Use of a Virtual Demonstrator in a Social Learning Experiment with Cottontop Tamarins

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Abstract

Social learning is a means by which animals can acquire information from their surroundings through observation. The propensity for social learning is at least partly predicted by the nature of the social network in which an individual is embedded. Cottontop tamarins, *Saguinus oedipus*, are cooperative breeding primates with high social tolerance and relaxed social interactions, attributes that are thought to facilitate social learning. We conducted a social learning experiment at Perth Zoo to test whether tamarins were able to learn to solve a food acquisition task by observing a demonstrational video involving a trained conspecific. Two test groups were used; each was presented with a different demonstration video of how to open a two-action test box (lifting vs. swinging a door). A third group (control) was presented with the two-action test box with no demonstration video. However, discovery of the alternate technique by one individual in the 'swing group' early in the study forced us to turn off the demonstration video so as to avoid having two demonstrators in that group. There was no evidence for social learning through observing a conspecific video model: all three groups preferentially used the lift method to retrieve the food reward. However, the tamarins demonstrated rudimentary forms of social learning by observing live conspecifics: the more times an individual observed a conspecific in the group interacting with the test box, the greater the number of times they themselves interacted with the test box. Moreover, the dominant breeding females in both test groups were observed by significantly more conspecifics when they were interacting with the test box compared to the other individuals in the group.

Key words: primates, tamarins, video demonstration, social learning

1. Introduction

Social learning refers to behavior that is influenced by observation of, or interaction with, another individual or its products (Heyes 1994). Social learning allows animals to acquire adaptive information from their surroundings through observation rather than through costly trial-and-error learning (Boyd and Richerson 1985; Galef 2009). Acquiring relevant information from the individuals in the immediate environment permits a faster transmission of solutions to potential environmental problems (Boyd and Richerson 1988).

Social learning plays also plays a key role in generating local traditions in humans and some nonhuman primates, i.e. behavioral practises which are performed repeatedly over an extended period of time by members of the same social unit (Bonner 1980; Boyd and Richerson 1985; Fragaszy and Perry 2008). The data sets collated by Santorelli et al. (2011), van Schaik et al. (2003) and Whiten et al. (1999) illustrate the rich complexity of primate behavior and the establishment of multiple local traditions. These local traditions in non-human primate groups are of interest to both primatologists and anthropologists as they are considered to be important precursors to culture as we know it in humans (Fragaszy and Perry 2008; Richerson and Boyd 1984).

Social learning is taxonomically widespread in primates and has been demonstrated in both captive and wild settings and in species exhibiting different social systems, e.g. redfronted lemurs *Eulemur rufifrons* (Schnoell and Fichtel 2012), vervet monkeys *Chlorocebus pygerythrus* (van de Waal et al. 2010), brown capuchins *Cebus apella* (Dindo et al. 2008), squirrel monkeys *Saimiri boliviensis* (Hopper et al 2013) and colobus monkeys *Colobus guereza* (Price and Caldwell 2007), orangutans *Pongo spp*. (Dindo et al. 2011), and chimpanzees *Pan troglodytes* (Hobaiter et al. 2014; Whiten et al. 2005). There are many different types of social learning including stimulus enhancement and more complex emulation and imitation (see Hoppitt and Laland 2008). Stimulus enhancement involves the direction of an individual's attention to a particular object or place on an object with which another individual is interacting; this enhances an individual's opportunity to learn by drawing their attention to it (Whiten and Ham 1992). In comparison to stimulus enhancement, imitative social learning occurs when behavior is formed by observing and replicating the exact sequence of events being modeled (Heyes 1993).

Currently, the most common method used to test for imitation is the two-action test (Fawcett et al. 2002; Price and Caldwell 2007; Stoinski et al. 2011; Whiten et al. 1996). The two-action test requires an apparatus that can be manipulated by using two distinct methods. A demonstrator models one of the two methods to an observer or group of observers who are expected to solve the task by using the same opening method as presented by the demonstrator. Three different types of demonstrators have been used to model opening methods in two-action tests: live, trained human demonstrators (Whiten et al. 1996); live, trained conspecifics (Caldwell and Whiten 2004); and, most recently, prerecorded video footage of trained animals of the same species as the test subjects (Burkart et al. 2009b; Gunhold et al. 2014b; Price and Caldwell 2007).

