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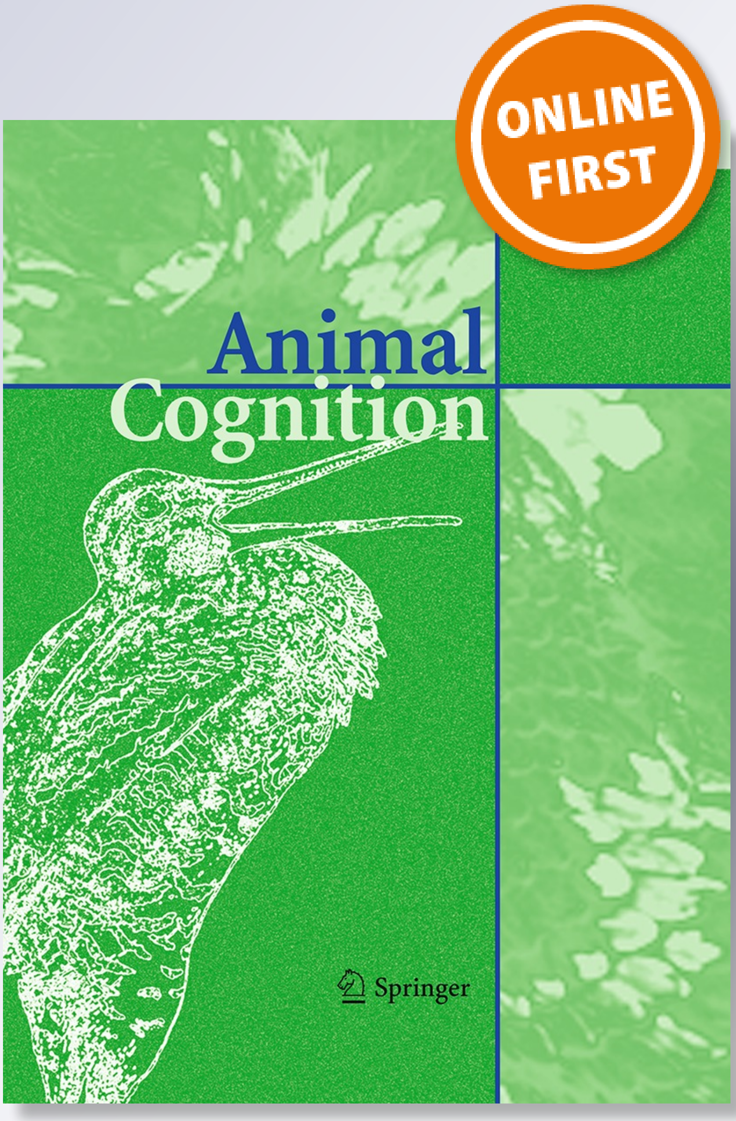

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ORIGINAL PAPER

Wild vervet monkeys copy alternative methods for opening an artificial fruit

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Abstract Experimental studies of animal social learning in the wild remain rare, especially those that employ the most discriminating tests in which alternative means to complete naturalistic tasks are seeded in different groups. We applied this approach to wild vervet monkeys (*Chlorocebus aethiops*) using an artificial fruit ('vervetable') opened by either lifting a door panel or sliding it left or right. In one group, a trained model lifted the door, and in two others, the model slid it either left or right. Members of each group then watched their model before being given access to multiple baited vervetables with all opening techniques possible. Thirteen of these monkeys opened vervetables, displaying a significant tendency to use the seeded technique on their first opening and over the course of the experiment. The option preferred in these monkeys' first successful manipulation session was also highly correlated with the proportional frequency of the option they had previously witnessed. The social learning effects thus documented go beyond mere stimulus enhancement insofar as the same door knob was grasped for either technique. Results thus suggest that through imitation, emulation or both, new foraging techniques will spread across groups of wild vervet monkeys to create incipient foraging traditions.

Keywords Field experiments · Social learning · Imitation · Cultural transmission · Primates · Vervet monkeys

Introduction

Social learning, traditions and cultural transmission in primates and other animals have received increasing attention in recent years (Hoppitt and Laland 2008; Kendal et al. 2010a; Whiten et al. 2011; Nielsen et al. 2012). Here, we focus on social learning, defined by Heyes (1994, p. 207) as 'learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products'. A key methodological advance in the identification of social learning and dissection of the alternative processes underlying it occurred with the development of the 'two-action' method, in which experimental subjects witness a model proficient in using either of two different actions to manipulate an object such as an 'artificial fruit' (Whiten et al. 1996) and extract a reward from it. If subjects are subsequently more likely to match the alternative they witnessed in their own attempts at the task, we obtain evidence not only of the operation of social learning per se, but also some details of what is learned, as entailed by the differences in the witnessed alternatives that subjects subsequently match. After being first used by Dawson and Foss (1965), the two-action method has been employed

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effectively in numerous studies to identify the social learning of alternative actions such as the use of foot or beak to operate a foraging device by pigeons (Zentall et al. 1996); or blue tits' piercing or flipping a foil to access a reward (Aplin et al. 2013); alternative techniques to open artificial food objects by marmosets (Bugnyar and Huber 1997; Voelkl and Huber 2000); and alternative sequences of constituent behavioural elements by chimpanzees (Whiten 1998).

