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## Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys

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Two-action experiments, in which observer individuals watch models use one of two alternative methods to achieve the same goal, have become recognized as a powerful method for studying social learning. We applied this approach to vervet monkeys, *Chlorocebus aethiops*, using an artificial fruit ('vervetable') which could be opened by either lifting a door panel on its front, or alternatively by sliding the panel to the left or right. In each of two groups a model was trained to lift the door and in two others the model slid it to either the left or right. Members of each group could then watch their model before the group was given access to multiple baited vervetables. Over the course of 100 openings we found a significant tendency for the lift and slide approaches to spread preferentially in the groups in which they were seeded. The same was true for slide left versus slide right, indicating these monkeys can attend to and learn from a fine level of detail in what others do. This effect cannot be explained by mere local enhancement since monkeys grasped a knob centred in the door to perform all techniques. Instead, imitation or emulation is implicated. No significant diminution of the tendency to adopt the seeded technique occurred among individuals learning later rather earlier in the study. Our results show that vervet monkeys have the capacity to learn from others by either emulation or imitation and what they learn has the potential to spread across their group.

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Research on social learning, traditions and cultural transmission in primates and other animals has in recent years become a major endeavour in the life sciences (Hoppitt & Laland 2008; Kendal et al. 2010a; Whiten et al. 2011; Nielsen et al. 2012). An important 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 earlier when they make their own attempts at the task, we gain 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. First used by Dawson & Foss (1965), the two-action method has since been employed 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, *Columba livia* (Zentall et al. 1996), alternative techniques (e.g. manual versus oral) to open artificial food objects by marmosets, *Callithrix jacchus* (Bugnyar & Huber 1997; Voelkl & Huber 2000) and alternative sequences of constituent behavioural elements by chimpanzees, *Pan troglodytes* (Whiten 1998).

Such two-action studies have typically been dyadic, based on an isolated subject learning from a single model (Zentall 2012). Such a configuration can be optimal in tightly controlling and identifying the information available to the learner, and thus circumscribing the social-learning processes involved. However, the two-action concept has more recently been enlisted in the design of experiments in which the interest lies in the social transmission and spread of action patterns in groups and broader populations (Galef & Allen 1995). In a review of 33 such 'diffusion experiments' in nonhuman species, Whiten & Mesoudi (2008) identified 17 that had 'seeded' alternative actions in an individual in each of at least two different groups of birds or mammals, and then documented any subsequent differential spread of the alternatives that occurred in the groups in which they were seeded, creating incipient local traditions. Among primate studies, such differential spread has been

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shown to occur with substantial fidelity in captive groups of both capuchin monkeys, *Cebus apella* (Dindo et al. 2008, 2009) and chimpanzees (Whiten et al. 2005, 2007; Horner et al. 2006).

Comparable studies remain in their infancy in the wild (Whiten & Mesoudi 2008; Thornton & Clutton-Brock 2011), where they are inherently more difficult to engineer because there is less scope to control what an observer monkey witnessed. For primates, such experiments have begun only recently, with studies by Kendal et al. (2010b), van de Waal et al. (2010), van de Waal & Bshary (2011) and Schnoell & Fichtel (2012). In the van de Waal studies, boxes acting as 'artificial fruits' were presented to wild vervet monkeys, *Chlorocebus aethiops*. A door at one end of the box could be opened by sliding it and a differently coloured door at the other end could be opened by lifting it, to obtain food inside. These two alternatives were seeded in different groups by initially locking the box so that only one technique could be used, until a single dominant individual mastered it. Then both methods were made available. This study demonstrated social learning from the initial model, so long as the model was a female monkey. However, because the different actions were modelled on different doors at either end of the box, it was not possible to determine whether the results reflected only local enhancement (Thorpe 1963), where the observer is simply more likely to focus their efforts on the end of the box to which a model had drawn attention, or more complex social learning.

