

Observational learning in orangutan cultural transmission chains

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Field reports suggest that orangutans acquire local traditions by observing neighbouring conspecifics. However, there is little direct evidence of social learning to support this conclusion. The present study investigated whether orangutans would learn a novel foraging method through observation of a conspecific in a diffusion-chain paradigm testing for the spread of the behaviour. A foraging box with two possible methods for extracting food was used to investigate the transmission of a foraging tradition among zoo-living subjects. In a socially housed group of five orangutans, the dominant male was trained to use one technique exclusively to retrieve food. He then performed this technique in the presence of another group member, who was then allowed to forage. After several trials, the observer became the model for the next individual. A second experimental group of six individuals was introduced to the alternative method. The model-seeded technique was successfully transmitted along both experimental chains, with significant preferences for the model method. These results are consistent with claims for social transmission of foraging methods in wild orangutans.

Keywords: culture; social learning; copying; orangutans

1. INTRODUCTION

Orangutans are interesting primates in which to study the development and the transmission of cultural behaviours, because of their ‘solitary yet social’ behaviour. By contrast to highly social chimpanzees that live in large fission–fusion groups, orangutans forage primarily on their own and do not gather in groups larger than a few individuals at a time [1,2]. Compared with chimpanzees and other species described as cultural [3], orangutans appear to have relatively few potential opportunities for learning from others [1,2]. Despite this, population-specific feeding techniques, social behaviours and signals attributed to cultural transmission have been identified in wild populations in both Borneo and Sumatra [4,5].

Orangutans inhabit a demanding forest environment in which complex food-processing techniques are necessary for their survival [6]. This may make it

adaptive for them to learn from others how to fully exploit resources in their environment. However, evidence for social learning in the wild is limited to mother–offspring interactions [7,8,9]. Jaeggi and colleagues found that orangutan mothers maintain different foraging practices, which are later seen in their offspring [7]. Beyond this mother–infant context, there have been limited reports suggesting social learning in the wild. Adult orangutans have been seen closely observing tool-use in other adults, but these instances remain unquantified [10]. Experimental evidence for social learning among orangutans thus remains much needed. In particular, little is known about horizontal (within-generation) and oblique transmission of behaviours across a population [7,8].

The present study aimed to investigate the potential spread of a foraging tradition in two groups of orangutans by using an experimental paradigm known as the *diffusion chain* [11–13]. In a diffusion chain, the innovator of a new behaviour is observed by another individual. If that individual is successful in the task, a further individual is allowed to observe and potentially learn from them, and so on along the chain. Unless the behaviour is transmitted with adequate fidelity, it will not spread and endure as a population-specific tradition.

Our study used a foraging apparatus that allowed us to introduce either of two distinct methods for extracting food from a box acting as an ‘artificial fruit’ [14]. A subject could either lift or slide a door panel and reveal a hidden food item. Both methods were always possible, but only one method was introduced to the first individual in each chain. Here, we present the resulting first evidence for the faithful transmission of foraging traditions across these small populations of orangutans.

(a) *Subjects and housing*

Seven male and four female orangutans (*Pongo pygmaeus*, *Pongo abelii* and one hybrid) at Zoo Atlanta, participated in this study (figure 1). Two males were trained as models, making the total number of test subjects nine. The orangutans ranged in age from 2 to 38 years at the time of the study (mean = 20 years, median = 19 years).

Testing took place between 7.30 and 9.30 h in the indoor living quarters in May and June of 2008. Subjects were never food or water deprived. Dried fruits and mini pepperidge farm goldfish crackers were used for forage.

(b) *Apparatus*

The same foraging box used by Dindo *et al.* [11,15] was used in the present study. In this box, an opaque door could either be slid or lifted (figure 2). Each method required a different action to be performed at the same location on the same door, thus controlling for stimulus enhancement. If a subject was drawn to the door by the demonstrator’s presence, they could independently discover either method. We wanted to determine whether or not, through attending to the actions of the demonstrator and/or the movements of the door, subjects would copy the observed technique.