The opportunity for social learning is partly contingent on the extent of tolerance expressed in a social setting (Coussi-Korbel and Fragaszy 1995). Cooperative breeding systems, i.e. systems in which individuals stay with their natal family and assist in raising offspring which are not their own (Emlen 1982), are generally characterized by high levels of social tolerance. Among primates, cooperative breeding is found in New World monkeys in the family Callitrichidae (tamarins and marmosets) as well as in humans. Cooperative breeding in primates results in groups having a high level of relatedness and generational overlap (Clutton-Brock 2006; Lukas and Clutton-Brock 2012). Cooperative breeding might produce changes in psychology, facilitating greater prosociality, reduced response to inequity (Freeman et al. 2013) and enhanced cognition (Burkart et al. 2014; Burkart et al. 2009a; but see Thornton and McAuliffe 2015). Cooperatively breeding callitrichids are predicted to have high levels of conspecific monitoring, associated with greater cognitive performance and social learning (Snowdon 2001).

Previous work on callitrichids has shown that both marmosets and tamarins are capable of social learning. In Voelkl and Huber's (2000) experiment, one group of common marmosets Callithrix *jacchus* was shown a trained conspecific taking the lid off a film canister using its mouth and the other group was shown a demonstration of the trained conspecific taking the lid off the film canister using its hands. Both test groups imitated the behavior being shown to them and opened the lid of the canister using the matching method. Caldwell and Whiten (2004) tested juvenile common marmosets with a two-action apparatus and a live, trained conspecific demonstrator. The study included the comparison of a full demonstration group and a non-demonstration control group, as well as controlling for stimulus enhancement effects by including a partial demonstration, presented to a third group. None of the three tests groups were successful at retrieving the food reward, but the full demonstration group spent the most time manipulating the box at the targeted area. Burkart et al. (2009b) tested whether common marmosets were capable of demonstrating social learning by observing a conspecific modelling a task on a demonstration video. Only individuals from the test group presented with the video and none from the control group were able to solve the task and obtain the food reward. Most recently, Gunhold et al. (2014b) tested wild common marmosets and found that those exposed to video demonstrator showed higher levels of manipulative behavior of an artificial fruit and were more successful at opening the fruit than controls and were also more likely to use the technique they had seen).

Social learning in captive cottontop tamarins *Saguinus oedipus* was examined by Moscovice and Snowdon (2006) who exposed captive individuals to a novel foraging task which involved learning how to detect and retrieve hidden food rewards from a number of differently cued forage sites. The authors reported rapid social learning by naive animals that followed their knowledgeable mates and solved the task within a median of three trials. In another study, parent cottontop tamarins were trained to access a food reward from a two-action apparatus using one of two different methods (Humle and Snowdon 2008). When the trained adults were paired with a juvenile, not all juveniles matched the solution being modeled by their parent but they spent significantly more time at the parts of the apparatus that were modeled to them. In a follow-up study testing adult individuals observing adult demonstrators, Dillis et al. (2010) found that observation was a key factor in solving the novel foraging task even though matching of the behavior of the demonstrator was not consistently recorded.