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 & Ham (1992, page 250) as 'learning some aspect(s) of the intrinsic form of an act' from another individual) or 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 have created an artificial food item we have dubbed a 'vervetable'. This 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. Preparatory to field experiments with this device we have initially tested captive vervet monkeys, some of them wild born, living in sanctuaries in South Africa prior to release into the wild. We seeded each of the different techniques (slide left, slide right or lift) in a single individual in each of four groups and investigated (1) 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 findings of van de Waal et al. (2010) as discussed above; and (2) whether there was evidence for the spread and maintenance of the alternative sliding and lifting techniques in the groups in which they were seeded, consistent with a capacity for behavioural traditions in this species.

## METHODS

### Study Animals

Experiments were conducted by E.W., with the help in each experiment of one of several staff members of the Inkawu Vervet Project, between December 2010 and August 2011 on four groups of captive vervet monkeys. Three groups ('Hammer' (H), 'Hamptons' (P) and 'Sturrell' (S)) were housed at the Wild Animal Trauma Centre and Haven (WATCH) in Vryheid, KwaZulu-Natal, South Africa and one group ('Lisa' (L)) was at Bamblela Wildlife Care, Limpopo, South Africa. Both centres play a key role in the rehabilitation and release of vervet monkeys in South Africa. They are home to numerous groups of vervet monkeys at various stages of rehabilitation, and have already released groups to the wild.

All participating monkeys lived in groups of 19–37 individuals, typically composed of one adult male with many adult females and juveniles (Table 1). Group compositions were thus similar to those in the wild even if individuals were of course less related than natural groups. All groups were kept in conditions to prepare them to be released. Individuals were recognizable from their faces and other features such as scars, fur colour and tail shape already documented by sanctuary staff. The hierarchy within each group was documented by sanctuary staff on the basis of the outcomes of conflicts between pairs of individuals and priority of access to food sources. Rank is typically stable between adult female vervets and given only one male per group, there were no changes in the hierarchies during the study.

The enclosures at WATCH were enriched with grass, trees and climbing structures, with a ground area of 80 m<sup>2</sup> (P), 130 m<sup>2</sup> (H) and 420 m<sup>2</sup> (S) and a height of 3.2 m in all three enclosures. The enclosure of (L) group at Bamblela consisted of a concrete floor and climbing structures, with a ground area of about 50 m<sup>2</sup> and a height of 3 m. The monkeys' diet was very diverse, but consisted mainly of fruits, vegetables and some cereals.

### Experimental Procedures

The experimental apparatus 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 gain access to the contents (Fig. 1a–d, Supplementary Video S1, S2). The food reward inside was grapes, raisins, peanuts or fruit candies depending on the group, but all food rewards were part of the monkeys' usual diet. 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 sliding 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.

At WATCH, experiments took place in the entrances of the enclosures, which could be isolated from the main enclosures so that vervetables could be refilled with no monkeys present. As soon as all vervetables were opened and empty, the monkeys were herded back into their enclosure and the vervetables were refilled by the experimenter or assistant and closed (one box during demonstration, up to four during later experimental trials). These entrances were shaded by cloths to avoid monkeys from other groups observing the experiment. In Bamblela these experiments took place in the enclosure.

**Table 1**  
The composition of the study groups

Group	Adult males	Adult females	Juveniles	Infants	Total	Model+technique
H=Hammer	0	5	10	7	22	Dominant adult female+slide left
P=Hamptons	2	7	10	0	19	Dominant adult female+slide right
S=Sturrell	1	5	20	11	37	Subordinate juvenile male+lift
L=Lisa	1	2	16	8	27	Control=lift

Males were scored as adults by size and testis colour, while females were scored as adults once they had given birth. Group members that did not fulfil these criteria were scored as juveniles if they were over 1 year old. The individuals under 1 year old were categorized as infants and were not included in our analyses. Identity of the model is shown in the last column.



