ants and fishes are socially learned preferences and may persist because learning alternative routes (breaking the norm) would involve leaving the safety of the group (*3*). Similarly, food preferences may remain stable within groups because deviating from the conformity by eating unknown foods is risky as it might be toxic (*4*). In contrast, it remains an open question in how far animals may maintain arbitrary traditions due to conformity.

Laboratory experiments demonstrate that chimpanzees may keep arbitrary traditions due to conformity. In one experiment, two models learned in two different ways to access a food item in a box (*5*). Following a demonstration period, subjects adopted the method that was prominent in their group even though many individuals had learned through individual experience that there was an alternative method. Similar results were obtained in another social learning task (*6*). More recently, data on rats suggest that conformity may be more widespread in animals: rats that had

learned to avoid a toxic food started eating that food after exposure to a group member eating it (*7*).

In the field, evidence for arbitrary traditions is even rarer than in captivity. In primates, the existence of traditions has been inferred by identifying differences in a broad range of behaviors between populations that do not seem to be based on differences in ecology (*8, 9*). However, these comparative studies were not designed to provide direct evidence for social learning and its mechanisms. Recent experimental field studies on meerkats (*10*) and marmosets (*11*) tested whether initially useful specific techniques may persist once the experimenter allows an alternative solution to the problem. Both studies seem to reject social conformity as the mechanism allowing traditions to be maintained on a group level in wild animals. Only wild capuchin monkeys provide some evidence for arbitrary traditions. In this species, social conventions have been reported as inserting fingers into the mouth, nostrils and even eyes of group members and a variety of 'games' in which small objects such as hairs are put in one monkey's mouth and extracted by another (*12*). Arbitrary variation in food processing has also been reported in capuchins, where the seeds of *Luhea* fruits can be extracted in two alternative ways of similar efficiency, and while juveniles eventually try both methods during their development, at least young females converge on the technique their mothers used (*13*). Clearly, more data and in particular experimental manipulations are needed to get more evidence.

Here we tested six groups of wild vervet monkeys for their ability to develop a conformist solution in a novel foraging task. The experiment simulated the food cleaning context that provided the first example of a tradition in wild primates, the sweet potato washing Japanese macaques (*14*). We offered the monkeys' grapes covered with sand and noted who cleaned the food before eating and how. We conducted 15 trials to test whether cleaning techniques would become more uniform within social units. With respect to social units, we distinguished between matrilines

(mother and offspring), females only as the philopatric members of the group, and the entire group.

We identified five different feeding techniques and all were already used during the first trial where a total of 63 monkeys ate. Individuals already used typically more than one technique during the first trial. The most common techniques used during the first trial were no cleaning (used by 78% of individuals) and rubbing the grapes in the hands (used by 51%). Less common were rubbing the grapes on substrate (ground, branches, stones, the plastic box, 25%), opening the grape in the mouth and not eating the peel (25%). The fifth method, opening the grape with the hands and eating the inside, was done by only one monkey at this stage (1%). As all cleaning behaviors appear from the first trial, it seems likely that the techniques used are part of the vervet's behavioral repertoire.

We used generalized linear mixed effect models to test simultaneously for the effect of group, matriline, individual, sex and age on the feeding technique used. We found a significant proportion of the variance was accounted for by matriline membership on conformity with respect to all five feeding techniques (all five 99.9% highest posterior density (HPD) intervals did not overlap with 0, Fig. 1, Table 1.A.). For the rubbing grapes in hands, we additionally found an age effect as this technique was more frequently used by adults than by juveniles (p-value < 0.001, Fig. 1, Table 1.A.). Whereas for the opening grapes with the mouth, we also found an age effect as this technique was more frequently used by juveniles than by adults (p-value < 0.001, Fig. 1, Table 1.A.). Also, males were more likely than females to open fruits with their hands (p-value < 0.001, Fig. 1, Table 1.A.). In contrast, we never found significant effects of group identity (p-value > 0.2, all HPD intervals at 80% overlapped with 0, Fig. 1). The lack of a group effect cannot be attributed to adult males using different techniques than the resident females as the results remained stable when we considered only females for our analyses.

In principle, the above results could be explained in three different ways. First, similarities within matrilines might be due to social facilitation (*15*) if members eat more often together than with other group members. Second, similarities may be due to contextual imitation (*15*) of behaviors. Finally, similarities in cleaning techniques might have a strong genetic component. We found that members of the same matriline were indeed more likely to feed at the box with each other than with other group members (Wilcoxon signed ranks test, n = 6, Z = -2.201, p-value = 0.028, Fig. 2). However, when we excluded all data where individuals were feeding in the presence of matriline members, the matriline effects persisted (all $p < 0.001$, Table 1.B.). When we investigated the potential importance of relatedness, we found that the mean value of Gower's similarity coefficient (*16*) of nine full sister pairs was very similar to the coefficients for mothers - offspring pairs (Wilcoxon one sample test, n = 49 mother – offspring pairs, Z= -0.37, p-value = 0.71). Thus, similarity in techniques is not restricted to members of the same matrilines. However, it seems unlikely that the effect is due to genetic similarity as we found that Gower's similarity coefficient between juvenile matriline members and their aunts was similarly high (Wilcoxon one sample test, n = 43 aunt – offspring pairs, Z= -1.7, p-value = 0.09, Fig. 3) even though the relatedness is typically 0.25 instead of 0.5. Another result that favors the hypothesis that social learning took place in our experiment is that we found a trial effect for the most common techniques, non cleaning and rubbing in hands (in both cases $p < 0.001$, Fig. A, Table 1.A.) meaning that individuals were flexible in their techniques while at the same time adapting their choice to the techniques used within their matriline.

Our data provide experimental evidence for conformity in wild primates. Conformity persists over trials even though the frequency of certain techniques may change. We found conformity first within matrilines and after additional analyses also between members of full sister - matrilines. Similarity was not due to simultaneous feeding and there was no effect of genetic relatedness on similarity when we compared full sister pairs to offspring-aunt dyads. Therefore, it seems that the cleaning

techniques are really learned and not just due to response facilitation or genetics. As individuals had in total five behavioral options to choose from, simple social learning mechanisms like stimulus enhancement or local enhancement fail to explain our results. Instead, the conformity of behavior where several options are present seems to be best explained by contextual imitation. Experimental evidence for imitation learning is accumulating in studies conducted in captivity (*17-20*) but evidence from wild animals is hitherto lacking. It remains an open question whether specific members of a matriline are most likely to act as models while the others are most likely to imitate, or whether the conformity is due to 'ontogenetic ritualization' (*21*) where participants shape one another's behavior during the course of repeated interaction.