Based on the combined evidence cited above of common marmosets being able to interpret social information from video demonstrators and cottontop tamarins being able to solve a foraging task by observing a live conspecific, we predict that cottontop tamarins can also demonstrate social learning in a two-action food acquisition task through observing a demonstrational video of a trained conspecific. Using a video offers greater control on part of the experimenter and does not require potentially stressful handling of the animals (e.g. temporarily removing an individual from its social group). We initially hypothesized that a socially mediated opening preference will be established in the two test groups, i.e. that the test groups will access the food reward using the method shown in the demonstration video more frequently than the alternative method. The two methods were swinging and lifting a door. However, on trial day 1 an individual in the swing group successfully lifted the door. This resulted in the group now having two demonstrators, i.e. a live demonstrator using the lift opening method and a virtual video demonstrator using the swing opening method. As there were two conflicting methods being modelled, the swing video was turned off. With the swing video removed from the swing group, we no longer expected to see a difference in preference scores for opening methods between the individuals in the two groups. The second prediction was that the number of opening attempts made by an individual will increase as the number of real-life opening attempts observed by that individual increases. This would demonstrate stimulus enhancement, which occurs "when a demonstrator's behavior increases the probability that an observer is exposed to a stimulus [in our case two-action box], resulting in an increase in the observer's rate of interaction with stimuli of the same type" (Hoppitt and Laland 2013) (p. 65).

2. Methods

2.1. Study animals

The cottontop tamarins at Perth Zoo (Western Australia) were housed in four separate spacious enclosures. The four groups varied in group size and in age and sex composition (Table 1). Test group 1 contained three adult females and one juvenile, test group 2 three adult males, four adult females and one juvenile, and the control group six adult males. One of the four groups was used to obtain the demonstration footage needed for the study, and the remaining three groups represented our two test groups and our control group. The animals had not been subjected to previous experimental research such as extractive foraging tasks and were thus naïve to such studies. The test groups were habituated to the main observer prior to the onset of the experiment.

Study group	Adult 3	Adult ♀	Juvenile 👌	Juvenile ♀	Juvenile unsexed	Total
Video demonstration	1	1	0	0	0	2
Test group 1 (Lift)	0	3	0	0	2	5
Test group 2 (Swing)	3	4	1	0	0	8
Control group	6	0	0	0	0	6

 Table 1: Age/sex composition of the four study groups

Due to the inability to dye mark the tamarins, individual recognition was only partly achieved. Of the three study groups that were used for testing, we were able to confidently individually identify six individuals: three adult females from test group 1 and two adult females and one male juvenile from test group 2. We distinguished these individuals from the others using a combination of external sex organs, pelt coloration, and tail size and shape.

2.2. Data collection

Primary data collection took place from the 21st of January until the 14th of July 2013. We designed and built a two-action test box out of clear perspex and plywood which could be easily loaded with a food reward (Fig. 1). The food reward used was 'tamarin cake', a highly desired high protein food mixture for tamarins. The test box had two different methods by which the food reward could be retrieved from inside: via lifting or swinging a transparent door. The first method required that the white outlined square door be lifted and the second method that the round black outlined door be swung.

Fig. 1: Photo of the two-action test box. The white square door can be lifted to retrieve the food reward inside and the black round door can be swung to the right to retrieve the food reward from inside.



2.2.1. Obtaining demonstration footage

We trained and filmed a cottontop tamarin from the demonstration group opening the two-action test box using the two different methods. Whilst collecting the demonstration footage for the lift method, the swinging mechanism of the door was restricted by a bolt so it could not be opened. Similarly, when the footage for the swing method was collected, the lift mechanism of the door was restricted. In order to obtain good demonstration footage of the swinging technique, the door had to be swung from left to right.

A solo male tamarin housed in the enclosure was provided with the test box for four trial days. He was unable to successfully open the door using the lift method (the swing door was temporarily restricted). On trial day 5, an adult female was added to the enclosure. The test box was provided to the two individuals, with the female successfully lifting the door on trial day 5, her first day with the test box. On trial day 12 we temporarily restricted the lift door, allowing for manipulation of the swing door. The female successfully swung the door on trial day 12. Only footage of the female was used for the experiments. Members of the test group were unfamiliar with this individual.

The video footage was edited in Windows Live Movie Maker to create two demonstrational DVDs, one showing a continual loop of one good demonstration (10 secs) of the lift opening method and the other showing a continual loop of one good demonstration (8 secs) of the swing opening method. These video loops were transferred onto DVD in the form of two digital QuickTime movies (Price and Caldwell 2007). To ensure the demonstration video was as clear as possible, the footage was played on a DELL LCD (liquid crystal display) monitor which does not have a flicker effect (Price and Caldwell 2007).