**Figure 1.** The 'vervetable': (a) door closed, (b) door lifted, (c) door slid to left, (d) door slid to right.

The experimental procedure began with a stepwise 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. Once an individual mastered the opening technique it was allowed to perform 20 openings, ('demonstrations') each time being provided with 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. Dominant females were preferred models, as van de Waal et al. (2010) found that in the wild, adult female vervets are watched and more likely to be learned from than males, but in practice experimenter selection of models was limited. In one group (H) the dominant female (wild-born, taken in after a car accident) could be comfortably separated in the entranceway such that others observed her 20 initial demonstrations of sliding to the left, through the mesh. However, it was not possible to separate the dominant females in the other groups. Fortunately, one human-raised dominant female self-selected to perform the 20 initial openings in group P, the vervetable being locked so she demonstrated only sliding to the right. In the third group (S) this role was taken by a human-raised juvenile male restricted to the lift method for 20 demonstrations. Having succeeded in achieving models for all three opening techniques, in the fourth group (L) we then conducted an exploratory trial with no demonstration and the vervetable initially free to be opened in all ways, to discover which method might emerge spontaneously. A single human-raised juvenile male monopolized the first three openings, showing consistent lifts, and thereby became the initial model; he was joined by the dominant female also lifting on four occasions during the first 20 openings. We thus designated this to be a second 'lift' group. In all cases, other monkeys were next to the model as they performed the initial demonstrations.

After the demonstration phase, an experimental phase consisted of 100 openings in four groups with up to four vervetables offered at one time. 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 varied. Each experimental session had between 20 and 80 openings

depending on monkeys' motivation and was completed with a maximum of a week between experimental sessions. The experimental trials were spread over 2 days for each of H, P and L groups and 3 days for S group. All interactions with the vervetables were recorded using one video camera during the demonstration phase and two during the experimental phase, which involved multiple vervetables.

#### *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 left) and whether the monkey managed successfully to open the door and gain the reward or not. We found that all codings were unambiguous as they involved very different manipulations of the apparatus (lift, slide right or left), and such measures were always taken by two coders (E.W. and one other staff member of IVP); thus interobserver reliability was 100%.

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 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 binomial generalized 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. Finally, we focused on the evolution of the difference between groups across trials and tested for the maintenance of any initial group differences in behaviour. To do this we compared the proportion of actions matching those of the initial model in the approximately half of all individuals who succeeded in the first 20 openings with the same index of matching for those later-learning individuals who succeeded in subsequent trials. We also tested whether in the early-learning individuals, this index of matching later diminished. To analyse these results we used a binomial generalized estimating equation (GEE) for repeated measures procedure with a logit link. All statistical analyses were performed using IBM SPSS 19 (SPSS INC, Chicago, IL, U.S.A.).

### Ethical Note

Our experiments were approved by the relevant local authority, Ezemvelo KZN Wildlife, South Africa; by the funder, Swiss National Science Foundation as well as the Ethics Committee of the School of Psychology, University of St Andrews, U.K. Our set-up involved some feeding competition. However, as we were mainly interested in individuals' first manipulation we offered multiple test boxes to minimize conflict. We also kept the amount of food relatively small (five raisins, or five peanuts or one fruit jelly depending on the group) both in the demonstration and experimental phases.

### RESULTS

Thirty-four individuals, out of 79 in the four groups, successfully opened a vervetable at least once. Both adults and juveniles were successful (65% of adults and 35% of juveniles). While most of the recruitment occurred in the first 20 openings, it continued through later trials with the number of monkeys first opening vervetables in consecutive sets of 20 openings being 9, 0, 1, 2 and 2 in the lift groups and 10, 3, 4, 1 and 2 in the slide groups. Individuals younger than 1 year old never participated in the experiments. Evidence for social learning was evaluated in the following three analyses.