Social transmission in our experiment was restricted to units of closely related individuals, i. e. members of the same matriline or full sister matrilines. In contrast, social transmission did not extend to members of the philopatric sex or even the whole group. Evidence for the importance of matriline membership for social learning has been reported before in a study on the diet and foraging skills of wild orangutans (*22*) as well as in various studies on Japanese macaques (*23-25*). Nevertheless, the present results are somewhat surprising given that dominant females as models caused social learning in an artificial fruit experiment on the same study groups. In contrast, the dominant males did not elicit such social learning, and the difference was due to group members paying more selective attention to dominant females (*26*). We would have therefore expected to find conformity also on the group level: dominant matriline members fed first on the grapes while other group members could observe, similarly to the artificial fruit experiment. The reason why the two studies provide different conclusions could be that in the current experiment, individuals did not have to learn new techniques but they adjusted the use of established techniques to what others were doing. Our results on matriline members feeding simultaneously emphasize the likely importance of tolerance and proximity for social learning and resulting conformity.

Our findings offer several intriguing perspectives for future research. First, our results suggest a refined version of the 'BIOL' hypothesis ('Bonding- and Identification-based Observational Learning Model' (*27*), which proposes that individuals mainly copy the behaviors of individuals that are central for their life, like older and more dominant group members and the mother, even when there is no advantage of copying the particular behavioral variant in question. Our results suggest that in vervet monkeys the close social bonds with the mother and/or siblings are a more important source of conformity than a motivation to conform to dominant group members. However, the advantages of such decision rules remain currently obscure. Models that explore under which conditions such decision rules are favored by natural selection are clearly needed. Finally, it has been proposed that conformity on the group level is only prominent in humans and chimpanzees (*28*). We believe that our experimental design would yield variable behavior in many species, which would set the stage for exploring the distribution and the units of conformity across species.

References

1. P. J. Richerson, R. Boyd. In *Not by Genes Alone: How Culture Transformed Human Evolution* (Chicago Univ. Press, Chicago, 2005).

2. A. Whiten, in *The Question of Animal Culture*, K. N. Laland, B. G. Galef, Jr., Eds. (Harvard University Press, Cambridge, Mass., US, 2009), pp. 99-124.

3. R. L. Day, R. Macdonald, C. Brown, K. N. Laland, S. M. Reader, Interactions between shoal size and conformity in guppy social foraging. *Anim. Behav.* **62,** 917-925 (2001).

4. B. G. Galef, Jr., Function of social learning about food: a causal analysis of effects of diet novelty on preference transmission. *Anim. Behav.* **46**, 257-265 (1993).

5. A. Whiten, V. Horner, F. B. M. de Waal, Conformity to cultural norms of tool use in chimpanzees. *Nature* **437**, 737-740 (2005).

6. K. E. Bonnie, V. Horner, A. Whiten, F. B. M. de Waal, Spread of arbitrary customs among chimpanzees: a controlled experiment. *Proc. R. Soc. B.* **274**, 367-372 (2007).

7. B. G. Galef, Jr., E. E. Whiskin, 'Conformity' in Norway rats? *Anim. Behav.* **75**, 2035-2039 (2008).

8. Whiten A *et al.* Cultures in chimpanzees. *Nature* **399**, 682-685 (1999).

9. C. P. van Schaik CP *et al.*, Orangutan cultures and the evolution of material culture. *Science* **299**, 102-105 (2003).

10. A. Thornton, A. Malapert, The rise and fall of an arbitrary tradition: an experiment with wild meerkats. *Pro. R. Soc. B.* **276**, 1269-1276 (2008).

11. M. B. Pesendorfer, *et al.*, The Maintenance of Traditions in Marmosets: Individual Habit, Not Social Conformity? A Field Experiment. *PLoS ONE* **4**, e4472 (2009), doi:10.1371/journal.pone.0004472.

12. S. Perry, *et al.* Social conventions in wild white-faced capuchin monkeys: evidence for traditions in a neotropical primate. *Curr. Anthropol.* **44**, 241-268 (2003).

13. S. Perry, Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). *Anim. Cogn.* **12**, 705-716 (2009).

14. J. Itani, A. Nishimura, in *Precultural behaviour*, E. W. Menzel, Jr., Ed (Karger, Basel, Switzerland, 1973), pp. 26-50.

15. W. Hoppitt, K. N. Laland Social processes influencing learning in animals: a review of the evidence. *Adv. Study Behav*. **38**, 105-165 (2008).

16. P. Legendre, L. Legendre. *Numerical ecology* (second english edition, Amsterdam: Elsevier Science, 1998).

17. K. N. Laland, H. C. Plotkin, Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Anim. Learn. Behav.* **18**, 246-251 (1990).

18. V. Horner, A. Whiten, E. Flynn, F. B. M. de Waal, Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proc. Natl. Acad. Sci. U.S.A.* **103**, 13878-13883 (2006).

19. M. Dindo, B. Thierry, A. Whiten, Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proc. R. Soc. B.* **275**, 187-193 (2008).

20. G. Gajdon, N. Fijn, L. Huber, Testing social learning in a wild mountain parrot, the Kea (*Nestor notabilis*). *Learn. Behav.* **32**, 62-71 (2004).

21. M. Tomasello, J Call, in *Primate cognition*. (Oxford University Press, Oxford , 1997).

22. A. V. Jaeggli *et al*. Social Learning of Diet and Foraging Skills by Wild Immature Bornean Orangutans: Implications for Culture. *Am. J. Primatol.* **72**, 62-71 (2010).

23. I. Tanaka, Social diffusion of modified louse egg-handling techniques during grooming in free-ranging Japanese macaques. *Anim. Behav.* **56**, 1229-1236 (1998).

24. J.-B. Leca, N. Gunst, M. A. Huffman, Indirect social influence in the maintenance of the stone-handling tradition in Japanese macaques, *Macaca fuscata*. *Anim. Behav*. **79**, 117-126 (2010).

25. K. Hikami, Y.Hasegawa, T. Matsuzawa, Social transmission of food preferences in Japanese monkeys (Macaca fuscata) after mere exposure or aversion training. *J. Comp. Psychol.* **104**, 233-237 (1990).

26. E. van de Waal, N. Renevey, C. M. Favre, R. Bshary, Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proc. R. Soc. B.* (2010). doi:10.1098/rspb.2009.2260.

27. F. B. M. de Waal, in *The ape and the sushi master: cultural reflections of a primatologist*. (New York, NY: Basic Books, 2001).

28. A. Whiten, C. P. van Schaik, The evolution of animal 'cultures' and social intelligence. *Phil. Trans. R. Soc. B* **362**, 603-620 (2007).

29. We thank Mpumalanga parks board for permission to work at Loskop Dam Nature Reserve and their help in the field. We thank L. Brown, L. Barrett, P. Henzi, R. Noë and T. de Beer for their logistic support. The project was funded by the Swiss Science Foundation (grant to RB) and the Fonds Marguerite Wütrich et A. Mathey-Dupraz from the University of Neuchâtel. We are very grateful to C. Borgeaud, Y. Bouquet, C. Favre, S. Mercier, A. Piller, N. Renevey, M. Spinelli, E. Tournier, V. Tournier, and A. Vail for their great help with the field experiments. We are thankful to Simon Reader and Heather Murray for comments on the manuscript.