2.2.2. Experimental set-up

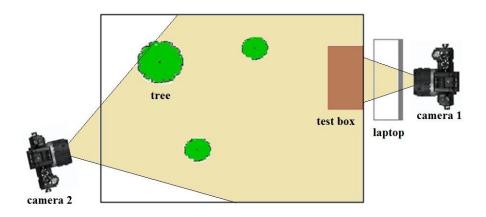
Following Price and Caldwell (2007), an acclimation period habituated the test animals to the equipment. Prior to the demonstration footage and test box being introduced, the filming equipment and a blank laptop screen were set up for two trial days outside the enclosures of the three test groups. After these two trial days, a still image of a tamarin was shown on the laptop to the two test groups. On the fourth day, a movie video loop of native South American birds was played on the laptop to the two test groups; this introduced the tamarins to movement on the screen. The screen remained black for the control group over the four days.

The laptop screen which was used to show the demonstration footage to test groups 1 and 2 and the blank screen which was used for to the control group were placed directly behind the box outside the wire mesh of the enclosure. This ensured that when the individuals were on the feeding platform of

the test box, they were able to manipulate the door concurrently with watching the demonstration footage.

Two video cameras were used to film all interactions with the box as well as the behavior of the observing individuals. Camera 1 was set up on a tripod outside the enclosure directly behind the laptop. This allowed us to observe and record which method of opening was attempted. Camera 2 was set up outside and across the enclosure from where the box was placed. This camera filmed a wide view of the enclosure, allowing us to observe and record the behavior of the other tamarins in the enclosure while one individual was manipulating the test box (Fig. 2).

Fig. 2: Diagram of a test group enclosure showing the experimental setup. This diagram is not drawn to scale.



The box was placed in the enclosure for one 30-minute trial each morning, beginning at approximately 08:15 after the morning food was distributed by the keepers. For test group 1 this was repeated for 24 trial days, for test group 2 it was repeated for 20 trial days, and for the control group it was repeated for 5 trial days. We were able to test the control group for only 5 days as the group was moved to another zoo.

When the test box with two access options was placed in the enclosure with test group 1 (the 'lift group'), the lift demonstration video was played on the laptop screen. When the test box was placed in the enclosure with test group 2 (the 'swing group'), the swing demonstration video was played. When the test box was placed in with the control group, no demonstration video was shown. The three groups tested did not have visual access to one another. If, at any stage in testing, an individual in the 'lift group' successfully retrieved the food using the swing method, the lift video demonstration video was turned off. Similarly, if an individual in the 'swing group' successfully retrieved the food using the lift method, the swing video demonstration video was turned off. This switched the test from a video demonstrator to a live demonstrator and reduced the potential for conflicting models.

2.2.3. Tests

During the testing phase (test group 1, test group 2 and the control group), all interactions with the box were filmed and additional observations voiced onto the video. The following information was noted in a notepad on each trial; trial date, trial time, trial duration, and any other key notes which might help to contextualise the results recorded from that day. From the video footage, events of individuals interacting with the box (i.e. touching any part of the box and/or handling the door) were extracted. For each event the following data were entered into the datasheet: event time, age, sex and

identity of individual performing the event (if identifiable), opening method being attempted (lift or swing) and whether the opening attempt was successful. A tamarin was considered to be observing the video when their eyes were directed at the video screen. In addition, using the footage from camera 2 and the audio recordings, the age, sex and identity (if known) of the individuals observing the event was recorded. DJT did all the coding of the video footage.

The lift group was unable to open the door to the food during the first 11 days of exposure. Similarly, the swing group was unable to swing the door open during the first 7 day of exposure. As failures accumulated, interest in the box abated. For both of these groups a remedial period was used during which the door was removed from the test box for 4 days. This allowed the tamarins to reach straight through the hole to retrieve the food reward and reinforced a positive experience with the test box. After the remedial periods, the door was replaced.