#### Testing for Social Learning: First Successes

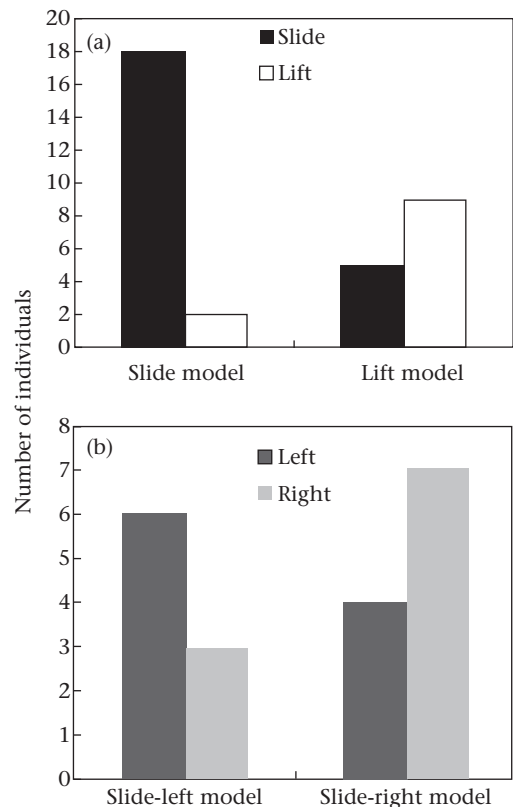
On their first opening, most group members adopted the technique their model had used. We found that members of the 'slide' groups were significantly more likely to use 'slide' in their first success than members of the 'lift' groups (exact permutation test:  $N = 34$ ,  $P < 0.001$ ; Fig. 2a).

The difference between the 'slide-left' and the 'slide-right' groups regarding the direction of movement on the first 'slide' success was not significant (exact permutation test:  $N = 20$ ,  $P = 0.21$ ; Fig. 2b). However, the number of individuals in the two slide groups was small (nine and 11 in each group, respectively), limiting the power of the test compared to that for the lift versus slide contrast above, which used data from 34 individuals.

#### 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  $\chi^2_1 = 8.77$ ,  $N = 34$ ,  $P = 0.003$ ; Fig. 3a).

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 two groups in which the models had been trained to perform 'lift' were used as a contrast additional to the direct left–right comparison because these models provided no information regarding the direction in which the door could slide. We found that the technique demonstrated had a significant main effect (Wald  $\chi^2_2 = 22.13$ ,  $N = 33$ ,  $P < 0.001$ ; Fig. 3b) and that the effect resulted from the fact that individuals who had been exposed to a model using 'slide-right' were more likely to use that technique than individuals who had a 'slide-left' (Wald  $\chi^2_1 = 11.99$ ,  $N = 20$ ,  $P = 0.001$ ) or a lift model in their group (Wald  $\chi^2_1 = 20.65$ ,  $N = 24$ ,



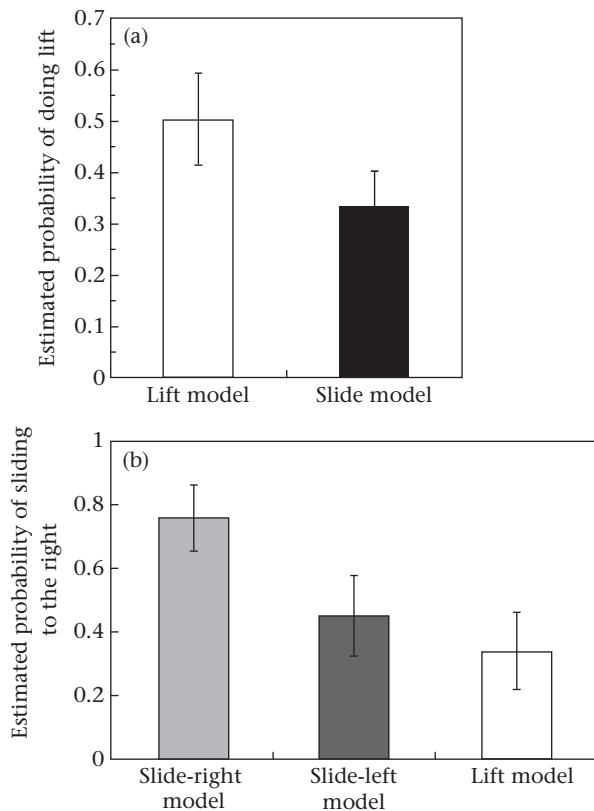
**Figure 2.** Preferences for the technique used by the model on their first success. (a) Total number of individuals using 'lift' or 'slide' on their first success in the four groups seeded with a 'lift' or 'slide' model. (b) Total number of individuals using 'right' or 'left' on their first 'slide' success in the two groups seeded with a 'slide-right' or 'slide-left' model.