The foraging box was presented against the 2 × 2-inch mesh of the orangutans’ enclosures, allowing them to manipulate the front of the box. The experimenter

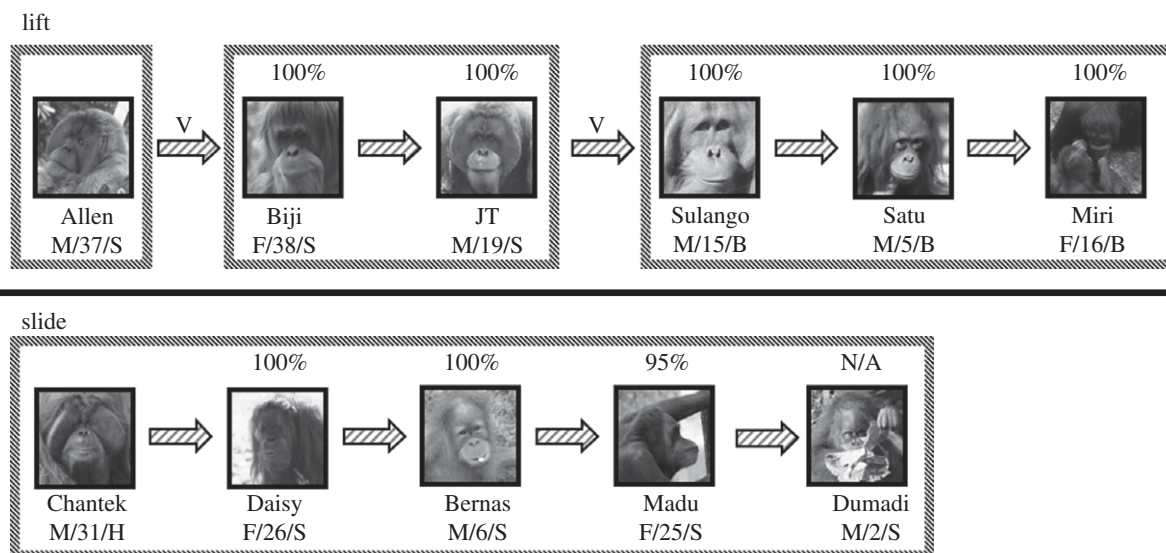


Figure 1. Individuals are shown in the order in which they participated in the chain, with the percentage of trials they performed using the observed method. A 'V' indicates video demonstrations. Striped boxes indicate how individuals were separated by housing barriers. The sex/age/species is marked below each individual with M for male, F for female, H for hybrid, B for Bornean and S for Sumatran.

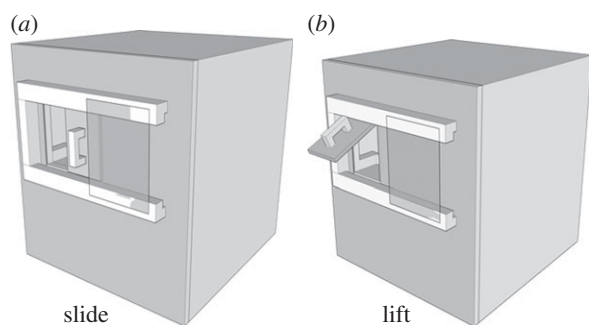


Figure 2. The box is shown (a) when the door is slid open and (b) when the door is lifted open.

(MD) baited the hidden tray from an opening at the back of the box.

(c) Procedure

(i) Model training

Each diffusion chain began with a model trained to perform either the lift or slide method, beginning with the model taking food from behind an already opened door. The door was then closed, and a new piece of food was shown to the model, placed inside the apparatus behind the closed door. Only one method was possible during the first training session, and each model performed three 10-trial sessions.