Tables & Figures

Table 1A. 99.9% Highest Posterior Density intervals from linear mixed effects models.

Model is
resp ~ Sex * Age class +(1 | Experiments) + (1 | Groups) + (1 | Matrilines)

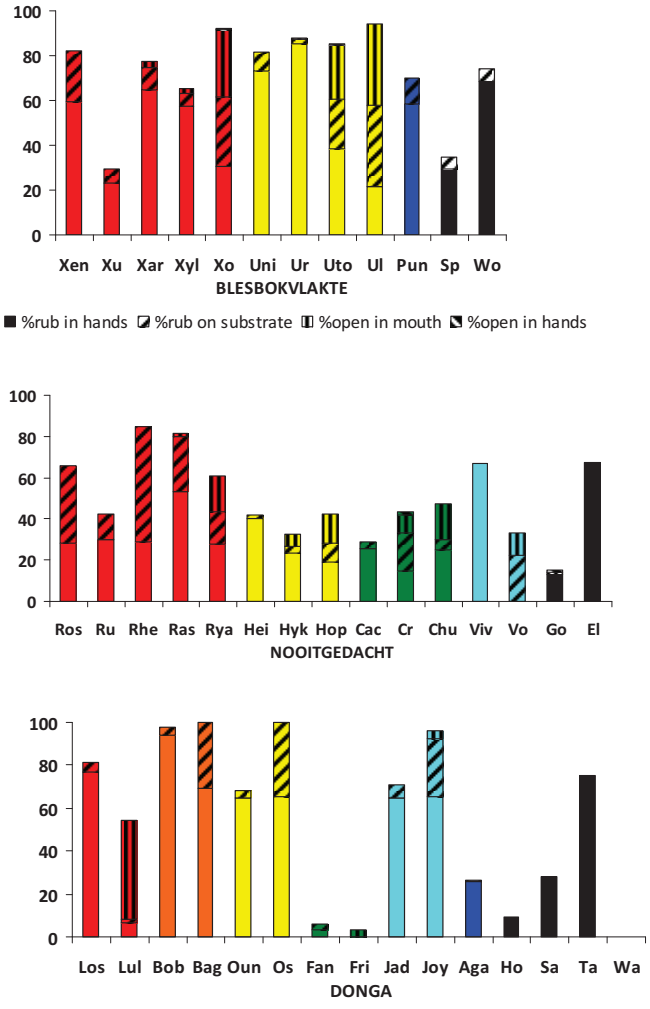
where resp is one of No cleaning, Rub in hands, Rub on substrate, Open in mouths or Open in hands.
Observed effect and 99.9% highest posterior density intervals for the different explanatory variables in the linear mixed effect models. The intercept is the predicted value for juvenile females, line Sex gives what needs to be added to the intercept to obtain the predicted value for males, line Age class gives what should be added to the intercept to obtain the predicted value for adults. For random effects, the standard deviation of the effect is given, and the HPD represents the proportion of standard deviation relative to the residual standard deviation explained by the effect. Intervals that do not include 0 are significant at the 0.001 level and are shown in bold.

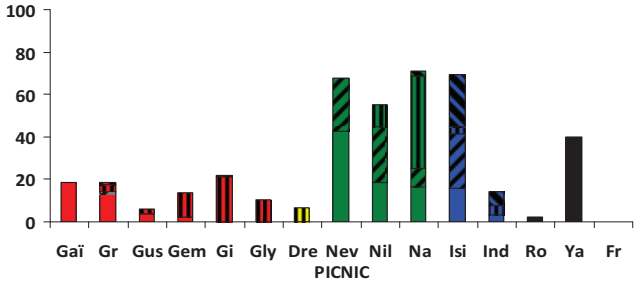
	No cleaning	Rub in hands	Rub on substrate	open in mouth	open in hands
			Fixed effects		
Intercept	[1.42, 7.15]	[-0.15, 5.32]	[0.03, 1.64]	[0.54, 1.36]	[-0.34, 0.34]
Sex	[-0.51, 1.19]	[-0.96, 0.53]	[-0.55, 0.29]	[-0.30, 0.31]	**[0.02, 0.30]**
Age class	[-0.10, 1.55]	**[0.62, 2.10]**	[-0.61, 0.18]	**[-1.22,-0.63]**	[0.00, 0.26]
Sex : Age Class	[-1.54, 3.01]	[-1.90, 2.09]	[-1.15, 0.45]	[-0.58, 0.49]	[-0.57, 0.03]
			Random effects		
Matrilines	**2.47[0.45, 0.85]**	**2.27[0.45, 0.89]**	**0.54[0.21, 0.55]**	**0.28[0.12, 0.41]**	**0.26[0.32, 0.68]**
Groups	0.79[0.00, 1.66]	0.70[0.00, 1.34]	0.10[0.00, 1.16]	0.00[0.00, 0.51]	0.06[0.00, 1.13]
Experiments	**0.63[0.09, 0.54]**	**0.57[0.09, 0.53]**	0.00[0.00, 0.22]	0.00[0.00, 0.19]	0.02[0.00, 0.23]
Residuals	2.80[2.65, 3.04]	2.58[2.45, 2.80]	1.43[1.34, 1.53]	1.10[1.03, 1.18]	0.47[0.44, 0.50]

Table 1B. Sub-sample of Table 1.A for matrilineal members feeding without their matrilines. 99.9% Highest Posterior Density intervals from linear mixed effects models.

	No cleaning	Rub in hands	Rub on substrate	open in mouth	open in hands
			Random effects		
Matrilines	**[0.29, 0.74]**	**[0.26, 0.78]**	**[0.13; 0.51]**	**[0.13; 0.47]**	**[0.13; 0.51]**
Groups	[0.00, 1.75]	[0.00, 1.16]	[0.00, 0.77]	[0.00, 0.50]	[0.00, 0.93]
Experiments	**[0.11, 0.47]**	**[0.09, 0.38]**	**[0.07; 0.34]**	[0.00; 0.18]	**[0.05; 0.30]**

Figure 1. Percentage of cleaning techniques used over the 15 trials in the 6 groups. Each bar represents one individual, where three letter codes represent females and two letter codes represent males. The same color bars are used to represent members of the same matrilines. Matrilines are ordered following the hierarchical structure (dominant on the left-subordinate on the right). Adult males are in black, again ordered following hierarchy.