2.3. Data analysis

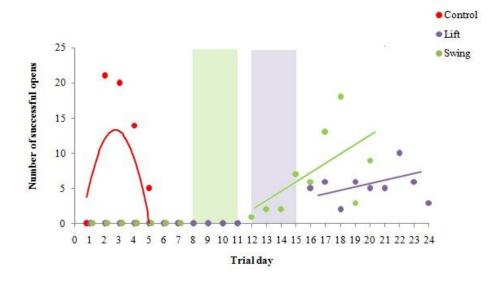
SPSS 20 was used for statistical analysis. As the data did not meet the requirements for parametric analysis, non-parametric tests were used. For all statistical tests performed, the alpha level was set at p<0.05. For the individual data, the lifting preferences of the 3 identifiable individuals in the lift test group were compared to the lifting preferences of the 3 identifiable individuals in the swing test group using a Mann-Whitney U test. To test whether the mean number of individuals observing a live demonstrator varied with the identity of the demonstrator, a Kruskal-Wallis analysis of variance was performed, followed by three Mann-Whitney U 'post hoc' tests with Bonferroni correction. The same procedure was repeated for the swing group.

3. Results

3.1. Group results

We recorded 110 events of an individual in the two test groups viewing the demonstration footage, but in only two of these did the individual manipulate the box right after watching the footage. The total number of successful openings achieved by each of the three test groups using either method was calculated across the trial days (Fig. 3). The all-male control group successfully opened the door most rapidly (trial day 2) and achieved the highest number of successful openings in one trial day of the three groups (21). The mixed-sex swing group successfully opened the test box on day 12, after a remedial period, and the all-female lift group successfully opened the test box on day 16, after a remedial period. The number of successful openings achieved by the control group decreased over the 5 trial days in comparison to the lift and swing groups where the number of successful openings increased over the trial days. The number of successful openings before and after the remedial period was significantly different for both the lift group (Wilcoxon Signed Rank Test, w = 36, p = 0.011) and the swing group (w = 28, p = 0.018).

Fig. 3: Number of successful (lift or swing) openings performed by each of the three test groups across the trial days. Shaded areas indicate the trial days where the door was removed. For the swing group this was from day 8 to 11 and for the lift group from day 12 to 15.



3.2. Individual results

The following results are for the individually identifiable animals only. Of the 3 identified individuals in the lift group, 2 solved the task using the lift method (Laura on trial 16, Fiona on day 24). Of the 3 identified individuals in the swing group, 2 solved the task using the swing method (Kate on trial 18, Ben on day 12). For all individuals combined, the number of successful lifts relative to all lift opening attempts was 94/401 (23%) whereas the number of successful swings relative to all swing opening attempts was 6/37 (16%) (Table 2). All individuals, except Kate (swing group), were more successful at the lift method. Kate was the only individual to successfully open the door using the swing method (on trial day 15), with a swing success rate of 23% compared to her lift success rate of 12%. Kate had a strong influence on the swing group members'' hourly rate of swing attempts.

Group	Individual	Age/sex class	Overall success rate	
			Lifts	Swings
Lift	Mum	Adult female	0/17 (0%)	0/0 (0%)
	Lauren	Adult female	45/94 (48%)	0/1 (0%)
	Fiona	Adult female	3/20 (15%)	0/1 (0%)
Swing	Morticia	Adult female	0/75 (0%)	0/2 (0%)
	Kate	Adult female	3/25 (12%)	6/26 (23%)
	Ben	Juvenile male	43/170 (25%)	0/7 (0%)
Median success			13.5%	0%
rate				
Total success *			94/401 (23%)	6/37 (16%)

Table 2: The success rates for each individual (number of successful attempts divided by the number of total attempts) for the lift and swing method.

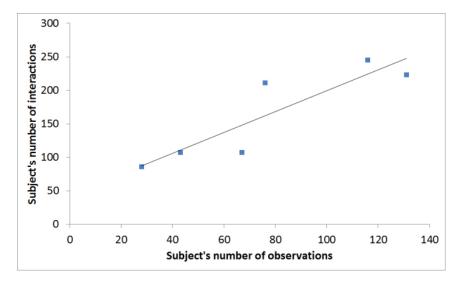
*Number of successful lifts relative to all lift opening attempts and number of successful swings relative to all swing opening attempts, respectively.

