American Journal of Primatology 73:1–8 (2011)

RESEARCH ARTICLE

Observer Choices During Experimental Foraging Tasks in Brown Capuchin Monkeys (*Cebus apella*)

MARIETTA DINDO[1–3]*, K.L. LEIMGRUBER[4,5], RIAAN AHMED[2], ANDREW WHITEN[1], AND FRANS B.M. DE WAAL[4]
[1]*Centre for Social Learning and Cognitive Evolution, School of Psychology, University of St Andrews, Fife, Scotland, United Kingdom*
[2]*Mind Brain and Evolution Cluster, The George Washington University, Washington, District of Columbia*
[3]*Zoo Atlanta, Atlanta, Georgia*
[4]*Living Links Center, Yerkes National Primate Research Center, Atlanta, Georgia*
[5]*Department of Psychology, Yale University, New Haven, Connecticut*

We investigated whether capuchin monkeys (*Cebus apella*) would choose to observe a high- or low-status adult female from their group during experimental foraging tests. The subject was located in the center of a test chamber, with a low- and high-ranking demonstrator on either side of two partitions. A peephole allowed the subject to observe the models by looking through either respective partition. Each model was trained on one of the two different methods, lift or pull, for retrieving food from a foraging apparatus. There were 22 subjects and four models. During the 40-trial test sessions, subjects could choose which model they would watch in each trial. It was predicted that subjects would prefer observing the model with whom it was closer in rank, and therefore share greater affiliation with. Results showed that only half the subjects showed a preference and that preference was not linked to status. Relatedness played a larger role in determining if a subject showed a preference for a model, and a correlation was found for relatedness and observer preference. After the observer preference tests, subjects were presented with the foraging apparatus to determine if they displayed a preference for one of the two tasks. The majority of subjects (17/22) showed a preference for the pull method, suggesting that this method may have been more salient to the monkeys in this study. Am. J. Primatol. 73:1–8, 2011. © 2011 Wiley-Liss, Inc.

Key words: observer preference; social learning; object movement reenactment; copying; social tolerance; *Cebus apella*

INTRODUCTION

The view that monkeys are unlikely to learn by imitation [Fragaszy & Visalberghi, 2004; Visalberghi & Fragaszy, 2002; Visalberghi & Munkenbeck-Fragaszy, 1990] has been challenged in the last decade, with increasing reports that monkeys copy familiar behavioral motion [Bugnyar & Huber, 1997; Dindo et al., 2008; Fredman & Whiten, 2008; Voelkl & Huber, 2000, 2007]. One reason for conflicting evidence may be that, as reported by Dindo et al. [2010], copying among capuchin monkeys can be context dependent, consistent with similar findings in chimpanzees, children, and dogs [Buttelmann et al., 2007; Gergely et al., 2002; Horner & Whiten, 2005; Range et al., 2007]. This context dependency should not be too surprising, given that capuchins have been shown to be sensitive to the presence of conspecifics under varying social conditions. For example, Brosnan and de Waal [2003] found that capuchin monkeys will accept cucumber as a food reward in a simple exchange task, but will refuse that same reward if their partner receives a much more desirable grape. The authors attributed the monkeys' refusal as an aversion to social inequity, suggesting that the monkeys were averse to working for less "pay" than their social partner. When the "work" (exchange task) element was removed from the experimental paradigm, the same capuchin monkeys readily collected cucumber presented to them, even when their partner received the more desirable food—grapes [Dindo & de Waal, 2007]. Additionally, capuchins increased their rate of consumption of cucumber pieces when their partner was also eating, but not when their partner's food was merely visible yet inaccessible to the partner, suggesting a social facilitation effect of a feeding conspecific on food consumption. Despite such findings, social context is often underreported or altogether ignored in the social learning literature, with

---

Contract grant sponsors: Royal Society Leverhulme Trust Senior Research; American Association for Accreditation of Laboratory Animal Care.

*Correspondence to: Marietta Dindo, Zoo Atlanta, 800 Cherokee Ave. SE, Atlanta, GA 30315. E-mail: mdindo@gmail.com

Received 23 February 2011; revised 28 March 2011; revision accepted 10 April 2011

DOI 10.1002/ajp.20962

relatively few studies providing information about the identity, age, sex, rank, or affiliation between subjects that may, in part, explain the differing results reported for copying complexity and fidelity in monkeys [Coussi-Korbel & Fragaszy, 1995; de Waal & Bonnie, 2011; Laland, 1993; Range & Huber, 2007].