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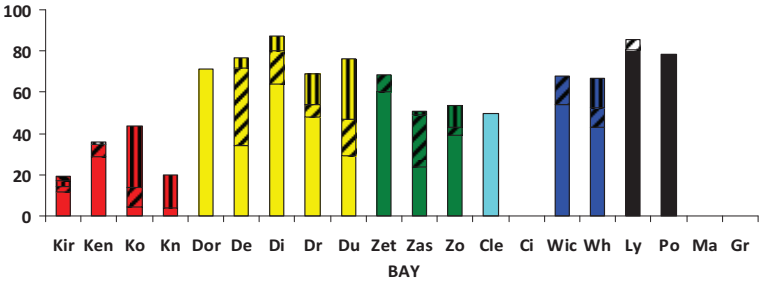
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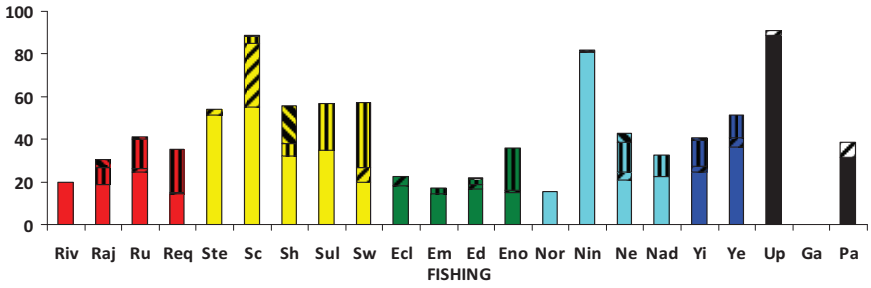
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Figure 2. The proportion of time matriline members spent foraging together with other group members, distinguishing between members of the same matriline and all other group members. Median and interquartiles using one value per group.

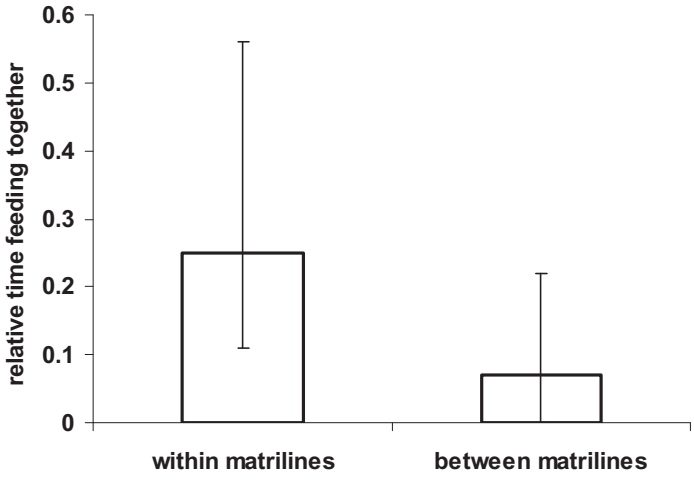


Figure 3. Gower's index of similarity of feeding techniques for full - sisters pairs of adult females, mother - offspring pairs and aunt - offspring pairs. For each category median and interquartiles of all dyads are shown.

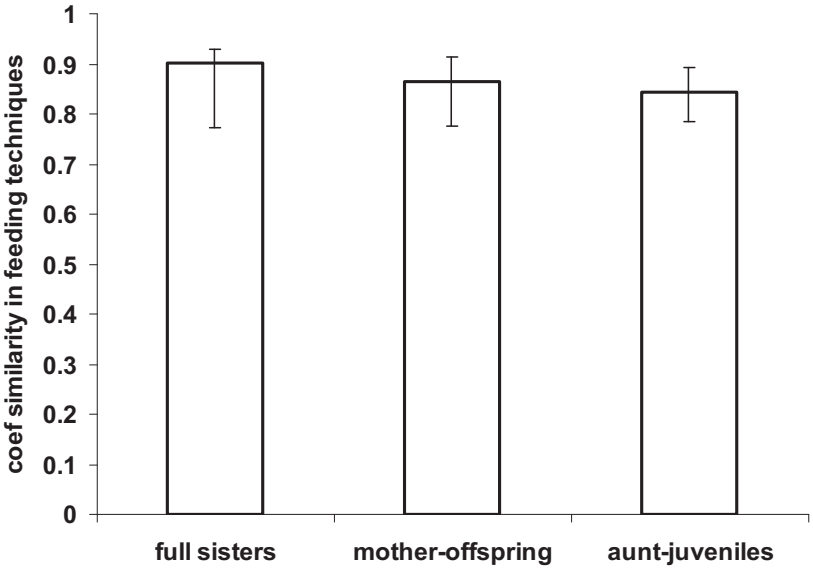
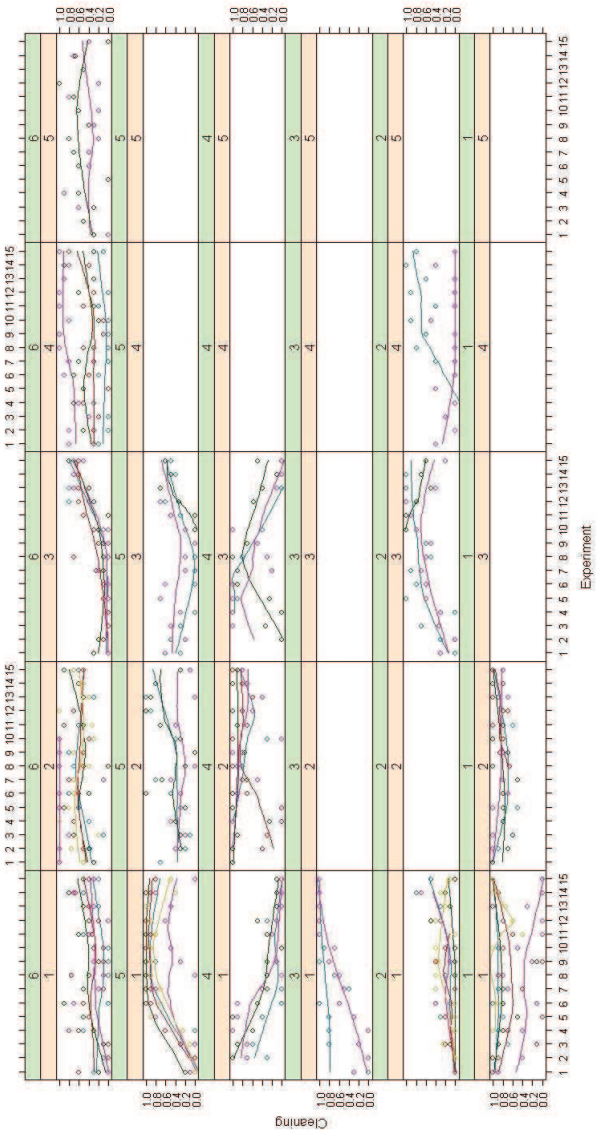


Figure 4. Evolution of the propagation of cleaning (all cleaning techniques pooled) in each matrilines of all 6 groups. Only matrilines for which 2 individuals or more participated to at least 6 experiments are represented. On each panel, the mother female is represented in blue, other individuals with different colors. The lines represent a running median smoother based on three consecutive data points.