Such two-action studies have typically been dyadic, particularly in the early years of the approach, with an isolated subject learning from a single trained conspecific (Zentall 2012). More recently, the two-action concept has been extended to the design of experiments where interest lies at the wider cultural level, concerning the social transmission and spread of action patterns in groups and broader populations (Galef and Allen 1995). Among primates, such spread has been shown to occur with substantial fidelity to experimentally seeded alternative foraging techniques in captive groups of capuchin monkeys (Dindo et al. 2008, 2009), chimpanzees (Whiten et al. 2005, 2007; Hopper et al. 2007) and vervet monkeys (van de Waal and Whiten 2012; van de Waal et al. 2013a).

However, the literature reviewed above is restricted to studies with captive populations that most easily afford the experimental controls involved. To know that the phenomena so identified are important in the wild, comparable field experiments are vital, yet they remain relatively rare (Whiten and Mesoudi 2008; Thornton and Clutton-Brock 2011). Most of the research on social learning and traditions in the wild have been observational, recording population differences in behavioural repertoires that are apparently not susceptible to straightforward environmental or genetic explanations and therefore attributed by this 'exclusion principle' to social learning. Examples include van Schaik et al. (2003) for orangutans, Santorelli et al. (2011) for spider monkeys and Panger et al. (2002) for capuchin monkeys. However, it is always difficult to be sure that the exclusion principle is being correctly applied, or whether there is some unrecognised, correlated factor other than social learning at the root of the behavioural differences. Studies of neighbouring semi-wild communities displaying behavioural differences (e.g. Rawlings et al. 2014; van Leeuwen et al. 2014) offer additional confidence that environmental and genetic explanation are not responsible, but do not provide the rigorous direct evidence for or against a causal role for social learning that is provided by controlled, two-action experiments.

Unfortunately, in the field it is inherently more difficult than in captivity to conduct such tests, controlling what an observer monkey witnesses by engineering particular model-observer configurations. Nevertheless, for primates, such field experiments have been pioneered recently in research by Kendal et al. (2010b) with ring-tailed lemurs, Schnoell and Fichtel (2012) and Schnoell et al. (2014) with red-fronted lemurs, van de Waal et al. (2010) and van de Waal and Bshary (2011) with vervets and Gunhold et al. (2014a, b) with marmosets. In the van de Waal studies, boxes acting as 'artificial fruits' were presented to the wild vervet monkeys. A door at one end of the box could be opened by lifting it, and a differently coloured door at the other end could be opened by sliding it, to obtain food inside. These two alternatives were seeded in different groups by initially locking the box, so that only one opening technique could be used, until one dominant individual mastered it. Then, both methods were made available to the rest of the group. This study demonstrated social learning from the initial model, but only when the model was a female monkey and not when it was the dominant male. However, because the different actions were modelled on different doors on the two ends of the box, the results may have reflected only local enhancement (Thorpe 1963), where the observer is simply more likely to focus their efforts on the side of the box that the model was manipulating.

To test for social learning that goes beyond local enhancement, and instead requires matching to what a subject witnessed either by imitation (defined by Whiten and Ham (1992) as 'learning some aspect(s) of the intrinsic form of an act' from another individual) or by emulation (replicating only the results of what the subject witnessed, such as the movements of parts of the object manipulated: Wood 1989; Tomasello 1990), we used the 'artificial fruit' (Whiten et al. 1996) we have dubbed a 'vervetable' and already employed successfully in studies with captive vervet monkeys, who discriminated and tended to copy whichever option they had witnessed (van de Waal et al. 2013a). The vervetable incorporates a single door that affords opening through alternative means, all of which involve contact with the same locus (a small knob in the centre of the door) such that local enhancement cannot explain any matching behaviour recorded. The door can be slid to either side, or alternatively lifted up, to gain access to the food reward inside. We seeded each of the different techniques (slide left, slide right or lift) in one adult female in each of three wild groups and investigated whether there was evidence for social learning of these alternative techniques by other group members, which would thus implicate emulation or imitation, and hence go beyond the local enhancement so far identified in the primate field experiments cited above, including our own studies of vervet monkeys (van de Waal et al. 2010; van de Waal and Bshary 2011).