(ii) Demonstrations and testing

The trained slide model, Chantek, performed the first demonstration session in front of an adult female from his social group, Daisy. A demonstration session consisted of 20 trials in the presence of the observer. If the observer walked away from the demonstrator, the researcher pulled the apparatus away until the individual returned, ensuring that the observer watched at least 50 per cent of the trials. After the demonstration, the model was shifted to an adjacent cage and the observer was presented with her test session. A test session consisted of up to 20 trials, regardless of which method was employed and was terminated if no action was taken

for 15 min. This occurred only for the single infant tested. After this single session, the subject became the model for the next group member. Because the third observer (Madu) in the slide chain was dominant over the demonstrator (Bernas), the first 10 trials were demonstrated with each animal on either side of a mesh barrier to prevent the observer from displacing the model. The mesh was removed for the last 10 trials and the observer was presented with the apparatus.

The lift group subjects were not all from the same social group (as the slide group subjects had been), therefore, videotapes of demonstrations were used for the first and third subjects' observation sessions (as noted by a 'V' in figure 1). A Canon Mini-DV camera was connected to a Mac Powerbook to display the videos in the iMOVIE programme. The Powerbook was presented to the orangutans within 60 cm of the mesh. Both orangutans presented with video-taped demonstrations showed interest and never left. Immediately after the video ended, the apparatus was presented to the subject. Live demonstrations for the other three lift group subjects were conducted using the same procedure as the slide group.

2. RESULTS

The number of food retrievals using either method was calculated for each subject during the experiment as it was clearly visible to the experimenter (MD) from behind the apparatus. All subjects in the lift group performed 20/20 lifts during their test session, including during the live demonstrations for the next subject in the chain. In the slide group, two subjects performed 20/20 slide, while one subject performed 19/20 slide. The last individual in the slide chain was a young 2 year old who did not complete the task by either method. Even with this small sample size there were significant differences between the two study groups in the percentage of slide/slide + lift (Wilcoxon signed-rank test, $\chi^2 = 6.67$, d.f. = 1, $p = 0.0098$).

3. DISCUSSION

Results confirm that orangutans will learn novel foraging behaviours through watching other conspecifics and that the learned technique is highly likely to be transmitted along chains of individuals in a population. The degree of fidelity for the method observed further supports the potential for a new behaviour to become a population-specific tradition in wild orangutans. Our results add to a small but growing corpus of diffusion chain experiments demonstrating the transmission of foraging techniques in other primates (see [13]). Whiten & Mesoudi [13] review an additional small number of experiments that have begun to use other variants of the diffusion design, such as 'open diffusion' in which a novel action is seeded in a single individual in a group and it is 'open' who watches and learns from this (e.g. [16]). Diffusion experiments have clearly been shown to have considerable power to test for cultural transmission across populations and have recently been extended to field studies [17].

The results of the video-taped demonstration sessions showed both that orangutans can learn from this medium and also that they are capable of extracting useful information from less familiar individuals. This study presents the first use of video-taped models in a social learning experiment with orangutans. Given the limited number of orangutans in most captive collections, this approach may provide future research endeavours with a means to test a larger sample size across populations and institutions (see [18] for evidence of chimpanzees' observational learning from video displays).

Previous studies on social learning in orangutans have shown less copying fidelity, as subjects copied most but not all aspects of a task performance they observed [19,20]. In the present study, success required just one specific action for each method, lift or slide, which may explain the high degree of fidelity observed. However, our objective here was not to be able to show direct evidence for imitation; rather, our experimental design focused on how foraging behaviours may spread among orangutans. Future work could usefully expand upon these results by more specifically investigating the learning mechanisms involved in the acquisition of behavioural traditions in orangutans.

Ethical approval was given by Zoo Atlanta's IACUC and veterinary staff. Zoo Atlanta is fully accredited by the Association of Zoos and Aquariums.

We thank Andy Burnley, Kristin Bonnie, Erin Vogel, Kate Markham, Charles Horton, Laura Mayo and the Zoo Atlanta keeper staff for their support.

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