A preference score was calculated by dividing the total number of lifts each individual attempted by the total number of lifts and swings they attempted (Dindo et al. 2009). There was no significant

difference between the two groups with the lift group showing a median lift preference score of 0.99 and the swing group 0.96 (Mann-Whitney U test, z = 2, p = 0.4).

For both test groups combined, there was a positive correlation between the number of times an individual observed a live conspecific in the group interacting with the test box and the number of times they themselves interacted with the test box (Spearman's Rank Correlation, $r_s = 0.93$, p = 0.0077) (Fig. 4). When these observations were broken down further into whether they were observing a lift or swing attempt and then attempting to perform a lift or swing attempt, there was no significant correlation ($r_s = -0.14$, p = 0.787).

Fig. 4: Subject's number of observations of conspecifics opening the test box and the number of opening attempts made.



There was a significant difference among the mean number of observers per event for the three identifiable individuals in the lift group (Kruskal-Wallis, k = 14.55, p = 0.001) and the three identifiable individuals in the swing group (k = 49.98, p < 0.0001). In the lift group, Mum (the breeding female) was observed by significantly more conspecifics than Lauren and Fiona (Mann-Whitney U 'post hoc' test with Bonferroni correction, z = 9515, p = 0.001). In the swing group, Morticia (the breeding female) was observed by significantly more conspecifics than Kate and Ben (z = 21026, p = 0.001)

4. Discussion

4.1. General

Burkart et al. (2009a) argued that cooperative breeding produces changes in psychology towards greater prosociality which can boost performance in the sociocognitive domain. Callitrichids are cooperative breeders and characterized by relatively high levels of relaxed social interactions with infrequent aggressive behavior. We reasoned that such social tolerance would be conducive to social learning by predisposing and motivationally attuning individuals to observe role models (Burkart and

van Schaik 2010; Coussi-Korbel and Fragaszy 1995; Dillis et al. 2010; Moscovice and Snowdon 2006).

In our experiment with captive cottontop tamarins at Perth Zoo, we failed to generate evidence in support of the expectation that they are able to demonstrate social learning by observing a conspecific video model. The tamarins in the test groups did not seem to relate the demonstration on the screen to the test box in their enclosure; only 2 out of a total of 110 events of an animal viewing the demonstration footage were followed by the same animal manipulating the box. However, the test groups exhibited social learning by observing live conspecifics. The more times an individual observed a conspecific in the group interacting with the test box, the more times they themselves interacted with the test box. In a similar vein, Gunhold et al. (2014a) noted that those common marmosets that spent the most time in close proximity with trained models excelled at learning a task.

4.2. Learning from video demonstrator

Burkart et al. (2009b) were the first to show that members of the Callitrichidae family are capable of social learning from a virtual video demonstrator. Recently, Gunhold et al. (2014b) confirmed in a field experiment that footage of unfamiliar conspecifics opening an artificial fruit can elicit social learning in watchers. Chimpanzees presented with a video demonstration showed comparable success in learning a novel task to that of chimpanzees presented with a live conspecific demonstrator, but chimpanzees with video models were less precise in their mimicry of the exact process of opening the apparatus (Hopper et al. 2012).