Discriminating these social learning processes has long been recognised as one of the most important goals in social learning research because they are thought to depend on cognitive operations that differ substantially in their nature and complexity (Whiten and Ham 1992; Hoppitt and Laland 2013). Local enhancement requires only that the observer registers cues such as a model's proximity to, or actions focused on, a certain element in the environment, and subsequently focuses its own attention and explorations on that same element. By contrast, imitation requires perceptual analysis of the form of a model's actions and the conversion of such analyses to generate outputs in the quite different medium of corresponding actions patterns in one's own effectors. Some authors have argued that while a prodigious capacity for such imitation is evident in humans, explaining our unique cultural achievements, evidence for imitation is lacking in other animals, including primates; thus, reviewing a large corpus of early research to answer the questions 'Do apes ape?' and 'Do monkeys ape?' (where 'to ape' meant to imitate), Tomasello (1996) and Visalberghi and Fragaszy (2002), respectively, delivered negative verdicts. Later research has subsequently provided experimental evidence for imitation in both apes (e.g. Buttelmann et al. 2007; Fuhrmann et al. 2014) and monkeys (e.g. Voelkl and Huber 2000; van de Waal and Whiten 2012) (for reviews, see Whiten et al. 2004; Whiten 2012), but the question remains controversial (e.g. Tennie et al. 2009) and there is a particular dearth of appropriately designed experiments in wild primates.

The Tomasello et al. (1996) and Tennie et al. (2009) position that apes do not imitate has been coupled with the claim that they instead 'only' emulate. However, these authors emphasised that emulation, like imitation, goes cognitively significantly beyond local enhancement. Depending on which of several forms emulation may take (Whiten et al. 2004), it may require a perceptual analysis of patterns of object movements, the causal factors involved and the generative re-creation of these. Efforts to identify emulation as distinct from imitation have principally been a preoccupation in the comparative psychology of humans (typically children) and apes (Tennie et al. 2009, 2010; Whiten et al. 2009). In monkeys, a growing corpus of studies has achieved the more tractable goal of identifying when social learning goes beyond local enhancement to imply either imitation *or* emulation (which are inherently more difficult to discriminate); these include the cultural diffusion studies cited earlier, as well as conventional dyadic experiments (Price and Caldwell 2007). However, this remains to be clearly done for primates in the wild, and this was our primary aim in the present study.

We first tested whether monkeys in the groups seeded with specific techniques were more likely to perform them. However, given that the extent of such matching varied, we also examined whether the proportion of either of the two techniques that individuals observed being performed by any or all other successful group members (i.e. not only the trained model demonstrations) predicted the technique first used, as well as that preferentially employed over the whole experimental set-up. Such a correlation was reported by Perry (2009) in relation to white-fronted capuchins (*Cebus capucinus*) adopting whichever of two methods of natural fruit processing they had observed most; here, we address this question for the two techniques experimentally seeded in the groups studied.

Methods

Study animals

Experiments were conducted by EW, with the help in each experiment of at least one of the several staff members of the Inkawu Vervet Project (IVP), between 26 April 2012 and 3 October 2013 on three groups of wild vervet monkeys (*Chlorocebus aethiops*). All three groups ['Ankhase' (AK), 'Baie Dankie' (BD) and 'Noha' (NH)] are part of the Inkawu Vervet Project conducted in a 12,000-hectares private game reserve, 'Mawana', in KwaZulu Natal, South Africa (S 28°00.327; E 031°12.348). The vegetation of the study site is classed as Savannah biome, characterised by areas of grasslands with dispersed clusters of trees forming a mosaic, with the typical savannah thornveld, bushveld and thicket patches. The home range sizes of our studied groups of vervet monkeys approximated 160 hectares (van de Waal et al. 2013b). The monkeys were totally wild before habituation started in 2010 and had human contact only with hunters and/or poachers within their territories. Experiments were mainly conducted in winter when food resources are scarce (documented in online material of van de Waal et al. 2013b), so monkeys were motivated to participate.

All participating monkeys lived in groups of 30–48 individuals, typically composed of a few adult males with many adult females and juveniles (detailed group composition in Table 1). The hierarchy within each group has been documented by field assistants on the basis of the

Table 1 Group composition 2012–2013

Group	AF	AM	JU	Total
Ankhase	8	4	21	33
Baie Dankie	12	4	32	48
Noha	11	4	25	40
total	31	12	78	121

Males (AM) were scored as adults once they migrated, while females (AF) were scored as adults once they gave birth. Group members that did not fulfil these criteria were scored as juveniles (JU). As some males migrated and some juvenile females gave birth during the study period, we present here average numbers outcomes of conflicts between pairs of individuals and priority of access to food sources. Rank is typically stable between adult female vervets and the males in each group, but there were some changes in the hierarchies during the study, with subadult females giving birth to their first infant and entering the adult female hierarchy as well as some changes in the male hierarchy, often resulting from migrations.

All individuals were identified by their faces. A recognition file with portrait photographs and specific individual features (scars, colour, etc.) was constructed for each group. Monkeys were named with letter codes. Matriline membership assignment was based on behavioural data: mothers nursing infants and adult females frequently being close to and tolerant of juveniles in feeding and resting contexts were taken as evidence for matriline membership.