$P < 0.001$ ; Fig. 3b). There was no significant difference between slide-left and lift (Wald  $\chi^2_1 = 1.53$ ,  $N = 22$ ,  $P = 0.217$ ).

#### Persistence of Socially Learned Group Differences Over Time

To examine the spread of the alternative techniques within the groups in which they were seeded we divided individuals into the approximately half of them that succeeded in the first 20 openings ( $N = 19$ ) and the remainder that learned in later trials ( $N = 15$ ). Any loss of group differences between these cohorts might be caused by one of two main effects. One hypothesis would be that the early learners later increasingly explored the vervetable, discovered one or more of the alternative techniques and went on to use these more. Alternatively, later learners, having observed more than one technique performed, might be less likely to perform the technique originally seeded. To address this second and arguably more important hypothesis related to social transmission, we compared the proportion of actions matching those of the initial model between the early learners and the later learners. To address the first hypothesis we compared this index of matching for early learners in the first 20 openings with their performance in the later trials.

We applied a GEE analysis, with the number of successes using the same technique as the initial model compared to the total number of successes, as the dependent variable. We first tested for main effects of, and interactions between, the technique used by the model ('lift' or 'slide') and the three 'Period' categories of early learner early actions, early learner late actions and later learners. We found no main effect of the Period category (Wald  $\chi^2_2 = 0.87$ ,  $N = 34$ ,  $P = 0.646$ ) and no interaction between the two factors



**Figure 3.** (a) Probability of performing 'lift' versus 'slide' as a function of what the model was trained to do (white for groups with 'lift' model and black for groups with 'slide' models). (b) Probability of performing 'slide-right' versus 'slide-left' as a function of what the model was trained to do (light grey for group with 'slide-right' model, dark grey for group with 'slide-left' model and white for groups with 'lift' model). The values are the estimated marginal means (unweighted means) and 95% Wald confidence interval from the GLM described in the text.

(Wald  $\chi^2 = 3.89$ ,  $N = 34$ ,  $P = 0.143$ ). Estimated marginal means and 95% Wald confidence intervals for the probability of matching the technique seeded were 0.53 [0.30;0.76] for early learners, 0.59 [0.37;0.81] for early learners in the later period and 0.64 [0.53;0.76] for later learners. Accordingly, there is no evidence for changes under either of the two hypotheses outlined above; rather, there is evidence for persistence of socially learned differences between groups in the later trials.

A similar analysis revealed the same effect regarding the direction of the slide movement. We compared model matching successes to the total number of slide actions and performed a similar GEE procedure to that outlined above. Again we found no main effect of Period (Wald  $\chi^2 = 3.70$ ,  $N = 20$ ,  $P = 0.157$ ) and no interaction with the technique modelled (Wald  $\chi^2 = 3.23$ ,  $N = 20$ ,  $P = 0.199$ ). Estimated marginal means for the probability of matching the technique seeded were 0.57 [0.31;0.83] for early learners, 0.83 [0.65;1] for early learners in the later period and 0.56 [0.40;0.71] for later learners.