We can envisage a number of reasons why, in our study, individuals did not pay attention to the presence of the video demonstrator¹. Glare may have been a confounding factor influencing the attending to the video demonstrator. Of possible positions, the laptop setup was located in an area which had the least amount of potential glare. The glare on the laptop screen however varied depending on the time in which the trial was conducted and the cloud cover present at each trial. In order to maximise the video clarity, we slightly tilted the laptop screen downwards, so that when the subjects were on the platform of the test box the demonstration video was as clear as possible. The result of orientating the screen to a subject located directly on the platform meant that individuals attempting to observe the video from a far from a tree branch or hanging above the screen on the enclosure fence were not able to clearly see the video playing on the screen. This dramatically limited the overall time which the tamarins had clear visual access to the demonstration video. To ensure that we maximised the clarity of the video when an individual was on the test box platform, a laptop with a LCD monitor was used as they do not have a flicker effect similar to CRT monitors (cathode ray tube) (Price & Caldwell 2007). Another reason for the limited attention we observed may be that the video of birds presented during the pre-test phase was not interesting enough to attract the tamarins to the monitor. The tamarins may also have habituated quickly to the presentation video because it was composed of a single sequence only that was played in a loop.

The study groups' unfamiliarity in partaking in experiments may have had an influence on the video demonstrator not being a successful model in this study. A number of primate studies with video demonstrators used test subjects which had either lived in a laboratory or had participated in previous experiments (Burkart et al. 2009b; Hopper et al. 2012; Platt and Novak 1997). For example, the eight common marmosets in Burkart et al.'s (2009) study which were confronted with a video demonstrator modelling a two-action task were all from a colony that had had previous exposure to experiments and were therefore more likely to be at ease in test situations. In comparison, the callitrichids in our study had never taken part in an experiment before. They therefore were not familiar with being put under test conditions, where they were expected to explore and engage with new unfamiliar stimuli in a natural way whilst being filmed and observed from multiple angles.

¹ Visual orientation to the screen was observed a number of times, but it was fleeting. We did not quantify levels of attentiveness to the stimulus, i.e. it is unclear whether the tamarins exhibited more focused or more diffuse attention.

As the video had to be removed from the swing group, our first hypothesis that the food reward is accessed using the method in the video model more frequently than the alternative (undemonstrated) method, could only be partially tested. While the lift group accessed the food reward using the lift method shown on the screen, we cannot unambiguously conclude that this opening technique was acquired via observational learning of the video demonstration. Given that the swing group spontaneously discovered lift, it is equally likely that the lift group also did not rely on social demos to learn this technique and that social facilitation may have been sufficient to encourage exploration which allowed them to discover the lift method independently (see Hopper et al. 2013).

It appears that the lift opening method was easier for the cottontop tamarins to perform, compared to the swing method; indeed, the control group showed a preference for the lift method. This is an interesting finding as in other studies which have tested for social learning by using a two-action task it has been assumed that the two methods available for solving the two-action task are of equal difficulty (Fawcett et al. 2002; Price and Caldwell 2007; Stoinski et al. 2011). The potential increased difficulty for the cottontop tamarins to perform the swing opening method may have counteracted the presence of a video demonstrator. This may explain the individual in the swing group lifting the door on trial day 12, instead of swinging the door as was being shown on the demonstration video.

4.3. Handedness

Cottontop tamarins' handedness may have introduced uneven difficulty of the two opening methods. Due to the layout of the enclosure in which the two demonstrator tamarins were housed, the test box was manipulated in order to obtain clear demonstration footage of the swing method. The swing door was altered with a bolt so that the door could only be swung from left to right. The test box used in the test groups and control group needed to remain the same as that shown on the demonstration video so the same bolt was installed on all the remaining two-action test boxes.

Diamond and McGrew (1994) suggest that cottontop tamarins have a strong right hand preference. The natural action for a right-hander to open the swing door would be to attempt to swing the door open by pushing from right to left. If this action was performed in our two-action test, the door swung into the bolt and would not open. In order to successfully swing the door open, the tamarin had to reserve the positioning of their hand and push the opposite way, left to right, as shown in the demonstration video. In comparison, the lifting method could be done by lifting either side of the door using either hand; no physical restrictions were in place to limit the movement of the lift door.