Supporting online information

Material and Methods

a) Study site and population

Experiments were conducted between 2006 and 2009 on six neighboring groups of habituated wild vervet monkeys (*Chlorocebus aethiops*) at Loskop Dam Nature Reserve, South Africa. The reserve situated 250km north-east of Johannesburg, covers 25'000 ha and was created in 1948. Vervet monkeys live in stable family groups which during our experiments varied from 10 to 27 individuals. Groups are typically composed of an alpha male, a few subordinate males and several matrilines, i. e. 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 around 4 years of age. Vervets are described as opportunistic omnivores and readily eat human food if available. 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 monkeys were named with different 2 first letter codes. The individuals belonging to the same matriline have the same first letter. We coded females using 3 letters and males using 2 letters. Matriline membership assignment was initially based on behavioral data with mother nursing infants as proximity and tolerance in feeding and resting context. We tested the accuracy of the assignments on 42 offspring-mother pairs using genetic data. As the genetic data were highly concordant with behavioral classifications, we kept the entire data set, including non sampled individuals in our analyses.

All groups had been exposed to the presence of human researchers for at least 6 months before they were tested. All individuals were recognized individually by their facial appearance, and a recognition file with portrait pictures and specific individual features (scars, ear shape, pigmentation of skin, etc) was constructed for each group. Two of the six groups were in regular contact with tourists; one at a picnic spot ('Picnic group') and the other one at a fishing camp ('Fishing camp group'). The 'Picnic group' and the 'Donga group' had been used for experiments before (*1*), and artificial fruit experiments (*2*) were conducted in parallel on all six groups.

b) Experimental design

We designed our own experiment based on the sweet potato washing observations among Japanese macaques (*3*) to test for food cleaning traditions in primates. We provided the vervets with a plastic box (34x14x12cm) containing grapes covered with sand (100g of sand for 2kg of grapes) in sufficient quantities (depending on each group composition) so that all monkeys were able to access to the food. The box was fixed on the ground using a rope and tent pegs. As the hierarchy is very strong in vervets, dominants needed to be satiated before subordinates could eat. We first conducted a control experiment offering clean grapes, to habituate the monkeys to eating grapes and to check that at least 80% of the group members would eat a minimum of 10 grapes. Then we did 10 experiments with grapes covered in sand. Every minute we noted who was eating at the box and who was within a diameter of 10meters. We used the focal sampling on each individual 104 participating individuals while eating 10 grapes to get 10 data points of cleaning techniques. For each focal data collection of 10 grapes feeding techniques, we noted who was eating simultaneously at the box while the focal individual was eating. We collected data only after a minimum of one minute since the focal monkey started feeding to avoid collecting data on unsettled individuals. We identified 5 different cleaning techniques: no cleaning, rubbing the grape in the hands, rubbing the grapes on substrate (ground, branches, stones, the

plastic box…), opening the grape in the mouth and not eating the peel, opening the grape with the hands and not eating the peel. Finally we conducted 5 more experiments where monkeys had access to a second plastic box of the same size with water. The same data were taken as in the other experiments with extra attention paid to use of water to clean the grapes. All individuals that took part to at least 10 experiments were included in our analyses and the experiments were excluded from the analyses only if alarm calls for predator occurred during the trial. With the help of linear mixed effects models we could compare the relative importance of sex, age, kinship, group affiliation, for the different cleaning techniques used, as well as the evolution of these techniques throughout the 15 trials.

As the monkeys became more habituated to our presence and to experimental setup with the more trials we did, we needed at some point to use a plate in Plexiglas (60x30x0.4cm) fixed in front of the box to force the monkeys to eat in front of us, thus allowing us to record feeding techniques. The plate has holes (1cm diameter) on each corner where ropes were fixed and one hole in the middle where the usual rope fixing the box could go through, enabling us to anchor the structure on the ground using tent pegs.

All experiments were video recorded with a digital video camera allowing us to visualize the experiment again in order to complete the data set when some of the 10 data points per individual were missing.

c) Genetic analyses

We extracted DNA from faecal vervet samples using the QIAamp DNA Stool Mini Kit (QIAGEN), following the manufacturer's protocol with one modification: samples were allowed to incubate for a minimum of 30 minutes before elution. We quantified DNA through real-time quantitative polymerase chain reaction (rtPCR) as in Morin et al. (*4*). This rtPCR assay allows determination of the number of positive PCR replicates

per extract necessary to obtain a 99% confidence level that a homozygous genotype is correct. For a heterozygous genotype, our criterion was each that of the two alleles needed to be observed at least twice in independent PCRs. Ten randomly chosen individuals were genotyped independently for a second time in order to calculate our genotyping error rate.

PCR amplifications for 13 human-derived microsatellite loci (*5, 6*) were performed as multiplex reactions in an 10 μL volume containing 1 μL DNA, 5 μL Multiplex Master Mix (QIAGEN), 1 μL primer mix (diluted 1:5), and 3 μL ddH_2O. Amplification conditions were: initial denaturation at 95°C for 15 minutes, followed by 40 cycles of 94°C for 30s, 58°C for 90s, 72°C for 1 min, and a final extension at 60°C for 30 mins. We performed capillary electrophoresis on the 3730xl DNA Analyzer (Applied Biosystems). Products were analysed using GeneMapper v4.0 (Applied Biosystems). We used Genepop v. 3.0 (*7*) to calculate deviation from Hardy Weinberg equilibrium and linkage disequilibrium. We checked for allelic dropout and null alleles using Microchecker 2.2.3 (*8*).