## DISCUSSION

### *Evidence for Social Learning by Copying*

Our study further confirms the capacity of vervet monkeys for social learning, first demonstrated in the field experiments of van de Waal et al. (2010). However, our results go beyond this to document the differential learning of either of two approaches to a task, both of which involve handling the same locus on the box,

namely the knob in the centre of the door, so that the effect cannot be explained as due only to local enhancement. This suggests a more elaborate level of social learning that discriminates how the artificial fruit is opened. One candidate for this is imitation (van de Waal & Whiten 2012), in which as defined in our Introduction, the monkeys are learning to use either the lift or slide action by copying the action they have witnessed. A second candidate is emulation, in which the monkeys have instead learned a particular affordance of the vervetable, either that the door slides open to left or right or that it lifts up, and this is what they attempt to copy. At present we are unable to determine which of these two mechanisms is involved, but future experiments, such as 'ghost' manipulations in which subjects witness only the object movements, permitting emulation but not imitation (Hopper 2010) should in principle be able to do so. Klein & Zentall (2003) completed such a study that indicated emulation learning in pigeons, and Hopper et al. (2008) extended this approach to chimpanzees and children, likewise finding evidence for emulation. However, it is also possible that the learning involved relies on some degree of replicating both the actions and their effects in the world. Experimental evidence already suggests this is the case for chimpanzees (Horner & Whiten 2005; Hopper et al. 2007, 2008).

### *Level of Granularity in What Is Learned*

We found that not only did the vervets show evidence of discriminating the different qualities of movement involved in either lifting or sliding the door, but they additionally discriminated between sliding the door to one side or the other. Much past experimental evidence has offered little support for social learning in monkeys that goes beyond local or stimulus enhancement (Visalberghi & Fragaszy 1990, 2002; Whiten 2012), so the present results are significant in showing that the species of monkey we studied does attend to such details of movement and may generate copies of them through its own actions. This level of granularity in what is matched, in this case discriminating laterality of movement, has to date been demonstrated in pigeons (Klein & Zentall 2003) and chimpanzees (Hopper et al. 2008) but we believe this is the first evidence of such a level of matching in monkeys. Perhaps the closest previous findings we are aware of are of copying pushing a door versus pulling it, in marmosets (Bugnyar & Huber 1997) and colobus monkeys, *Colobus guereza kikuyuensis* (Price & Caldwell 2007).

### *Spread of Alternative Socially Learned Options*

Our study was not limited to the dyadic context but instead seeded either the lift or slide method in a group and monitored its potential spread. Such spread was indeed observed to lead to different, socially transmitted behavioural profiles in the different groups we studied and there was a continued recruitment of individuals to open the vervetables over the 100 openings, with six monkeys opening one for the first time in the final set of 20 trials (trials 81–100). The approximately half of all monkeys we designated as the later learners were no less likely to adopt the technique of their model than were the earliest learners; nor were the early learners less likely to sustain the group differences in the later trials.

We were not able to study this process further because the subjects were released into the wild. However, our results suggest that the social-learning capacities of vervet monkeys are sufficient to sustain the spread of innovations across groups, which if adaptive are likely to become longer-term traditions. We would not wish to claim that the rather subtle differences in technique discriminated in our relatively short-term experiments would themselves be likely to continue as long-term cultural differences between groups. Rather, the two-action tests we applied here provide

rigorous means of testing for social learning at a level beyond mere local enhancement, and for capacities of cultural transmission that allow new techniques to spread across a group. In future, we hope to apply these methods to vervet monkeys in the wild, building on the studies of van de Waal et al. (2010) for this species, and Kendal et al. (2010b) and Schnoell & Fichtel (2012) for prosimian primates. Such studies remain rare. Whiten & Mesoudi (2008) identified just three on animals in the wild (all birds) among the 33 social diffusion studies they reviewed up to that date. More recently, Thornton & Clutton-Brock (2011) were able to identify a similarly small corpus of newer diffusion studies for nonprimate mammals in the wild, which include notable initiatives with meerkats, *Suricata suricatta* (Thornton & Malapert 2009) and mongooses, *Mungos mungo* (Müller & Cant 2010). It is to be hoped that the captive study reported here contributes to the expansion of this research effort both by refining the methodologies for application to field studies and by providing evidence of abilities for social learning and cultural transmission which beg to be tested for their application to monkeys' natural repertoires in the wild.

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### Supplementary Material

Supplementary material associated with this article is available, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2012.10.008>.

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