Experimental procedures

The experimental apparatus was that used in our earlier studies with vervets in sanctuaries (van de Waal et al. 2013a) and consisted of an opaque plastic box, 10 × 10 × 10 cm, with a door on one side that could be slid to either side or instead lifted up to access the contents (Fig. 1a–b, video 1–2). The food reward inside was 1/20th of an apple that all monkeys were used to in other experimental settings and captures. The box thus acted as an 'artificial fruit' (Whiten et al. 1996), here called a 'vervetable', designed for testing the social learning of alternative opening techniques. The alternative opening methods resemble those of a 'doorian' fruit used in previous studies with chimpanzees (Horner et al. 2006) and capuchin monkeys (Dindo et al. 2008, 2009), but the slide door in the vervetable could additionally move to either side (whereas it was restricted to one side in the 'doorian') and was larger than that used in the capuchin study. Holes on the sides of the vervetable allowed it to be anchored to the ground using rope and camping hooks.

The experiments took place at sunrise close to a sleeping site. Experimental boxes (one during demonstrations, four to eight during experimental phases) were anchored to the ground. The spacing between the boxes was a minimum of half a metre, and orientation was variable depending on vegetation density and visibility. The experimental procedure began with a step-wise training phase in which the individual most focused on the task could learn only one opening solution (either lift, slide to the right or slide to the left) by trial and error because other opening solutions were physically blocked through the tightening of appropriately located bolts, limiting opening to one technique in each group. Once an individual mastered the opening technique, it was allowed to perform over 50 openings ('demonstrations') and until a minimum of half of the group observed the demonstration from a 5 m radius of the vervetable (AK group 54 demonstrations, 17 observers; BD group 71 demonstrations, 23 observers; NH group 70 demonstrations, 24 observers). Demonstrations took place over an average of 9 days (range 6–12) with an average of 8 demonstrations per day (range 2–12), each time involving only a single vervetable to ensure its exclusive access and performance of a specific opening technique, alternative solutions remaining blocked. The remainder of the group were able to watch these demonstrations. By fixing the number of demonstrations to at least 50, we ensured that a minimum of 2/3 individuals of each group observed an opening at least once. Females were preferred models, as van de Waal et al. (2010) found that in the wild, adult female vervets are more likely to be watched and learned from than males. We first attempted to attract the dominant female of each group as a model by presenting the baited box open, in proximity to her. Where there was a lack of response, we trained the most food motivated and boldest

Fig. 1 The 'vervetable': **a** door being lifted, **b** door being slide to right. For more illustrations of vervetables manipulated by captive vervets in sanctuaries in prior experiments, see van de Waal et al. (2013a)

adult female of each group who approached the vervetable, namely Nkosikasi (4th in rank) in AK, Asis (3rd in rank) in BD and Paris (4th in rank) in NH. Our three groups were exposed to other experimental devices, but not to any other box with a door that opens through manipulation.

After the demonstration phase, an experimental phase consisted of 15 days in each of the three groups, with up to eight vervetables offered at one time. We initially offered four boxes but quickly decided to switch to eight as an optimal number to spread access across the group while being able to monitor all boxes; in this, number of sessions and boxes was kept comparable across all groups. We refer to each day of testing as a 'session', during which a monkey might achieve one or several openings. All vervetables were unlocked, so that any technique could now be used. All monkeys were free to interact with the vervetables repeatedly within the constraints of the social group dynamics, such as rank. As a result, the total number of openings per monkey naturally varied. Once any vervetable was opened, an experimenter slowly approached and re-baited it. All interactions with the vervetables were recorded using one video camera during the demonstration phase and two during the experimental phase, because the latter involved multiple vervetables to prevent monopolisation. The average duration of a demonstration session was 29 min, and the average duration of an experimental session was 1 h 21 min.

Data coding, analyses and statistics

For each manipulation of a vervetable, we recorded which monkey performed it, which technique was used (lift, slide to the right, slide to the left) and whether the monkey managed to open the door successfully and gain the reward or not. Most openings were coded live in the field, with the few openings that could not be followed during the experiment coded later from videos, concerning either the identity of the manipulating monkey or the opening technique. We found that all codings were unambiguous as they involved quite different manipulations of the apparatus (lift, slide right or left), and such measures were always taken by two coders (EW and one other staff member of IVP); inter-observer reliability was 100 %.

We also coded the ID of each monkey who was less than 5 m from a successful manipulation and attentive to the opener. The attention of these individuals was considered positive if the monkey was otherwise inactive and had its head orientated towards the manipulator. These data were coded in the field by EW and one other staff member of IVP; only if both observers had coded the monkey as attentive was this included in the analyses.