Pairwise relatedness estimates for 74 monkeys for which we were able to generate reliable genotypes for all 13 loci were calculated using the software SPAGeDi, v.1.2 (*9*). We calculated both the Queller & Goodnight (*10*) and Wang (*11*) estimators, as previous studies have shown that performance of relatedness depends mainly on the population relatedness composition (*12*). As both estimators performed equally well in identifying pairs of full-sibling adult females (relatedness > 0.45) and mother-offspring pairs (data not shown), we only report relatedness analyses based on the Queller & Goodnight estimator.

d) Scan data analyses

We calculated the total amount of scans where each monkey was present at the box, and who were the others present at the same time. Then for each dyads of group members we calculated the amount of scan present together at the box divided by the mean of the amount of scan each one was

present in total. We analyzed only the data involving females and juveniles to see if these individuals were more together at the box with their own matrilines than with other group members.

e) Coefficient of similarity of feeding techniques

We used Gower's coefficient (*13*) to quantify the similarity of techniques used by full-siblings adult females as well as mother and their offspring. Briefly, this coefficient takes the absolute value of the difference in counts of observations between two individuals, standardized by the largest possible difference in counts observed among all individuals. One minus this quantity is then the coefficient for one behavior. An average over the relevant behavior is then taken. We did not use the behavior "opening with mouth", as it is used mainly by juveniles. In order to compare the similarity between adult female full-siblings and mother-offspring as well as aunt and juveniles for full sister matrilines, we used a Wilcoxon one sample test, comparing the similarity index from the 49 mother-offspring pairs and the 43 aunt-juvenile pairs to the mean of the 9 full sister's pairs. This was done to avoid pseudo replication for the sister's pairs.

f) Statistical analyses

We analyzed our data set using linear mixed effect models as implemented in the lme4 package for R *(14)*. We modeled the number of occurrences of each behavior as a function of sex and age class (juveniles or adults) as fixed effects and experiment, matriline and group as random effects. In order to test whether these effects differed from 0, we used the HPDinterval function of the lme4 package. This function creates highest posterior density (HPD) intervals for the parameters of a linear mixed effect model from Markov Chain Monte Carlo sampling of the fitted model. The graph (Fig. 4) produced out of these analyses consists of lines representing a running median smoother based on three consecutive data points (*15*). To test whether the matriline effects were potentially caused by

simultaneous feeding or by learning, we ran another analysis on a sub-sample where we used for each individual only data points that were collected in the absence of matriline members.

All other tests were conducted on SPSS version 16.

Supporting references & Tables

1. C. Fruteau, B. Voelkl, E. van Damme, R. Noe, Supply and demand determine the market value of food providers in wild vervet monkeys. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 12007-12012 (2009).

2. E. van de Waal, N. Renevey, C. M. Favre, R. Bshary, Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proc. R. Soc. B.* (2010). doi:10.1098/rspb.2009.2260.

3. J. Itani, A. Nishimura, in *Precultural behaviour*, E. W. Menzel, Jr., Ed (Karger, Basel, Switzerland, 1973), pp. 26-50.

4. P. A. Morin, K. E. Chambers, C. Boesch, L. Vigilant. Quantitative polymerase chain reaction analysis of DNA from noninvasive samples for accurate microsatellite genotyping of wild chimpanzees (*Pan troglodytes verus*). *Mol. Ecol.* **10**, 1835-1844 (2001).

5. Y. Wang. Molecular polymorphisms for phylogeny, pedigree and population structure studies. PhD-thesis, University of Sydney, Australia (2006).

6. T. K. Newman, L. A. Fairbank, D. Pollack, J. Rogers. Effectiveness of human mircrosatellite loci for assessing paternity in a captive colony of vervets (*Chlorocebus aethiops sabaeus*). *Am. J. Primatol.* **56**, 237-243 (2002).

7. M. Raymond, F. Rousset. Population genetics software for exact tests and ecumenicism. *J. Hered.* **86**, 248-249 (1995).

8. C. van Oosterhout, W. F. Hutchinson, D. P. M. Wills, P. Shipley. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. *Mol. Ecol. Notes* **4**, 535-538 (2004).

9. O. J. Hardy, X. Vekemans. SPAGeDi: a versatile computer program to analyse spatial genetic structure at the individual or population levels. *Mol. Ecol. Notes* **2**, 618-620 (2002).

10. D. C. Queller, K. F. Goodnight, Estimating relatedness using genetic markers. *Evolution* **43**, 258-275 (1989).

11. J. L. Wang. An estimator for pairwise relatedness using molecular markers. *Genetics* **160**, 1203-1215 (2002).

12. K. Csillery, T. Johnson, D. Beraldi, T. Clutton-Brock, D. Coltman, B. Hansson, G. Spong, J. M. Pemberton. Performance of Marker-Based Relatedness Estimators in Natural Populations of Outbred Vertebrates. *Genetics* **173**, 2091-2101 (2006).

13. P. Legendre, L. Legendre. *Numerical ecology* (second english edition, Amsterdam: Elsevier Science, 1998).

14. D. Bates, D. Sarkar, lme4: Linear Mixed-Effects Models Using S4 Classes. R package version 0.9975-12, URL http://CRAN.R-project.org/ (2007).

15. J. W. Tukey. *Exploratory Data Analysis* (Reading Mass: Addison-Wesley, 1977).

Table 1. The composition of the study groups during the last experiment.

Males are scored as adults once they migrated, while females are scored as adults once they have given birth. Group members that did not fulfill these criteria were scored as juveniles.

Group	Adult male	Adult female	Juvenile	Total
Bay	4	5	12	21
Picnic	3	3	10	16
Blesbokvlakte	2	3	8	13
Donga	4	6	5	15
Nooitgedacht	3	4	10	17
Fishing Camp	3	4	15	22

General Discussion

The starting point of my PhD project was that though there was evidence for traditions in wild animals and detailed laboratory experiments on social learning mechanisms, field experiments on wild animals, in particular primates are missing. Similarly, laboratory experiments and theorists propose conditions under which social learning is favoured over individual learning or ignorance but again field experiments are missing. My results demonstrate the feasibility to conduct social learning experiment on wild primates. I successfully adapted a laboratory design, 'artificial fruit experiments' (Whiten et al. 1996, 1998) to the field, to test wild vervet monkeys' social learning abilities. I used two different versions of boxes creating an increase of complexity of the task. I designed myself the other experiment based on the famous example of sweet potatoes washing traditions in Japanese macaques (Itani & Nishimura 1973) to test if food cleaning techniques spread and stabilize in our study groups.

a) Evidence for social learning mechanisms

This research demonstrated experimentally for the first time the use of social learning in wild primates. With the results of my two-doors artificial fruit experiments I got evidences for the spreading of socially transmitted knowledge through 'stimulus enhancement' (Hoppitt & Laland 2008), with a higher participation in groups with female models and 'local enhancement' (Hoppitt & Laland 2008), as subjects chose the same door as a female model. In the two-step task local enhancement was also found in the form of subjects touching the bar during the first manipulation in groups with models, a behaviour that was totally absent in control groups. This last experimental set-up was designed to test for a more complex social learning ability, namely the copying of a sequence of actions. However, untrained vervets largely failed to master this more challenging experimental setup that consisted of removing the bar on the top of box and then opening the door.