Due to the design decision to have the swing door swinging from left to right to obtain the demonstration footage, we may have inadvertently made the swing opening method more difficult. In an attempt to minimise this influencing the results, we used 'attempted lifts' and 'attempted swings' rather than 'successful lifts' and 'successful swings'. This then included the unsuccessful swing attempts which were made where the door was swung from right to left and hit the bolt. This did not completely remove the bias from the results, as when a lift attempt was made, the door lifted slightly showing some positive feedback for the action. When a swing attempt was made, the door hit straight into the bolt not giving a positive feedback for the action. This may have influenced the next attempt made by that individual because it is more likely that the attempted method which gave some positive feedback (lifting) would be the method the individual would be more likely to pursue and continue to attempt.

4.4. Observing a live demonstrator

Our second hypothesis was supported, i.e. the number of opening attempts made by an individual increased as the number of opening attempts observed by that individual increased. This constitutes a case of stimulus enhancement, withthe two-action box being the stimulus. This form of social learning can result in social transmission which occurs "when the acquisition of information or a behavioural trait by one individual exerts a positive causal influence on the rate at which another acquires the same information or trait" (Hoppitt et al. 2010) (p. 544).

It appears that the tamarins in this study did not make a connection between the test box being manipulated on the screen and the test box in their enclosure. The three adult females in the lift group with the video demonstration spent more time observing live conspecifics manipulating the box compared to the virtual conspecific on the screen. Although the live demonstrator did not always successfully open the test box like the virtual demonstrator did, a potential advantage to observing a live demonstrator is that an observer can move themselves around the point of interest and gauge the behavior being demonstrated in a three-dimensional space. The live demonstrator may also have been more appealing for the other observing individuals to watch because the live demonstrators were all familiar individuals, unlike the virtual video demonstrator who was an unfamiliar female from another group at Perth Zoo. However the other publications of successful video demonstrations with callitrichids (Burkart et al. 2009b; Gunhold et al. 2014b) also used unfamiliar models, thus weakening the explanatory power of this argument.

4.5. Who makes a better demonstrator?

The dominant breeding female in both test groups was observed by significantly more conspecifics in the group when they were interacting with the test box compared to the other identifiable individuals in the group. Similarly, using a two-action task, van de Waal et al. (2010) observed a significantly higher interaction rate and method-matching to the demonstrator in wild vervet monkey groups with female demonstrators compared to groups with male demonstrators. In the case of vervet monkeys, females are philoptaric throughout their life compared to the males who disperse. It is hypothesized that due to this female philopatry bystanders pay more attention to the female demonstrators because they are likely to have closer ties to a large number of members in the group and females may have more extensive knowledge on the location of food resources in the region (van de Waal et al. 2010). In cottontop tamarins there is no sex difference in philopatry and dispersion; they exhibit both male and female philopatry (McGrew 1997; Savage et al. 1996). We therefore would expect there to be no difference between the mean numbers of observers watching an adult female interact with the test box compared to an adult male. Unfortunately we could not recognize individual adult males, so we are not able to make this comparison.

We were able to compare the mean number of observers watching the primary breeding female compared to the mean number of observers watching other adult females and a juvenile male. Cooperatively breeding cottontop tamarins have a breeding system where the primary breeding male and the primary breeding female are at the head of the dominance hierarchy (Savage et al. 1996). This coincides with our findings that the breeding female in both the test groups had the highest mean number of observers and the juvenile, being at the bottom of the social ranks, had the lowest mean number of observers.

4.6. Conclusion

This study contributes to the social learning literature by providing insight into the social learning and cognitive abilities of cooperatively breeding callitrichids. The results in conjunction with current literature highlight the need for further research in order to determine the ability of these primates to demonstrate social learning via observing a video conspecific demonstrator. The study also provides zoos with information regarding the kinds of novel stimuli which may be at an appropriate level for captive cottoptop tamarins. The use of novel stimuli, such as multi-functional two-action feeding box, may contribute to the development of appropriate enrichment materials which could be used in an effort to improve the welfare of captive cottontop tamarins at zoos. On a broader scale, we have observed the cottontop tamarins' ability to solve problems. Problem solving may be integral to survival in the wild when faced with environmental changes such as loss of habitats and food resources due to ongoing deforestation. The process of social learning and problem solving may play a critical role in the survival of dwindling populations of critically endangered primates.

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