We analysed the effects of monkeys observing 'lift' versus 'slide' techniques and 'slide right' versus 'slide left' techniques separately in terms of three principal hypotheses regarding social learning. First, we used R (R Core Team 2013) to perform two-tailed permutation tests with 10,000 permutations to test the prediction that the first successful technique used by each individual would be similar to the technique introduced into their group (whether because they learned from the model or another monkey). Second, focusing on the overall difference between groups' techniques, we used IBM SPSS Statistics 21.0 (SPSS Inc., Chicago, IL, USA) to create binomial generalised linear models (GLM) with a logit link to test whether the behaviour of individuals in the different groups was predicted by the technique used by their initial models and to calculate the correlation between attention and actions used.

Ethics guidelines

We adhered to the 'Guidelines for the Use of Animals in Research' of the Association for the Study of Animal Behaviour. Our experiments were approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa; by the funder, Swiss National Science Foundation and by the Ethics Committee of the School of Psychology and Neuroscience, University of St Andrews, UK. Our set-up involved potential opportunities for feeding competition. However, as we were mainly interested in individuals' first manipulation, we offered multiple test boxes, which minimised any conflict. We also kept the amount of food relatively small (1/20 of an apple in each trial) both in the demonstration and in experimental phases.

Results

Across all three groups, 49 out of 121 individuals approached the vervetable and touched the box. Seventeen individuals, out of 121 in the three groups, successfully opened a vervetable at least once. Only eight of the 32 unsuccessful manipulators touched the door during their manipulation. Excluding the models, it was mainly juveniles that successfully opened the apparatus (23 % of adults and 77 % of juveniles). We removed one individual from our analysis, 'Porto', as he interacted and successfully opened the apparatus during the demonstration phase, being tolerated by the model 'Paris', his mother; thus our sample size of successful openers, apart from the models, was 13. Individuals younger than 1 year never participated in the experiments. Evidence for social learning was evaluated in the following three analyses (see ESM for data set).

Testing for social learning: first successes

On their first opening, 11 out of 13 group members adopted the technique their model had used. We found that members of the 'slide' groups were significantly more likely to use 'slide' in their first success than members of the 'lift' groups (exact permutation test: $N = 13$, $P = 0.038$, Fig. 2).

The difference between the 'slide-left' and the 'slide-right' groups regarding the direction of movement on first 'slide' success was not significant (exact permutation test: $N = 6$, $P = 0.4$). However, only six monkeys in the two slide groups, three per group, solved the vervetable (two sliding to the right and one to the left in each group), limiting the power of the test.

Testing for social learning: differences between groups across all trials

To evaluate the strength of any socially learned differences between groups, we fitted a GLM with the number of successful 'lift' actions across all sessions relative to the total number of successes for each individual as the dependent variable and the technique used by the model, either 'lift' or 'slide' as a single factor. We found that individuals who had been exposed to a model using 'lift' were significantly more likely to use 'lift' than if the model had used 'slide' (Wald $\chi^2_1 = 28.28$, $N = 13$, $P < 0.001$, Fig. 3).

We used the same technique to fit a GLM with the number of successful 'slide-right' actions across all sessions relative to the total number of successful 'slide' actions for each individual as the dependent variable and the technique used by the model, either 'lift', 'slide right' or 'slide left' as a single factor. In this analysis, the group in which the models had been trained to perform 'lift' are used as a contrast because these models provided no information regarding the direction in which the door could slide. We found that the technique demonstrated had a small but significant main effect (Wald $\chi^2_2 = 6.35$, $N = 13$, $P = 0.042$) but that the effect resulted from the fact that individuals who had not been exposed to a model using 'slide' were more likely to use a 'slide-left' technique than individuals who had seen a 'slide-left' (Wald $\chi^2_1 = 3.84$, $N = 8$, $P = 0.050$) or a 'slide-right' model in their group (Wald $\chi^2_1 = 3.58$, $N = 10$, $P = 0.058$). There was no significant difference between 'slide left' and 'slide right' (Wald $\chi^2_1 = 1.36$, $N = 8$, $P = 0.24$).

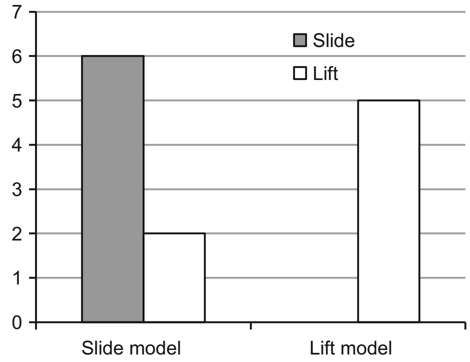

Fig. 2 Preferences for the technique used by the model on their first success: total number of individuals using 'lift' or 'slide' on their first success in the groups seeded with a 'lift' or 'slide' model (*grey* for 'slide' and *white* for 'lift')

Does the proportion of 'lift' versus 'slide' witnessed overall predict the option adopted?