The social learning mechanism, on which the conformity within matrilines and sister matrilines of the food cleaning techniques relies, seems to be 'contextual imitation' (Hoppitt & Laland 2008). Contextual imitation involves imitation of a known gesture in a new context. This finding is of great interest as it involves that wild primates might also use complex social learning mechanisms (and are not restricted to local enhancement) like imitation that was until now demonstrated only in captivity (Bonnie et al. 2006, Horner et al. 2006, Dindo et al. 2008). Thus these experiments should of course be repeated on captive vervets, this comparative approach should highlight the importance of the environment for social learning to occur. Even more importantly these experiments should be conducted on other species. Especially the food cleaning experiment seems to be promising for a broad range of primates, including neophobic species, as no manipulation is needed. The methods could be adapted with the use of naturally occurring fruits to the animals, therefore reducing even the ecological impact of the experiments.

b) Evidence for decision rules from whom to learn and their basis

The relevance of the model's identity for social learning to occur is shown in my 'simple' version of the artificial fruit, a two-door box (van de Waal et al. 2010). Following demonstrations by the model, a significantly higher participation rate and same-door manipulation in groups occurred, but only in groups with dominant females as models compared to groups with male models. Analysing the context of demonstrations, differences were found in the selective attention of bystanders to female model behaviour, rather than in the model's tolerance or aggression towards bystanders. These results demonstrate the eminent role of dominant females as a source for 'directed' social learning in a species with female philopatry. The importance of the status of the model for the spreading of social learning was already discussed in a few studies (Boyd & Richerson 1995, de Waal 2001, Laland 2004). Mainly dominance and age are assumed to be important factors. These two traits are argued to be the most reliable as they reflect the success of an individual with respect to group

leading and strength in the first case and survival as well as experience in the second. Based on my results, the most important variable seems to be the model's social role in the group. As all our models were dominants and adults, as well as successful in the task, the only relevant factor for group members to copy seems to be the sex, with females the philopatric sex being copied but not males the migrating sex. A very interesting comparative approach would be to conduct this experiment in a species like chimpanzees were females are the migrating sex and males the philopatric sex. Following the prediction based on my findings we should find that males are better models than females in this social structure.

The grape cleaning experiment demonstrates that individuals also take genetic relatedness into consideration. Females are generally more related to other group members than males are. On the basis of shared cleaning techniques, matrilines and full sister-matrilines rather than entire groups appeared to be the key units for social transmission that leads to conformity in vervet monkeys. This result appears to be mainly linked with the tolerance of close kin even during foraging, which enables simultaneous actions as well as observations while processing the grapes. The fact the five feeding techniques used were part of vervets behavioural repertoire and all techniques were already used during the first experiment cancelled the option to describe the pattern of spreading of an innovation. Thus, I could not investigate who initiates the feeding technique and who copies it, but just acknowledge the occurrence of conformity in the used techniques. During this foraging experiment, matriline members would generally eat simultaneously and not tolerate lower group members. My initial hypothesis was that I would find conformity of cleaning technique on the group level. This would have implied that individuals focussed on the dominants feeding first as models while they waited and then copied the dominants' behaviours once their turn to forage had come. However this explanation is not supported by the results. Furthermore, the results remained robust when I excluded males from the analyses. Thus members of the philopatric sex did not produce group-level foraging techniques. The results support the idea that if more models than the dominant female are

available, individuals will pay selective attention to closely related individuals.

c) Limited evidence for the formation of traditions

Conducting these social learning experiments I was hoping to document the establishment of new arbitrary traditions within each group. However, in the two-door artificial fruit experiment even models quickly adjusted to the experimental condition where both doors could be opened and used both options at their convenience. Similarly, during the food cleaning experiments the techniques used altered between trials and sometimes even during trials. Maybe the methodology accounts for the lack of fixed traditions. One possible explanation could be a too limited timeframe of exposure to the experimental set-up. Alternatively, the cost of switching methods may have been too small to force subjects to focus on one method. Alternatively, wild animals may be less willing to focus on the task because in parallel they have to be vigilant for predators and group competitors. In such an environment, variable behaviour might be the optimal solution to the trade-off between efficiency at a task and risk management.

My results made me hypothesise that two factors seem to be of importance for the theory and modelling on traditions in animals. First-of-all, the findings that the philopatric sex act as the key model imply that migration (by males) does not necessarily lead to an exchange of socially acquired information within populations, potentially maintaining quite localised traditions. Secondly our results on matrilines' and sister matrilines' similarity in feeding techniques suppose that conformity in the wild might not always happen in the entire social group, but still can spread and exist in sub-structures of the social unit. These findings imply that relatedness might be of broader importance that initially thought in assumptions on cultural transmission. Then one should wonder how much is based on social learning in an observed tradition and how much relies on shared genes. With the integration of these results we can argue that the

'second inheritance system' (Whiten 2005) that evolved on the back of genetic evolution and now forms a parallel evolutionary stream (Mesoudi et al. 2006) is maybe more linked to genetics than initially thought.

d) Limitations and perspectives

The poor rates of successful task-solving during the artificial fruit experiments highlight the limitation of the vervets' manipulative skills. Interestingly, when analysing the success of opening the two-door boxes, the sex of the model was not relevant anymore whereas the significant factor for success was membership in a group with contact to humans. Indeed, two groups of our study population have contact with humans and their structures in their home range. The Picnic group has a picnic site for the tourists visiting the reserve with toilets, dust bins and barbecue set-ups, and the Fishing camp group has three huts that can be rented by fishermen. The results imply that having the opportunity to interact with humans or their facilities might enhance some manipulative skills. This finding has important implications for the effect of the environment for the development of specific cognitive abilities. Thus, results of experiments conducted in the lab should be interpreted carefully as captivity seems to enhance capacities beyond standard natural abilities, known as 'enculturation effect' (Whiten & van Schaik 2007). Studies on marmosets (Hasley et al. 2006) and on baboons (Laidre 2008) already documented the low manipulation skills of wild primates. Therefore researchers should aim at testing wild animals to really know the species abilities and not only focus on laboratory subjects.

To increase the abilities of the subjects, a preliminary training of the wild vervets on sliding and pulling movements might be needed to find more successful manipulation. However we should then be also careful of the participants' previous experience. For example, the findings of our two-steps task might have been biased by the fact that nearly all participants had previous personal contact with the 'simple' artificial fruit. Other results might have been found if the tested subjects were vervet groups totally

naïve to artificial fruit experiments. In any case, the study highlights the problem that animals might fail at a task because some technical aspects are too difficult. For example, an obvious next experiment is to test the monkeys with an artificial fruit that allows testing for 'production imitation' (Hoppitt & Laland 2008). The set-up used in Dindo et al. (2008) would be ideal. They designed a 'Doorian' artificial fruit consisting of a box with a single door that could be either pulled or slide. After repeated demonstrations of a single gesture (other opening option blocked) by a model one could observe if others copy the detailed movement of opening by either pulling or sliding. As both opening techniques happen on a single door, local enhancement can be excluded. Thus, if copying occurs, production imitation should be the mechanism involved. According to the results presented in my thesis, however, most vervets would fail to open the box at first trial without prior training of relevant movements and then either give up or start with individual exploration.