Building on approaches developed in a two-action social diffusion study in young children (Whiten and Flynn 2010: compare Figs. 3 and 4 therein), Fig. 4 shows each successive monkey's openings during their first successful session of 'lift' versus 'slide' actions before the next monkey opened a vervetable, for each of the groups (Fig. 4a = Baie Dankie group, 4b = Ankhase group, 4c = Noha group). Arrows indicate the putative direction of information flow, because these arrows originate from each monkey that the focal individual had watched prior to its first success, and the proportion of 'lift' versus 'slide' actions witnessed as a result is indicated in each case. These data are important because they permitted us to address whether the proportion of 'lift' witnessed overall predicted a corresponding bias in an individual's actions. The illustrations in Fig. 4 are necessarily complex precisely because the reality of information flow in the diffusion process is inherently complex; we have sought to portray this reality in these figure formats, so allowing direct comparison with those for other species (Flynn and Whiten 2010).

We found that the percentage of the 'lift' technique witnessed overall was significantly correlated with the percentage of 'lift' that individuals used during their first successful session (Spearman correlation, $N = 13$, $\rho = 0.76$, $P = 0.003$; Fig. 5a) as well as to the percentage of 'lift' used during the whole experiment (Spearman correlation, $N = 13$, $\rho = 0.808$, $P = 0.001$, Fig. 5b).

One possible explanation for the correspondence between what monkeys saw and what they did is that it is determined by the angle of approach, as might be suggested by the video samples we offer showing a monkey arriving at the front and lifting, or approaching from the side and sliding. However, these videos were chosen to show most clearly the actions each model performs: overall, approaches and postures varied in similar ways across the different model conditions. To check this, we

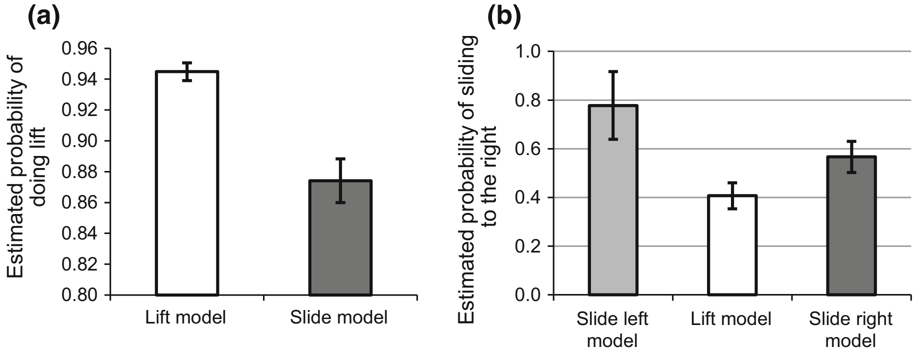

Fig. 3 Probability of performing 'lift' versus 'slide' across all sessions as a function of what the model was trained to do (*white* for the one group with 'lift' model and *grey* for the two groups with 'slide' model)

recorded the direction of first approach and successful manipulation from either left, right or front, and these were, respectively, 1, 2, 2 in the lift group and 2, 4, 2 in the slide groups. Similarly, body orientation towards the vervetable from left, right or front when opening it was, respectively, 1, 1, 4 in the lift group and 2, 1, 5 in the slide groups. Clearly, there is no pattern here that would explain the match between what monkeys saw and what they did.

Discussion

Our results provide evidence of a level of social learning in wild vervet monkeys that discriminates between different ways to process an artificial fruit item. We observed matching of whichever of two alternative methods had been experimentally seeded in a participant's group, both in the first opening and in overall behaviour subsequently. Overall, there was a strong positive correlation between techniques witnessed by each individual and the technique they adopted. This latter result took into account occurrences when individuals sometimes saw techniques different to those seeded, thereby permitting a finer-grained statistical analysis of what actions were done, contingent on those witnessed. Here, we address three principal implications of our results.

Two-action tests in the wild

Field experiments identifying social learning remain rare, but already cover taxa ranging from fish to birds and suricates (Helfman and Schultz 1984; Langen 1996; Lefebvre 1986; Thornton and Malapert 2009; Warner 1988; for a review, see Reader and Biro 2010). Such experiments on primates have only recently been completed and have begun to demonstrate social learning in the wild in just a handful of species so far (lemurs: Kendal et al. 2010b; Schnoell et al. 2014; vervet monkeys: van de Waal et al. 2010, 2012, 2013b, 2014; van de Waal and Bshary 2011; marmosets: Gunhold et al. 2014a, b). However, experiments with wild primates that incorporate the refinement of seeding alternative foraging techniques in trained models remain even more uncommon: just two on lemurs (Kendal et al. 2010b; Schnoell and Fichtel 2012; Schnoell et al. 2014 [same study]), two on marmosets (Gunhold et al. 2014a, b) and one on vervet monkeys (van de Waal et al. 2010).