A valuable extension of the food cleaning experiment could consist in running a single extra round of the food cleaning experiment on all six groups after at least a year from the last experiment. This extra-experiment would give insight on the stability of the matrilines preferred techniques even after a long time interval without exposure to the task. One would also be able to test whether the new generations again adopt the typical behaviour of the matriline they belong to. In particular the question whether rare techniques persist and even spread within matrilines would be interesting. In addition, a comparison with captive vervets should be conducted. This addition would allow testing whether matriline conformity is as important in a confined environment or whether captivity and possibly artificial group compositions lead to other social units becoming important units for the spreading of specific behaviours.

e) Conclusion

The different experiments realised for this thesis as well as all the time spent with wild vervets gave me the opportunity to discover a bit of

vervet social learning processes. This work emphasizes the possibility of traditions developing in different groups within the same population due to the lack of spreading of knowledge through migration. Until now, natural between-group variations were mainly found in groups belonging to different populations (Whiten et al. 1999, van Schaik et al. 2003). Critical reviews have argued that the variation observed might be due to undetected environmental factors (Laland & Janik 2006). Therefore, I think that further researches should aim at within-population comparisons. This method would have some advantages over between-population comparisons: ecology and genetics are more similar, and hence any differences between neighbouring groups are less likely to be due to genetic diversification or due to adaptations to different ecologies. In chimpanzees from different populations, variations in stick length for termite fishing can be explained with differences in the termite mounts. Whereas if two groups of the same population use different length of stick when fishing the same termite species then it would be a better proof of cultural differences. In vervet monkeys I think we should pay specific attention to natural feeding preferences, conflict resolution behaviour and communication as we found between-group variations in theses subjects in various studies done by master students on the Loskop population. Aiming at a long-term many-groups project one should find natural traditions also in monkeys.

To conclude, this work proves that social learning and its mechanisms can be tested in wild primates. I found evidences for stimulus enhancement, local enhancement and contextual imitation. My research discovered that in vervet monkeys a dominant of the philopatric sex is a better model than a dominant of the migrating sex and that genetic relatedness is a key factor as the social unit for the spread conformity. I hope that my work will encourage others conduct these field experiments on other species and taxa to see if similar patterns of social transmission are found. As noted by Whiten & Mesoudi (2008) the fact that the majority of social learning studies have been conducted on captive individuals limits the validity of the field as a whole. Thus this study joins few others field experiments (Helfman & Schultz 1984; Lefebvre 1986; Warner 1988;

Langen 1996; Reader et al. 2003, Thornton & Malapert 2009, Müller & Cant in press) to demonstrate the feasibility of social learning experiments on wild animals. Aiming at more studies of this kind, we should better understand the conditions under which animals may learn socially, what mechanisms are involved and when do these socially learned behaviours become traditions. By solving these questions, we will make a step closer in the knowledge of the human cultural specificity as well as what we share with other species.

References

Bonnie KE, Horner V, Whiten A & de Waal FBM 2006 Spread of arbitrary customs among chimpanzees: a controlled experiment. *Proceedings of the Royal Society 'B'*, **274**, 367-372

Boyd R & Richerson PJ 1985 *Culture and the evolutionary process.* Chicago, IL: University of Chicago Press.

Dindo M, Thierry B & Whiten A 2008 Social diffusion of novel foraging methods in brown capuchin monkeys (Cebus apella). *Proceedings of the Royal Society 'B'* **275**, 187-193.

Halsey LG, Bezerra BM & Souto AS 2006 Can wild common marmosets (*Callithrix jacchus*) solve the parallel strings task? *Animal Cognition* **9**, 229-233.

Helfman GS & Schultz ET 1984 Social transmission of behavioural traditions in a coral reef fish. *Animal Behaviour* **32**, 379-384.

Hoppitt W & Laland KN 2008 Social processes influencing learning in animals: a review of the evidence. *Advances in the Study of Behavior* **38**, 105-165.

Horner V, Whiten A, Flynn E & de Waal FBM 2006 Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences of the United States of America - Biological Sciences*, **103**, 13878-13883.

Itani J & Nishimura A, in *Precultural behaviour*, E. W. Menzel, Jr., Ed (Karger, Basel, Switzerland, 1973), pp. 26-50.

Laland KN & Janik V 2006 The animal cultures debate. *Trends in Ecology & Evolution* **21***,* 542-547.

Laidre ME 2008 Spontaneous performance of wild baboons on three novel food-access puzzles. *Animal Cognition* **11**, 223-230.

Laland KN 2004 Social learning strategies. *Learning & Behavior* **32**, 4-14.

Langen, TA 1996 Social learning of a novel foraging skill by white-throated magpie-jays (*Calocitta formosa, Corvidae*): a field experiment. *Ethology* **102**, 157-166.

Lefebvre L 1986 Cultural diffusion of a novel food-finding behaviour in urban pigeons: an experimental field test. *Ethology* **71**, 295-304.

Mesoudi A, Whiten A & Laland KN 2006 Towards a unified science of cultural evolution. *Behavioral and Brain Science* **29**, 329-383.

Müller CA & Cant MA (in press). Imitation and traditions in wild banded mongooses. *Current Biology*.

Reader SM, Kendal JR & Laland KN 2003 Social learning of foraging sites and escape routes in wild Trinidadian guppies. *Animal Behaviour* **66**, 729-739.

van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS & Merrill M 2003 Orangutan cultures and the evolution of material culture. *Science* **299**, 102-105.

Thornton A & Malapert A 2009 The rise and fall of an arbitrary tradition: an experiment with wild meerkats. *Proceedings of the Royal Society 'B'* **276,** 1269-1276.

de Waal FBM 2001 *The ape and the sushi master: cultural reflections of a primatologist*. New York: Basic Books.

van de Waal E, Renevey N, Favre CM, Bshary R 2010 Selective attention to philopatric models causes directed social learning in wild vervet monkeys. *Proceedings of the Royal Society of London 'B'* in press.

Warner RR 1988 Traditionality of mating site preferences in a coral reef fish. *Nature* **335**, 719-721.

Whiten A, Custance DM, Gomez J-C, Teixidor P & Bard KA 1996 Imitative learning of artificial fruit processing in children (Homo sapiens) and chimpanzees (Pan troglodytes). *Journal of Comparative Psychology* **110**, 3-14.

Whiten A 1998 Imitation of the sequential structure of actions by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology* **112**, 270-281.

Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW & Boesch C 1999 Cultures in chimpanzees. *Nature* **399**, 682-685.

Whiten A 2005 The second inheritance system of chimpanzees and humans. *Nature* **437**, 52-55.

Whiten A & van Schaik CP 2007 The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society 'B'* **362**, 603-620.

Whiten A & Mesoudi A 2008 Establishing an experimental science of culture: animal social diffusion experiments. *Philosophical Transactions of the Royal Society 'B'* **363**, 3477-34.

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