Even these have applied experimental designs that are inherently limited in identifying the social learning mechanism implicated. For example, Schnoell and Fichtel (2012) in a study incorporating a door that could be either pulled or pushed according to where lemurs put their muzzles, acknowledge that this does not exclude the simplest form of social learning, local enhancement. Kendal et al. (2010b) used a similar set-up. By contrast, in our study monkeys grasped the same knob on a door to perform either 'slide' or 'lift', so that the copying we observed could not be explained by local enhancement, but rather concerned alternative movements, involving either or both the actions of the model, thus implicating imitation, or the movement of the vervetable door, implicating emulation. We believe that our results and those recently reported for marmosets by Gunhold et al. (2014a) provide the first such evidence derived from two-action field experiments with wild primates. It is a further and more difficult step to discriminate imitation from emulation, because in nature, alternative actions (e.g. lift versus slide) and their contingent effects on the world (door rises versus door slides) are so intimately linked. In the controlled conditions permitted by captivity, these have been dissected by experimental manipulations such as 'ghost conditions' (Hopper et al. 2008), in which the object movement occurs without sight of causative actions, permitting only emulation and not imitation. Such manipulations naturally become particularly challenging in the wild, but may become more feasible through new developments like video presentations in the field (Gunhold et al. 2014b).

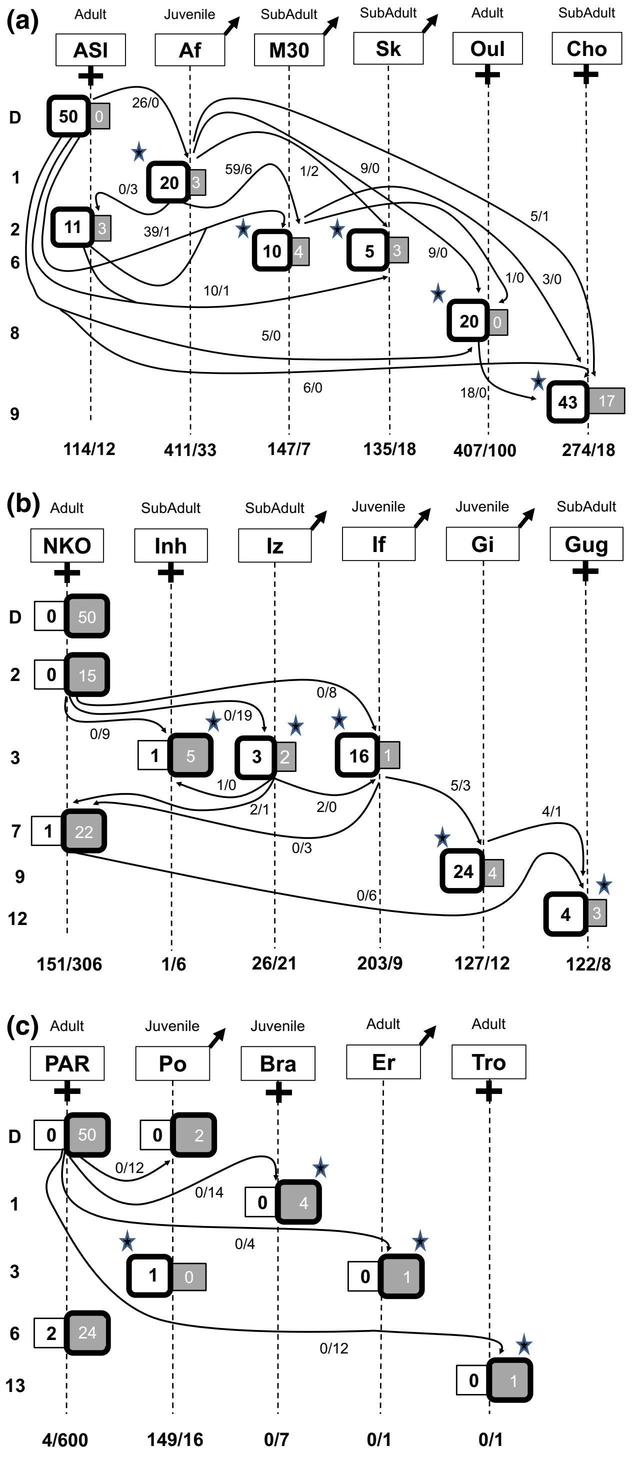

Fig. 4 Inferred information flow through each group: **a** group AK, **b** group BD, **c** group NH. Following the format of a similar diagram describing cultural transmission in groups of children (Whiten and Flynn 2010), *each column* represents one vervet (age class written above the name: adult, subadult, juvenile and sex as a symbol under the name ♀ = female, ♂ = male) and *each row* represents a session day (numbered), with entries *diagonally left* to *right* expressing each individual's first opening techniques on the relevant session: on *left* in *white box*, number of lifts; on *right* in *grey box*, number of slides. The *bold frame* indicates the most common action in each case. *Arrows* tracked backwards show whom an individual had been in a position to observe before starting to open vervetables, and the relative numbers of 'lift' versus 'slide' they were thus inferred to have witnessed before their first successful opening, so *arrow heads* indicate inferred information flow. *Numbers* across the *bottom* of the *diagram* show the total frequencies of alternative actions in the whole series of sessions. *Stars* indicate whether the first action done was lift or slide

Correlations between relative frequency seen and relative frequency done

Our detailed data on what each individual had been likely to see before it worked on our foraging task (Fig. 4) permitted computations of correlations that provide finer-grained support of the link between observation and learning a new task than obtained in a simple dichotomous comparison of two different treatment groups. The positive correlation we found is consistent with observational field evidence for primates suggesting vertical transmission, where tolerance and close observations allow juveniles to adopt their mother's foraging methods (Lonsdorf et al. 2004; Perry 2009; Jaeggi et al. 2010). Consistent with this, we have earlier shown experimentally that wild vervet monkeys display vertical social transmission in both food preference (van de Waal et al. 2013b) and forms of food manipulation (van de Waal et al. 2014). The correlation we observed is diagnostic of social learning that could reflect one or more process of (a) conformity to the preference of a majority of the several monkeys an individual watched (Claidière and Whiten 2012); (b) matching the overall total frequency of actions (rather than number of monkey) witnessed (Perry 2009); or (c) matching focussed on one key individual such as the mother (van de Waal et al. 2014) or a higher status individual (Horner et al. 2010). A plausible scenario that is also consistent with models of human cultural development (Henrich and Broesch 2011) would involve an initial focus on learning from the mother, extending to others of these kinds of learning rules as a young primate matures. We do not yet have enough data to discriminate such alternatives for the task described here, but in many cases in the present experiment individuals watched only one or few others, suggesting a conformity effect may be less likely than the other potential biases.

Minimal success across the group as a whole

The proportion of individuals in our groups who were successful in the study was low, at only 17 among 121 monkeys. As a result, we cannot address the level of granularity in what was learned compared to the larger sample of captive vervets in our earlier study that even revealed copying of whether the sliding of the door was to the right or to the left (van de Waal et al. 2013a). What

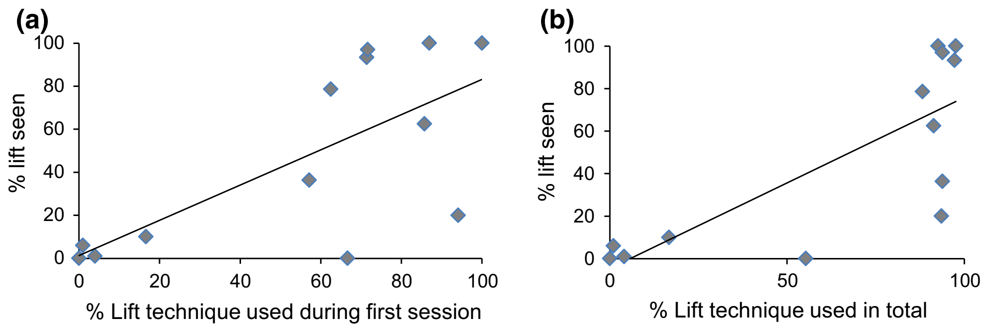

Fig. 5 **a** Correlation between the percentage of the lift technique used during the session when a monkey first successfully opened a vervetable and the percentage of lift actions that individuals witnessed beforehand. **b** Correlation between the percentage of lift technique used during the whole experiment and the percentage of lift that individuals witnessed before their first success

might have been responsible for the low rates of participation and successful openings? One possibility is that it is linked to model identities. All our models were determined by which individuals approached the task first, and these were adult females ranked only 3rd or 4th in the female hierarchy, perhaps consistent with earlier findings that lower-ranked individuals can be under pressure to be more ecologically exploratory than higher-ranked individuals (Sigg 1980). In turn, these lower-ranked individuals may be less likely to be attended to and copied, a phenomenon identified in chimpanzees (Horner et al. 2010; Kendal et al. 2014). However, van de Waal et al. (2010) found selective attention of wild vervets towards dominant females and not dominant males in another two-action test, consistent with the hypothesis that the philopatric sex should be more copied in a foraging task, but observations of gaze during adult vervet monkeys' foraging revealed that adult females are observed more than adult males *irrespective* of their rank (Renevey et al. 2013). The question of whether greater participation would follow the demonstration of new techniques by alpha females remains open and further investigations are needed.

Conclusions

We have described one of the first field experiments demonstrating that, in contrast to the conclusions of many earlier studies with captive primates, wild primates may discriminate and copy alternative means for processing difficult food types, and we have tracked the initial progress of social information transfer within the group. These approaches should be applicable to many other species and with sufficient sensitivity to the social dynamics of the groups concerned offer prospects for deeper analyses of social learning in wild animal populations in the future.

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