One of the first to acknowledge that individual personalities and life histories may play a role in social learning was Imanishi [1957] in his study of potato washing in Japanese macaques. Huffman [1984] and others [Huffman & Quiatt, 1986; Watanabe, 1994] have proposed that the spread of potato washing behavior began with juvenile females related to the female who invented the technique. Although it has been argued that the slow transmission rate was not consistent with social learning, Huffman and others have counterargued that the spread was relatively slow owing to the strict matrilineal hierarchy found in Japanese macaques, with limited opportunities for social learning reflecting a lack of social tolerance between unrelated females and male group members [de Waal, 2001; Galef, 1990, 1992; Huffman, 1996]. Coussi-Korbel and Fragaszy [1995] referred to such effects as "directed-social learning" and proposed that social learning opportunities would vary by species depending on the level of social tolerance exhibited. Socially acquired information would, therefore, spread unevenly in more despotic species, such as Japanese macaques. Similarly, Cambefort [1981] conducted studies involving the discovery of hidden food items in vervets and baboons. Cambefort reported species differences in the spread of the foraging behaviors, with baboons exhibiting directed social learning. According to Cambefort, baboon juveniles first acquired the behavior of harvesting the novel items followed by adults, whereas in vervets, the adults and juveniles both learned at equal rates from the first few that discovered the food. Coussi-Korbel and Fragaszy [1995] argued that, in the case of the baboons, individual relationships and group social structure meant that certain individuals would not maintain the same level of saliency to all members of their group. Therefore, directed social learning took place in the baboon group, but not in the vervet group where all members paid attention to the initiators of the foraging behavior.

Differences in motivational factors for social learning have also been reported in wild populations of chimpanzees. For example, the motivation for learning from mothers varied between males and females in Lonsdorf's study of termite fishing [2006]. She found that bouts of termite fishing were more often observed by juvenile females than juvenile males, with specific attention being given to mothers. This difference was explained by de Waal and Bonnie [2011] as a sign of gender identification, favoring daughters learning from mothers. Biro et al. [2003] also found that juvenile chimpanzees spent more time observing their mothers and more time in close proximity to nut-crackers than did older individuals. In capuchin monkeys, Ottoni et al. [2005] showed similar trends for juveniles to be tolerated in close proximity to nut-crackers, but in their case, found that capuchins were nonrandomly motivated to observe more proficient nut-crackers. These species differences in an individual's preference for whom to observe potentially result from differences in social organization between chimpanzees and capuchin monkeys [Day et al., 2003].

Given the extent of social context sensitivity in these studies, the purpose of this study was to create an experimental test of observer preference with regard to social context. Dindo et al. [2008] concluded that the high level of social tolerance and closeness in rank of their capuchin subjects was likely to have had a strong effect on the faithful social learning shown in their foraging task. Therefore, in this study, we present subjects from two colonies of capuchin monkeys with both a high-ranking model, the alpha female of their respective group, and a low-ranking adult female from the same group. Coussi-Korbel and Fragaszy [1995] predicted that more socially tolerant species, such as capuchins, would exhibit more flexibility in their motivation to watch other group members. However, they also predicted that extreme differences in rank (and therefore in the degree of affiliation) would affect the opportunity for observation to occur between high- and low-ranking individuals. We predicted that capuchin subjects would show an observer preference for the model with a rank most similar to their own. We based our experimental design, in part, on a Range and Huber [2007] study in which marmosets were presented with the opportunity to watch a conspecific through a peephole. If the subject was motivated to watch the test partner, they would approach the hole that allowed them to view that individual on the other side of an opaque panel. In our study, we taught a high- and a low-ranking female a different method for extracting food from a foraging box. Subjects were then presented with the opportunity to watch either model performing their respective foraging method by looking through a peephole on their left or on their right.

METHODS

Subjects and Housing

The subjects in this study were members of two social groups of capuchin monkeys at the Yerkes National Primate Research Center in Atlanta, Georgia. Each group had 15 members. This study was conducted from August 6 to 27, 2007.

Twenty-six capuchin monkeys served as subjects for this study. The highest and lowest ranking females from each group were selected as demonstrators for their group for four model subjects ranging in age from 23 to 33 years (median 24). Only females were chosen as models because the alpha males are not easily trainable as models. Alpha males become distracted when they are separated from the rest of their group and are not willing to participate in this kind of experiment. Additionally, the lowest ranking males were still higher ranking than many of the females in their group. Eleven observer subjects from colony A consisted of 5 males and 6 females ranging in age from 3 to 33 years (median 5). Eleven observer subjects from colony B included 4 males and 7 females ranging in age from 3 to 40 years (median 9).

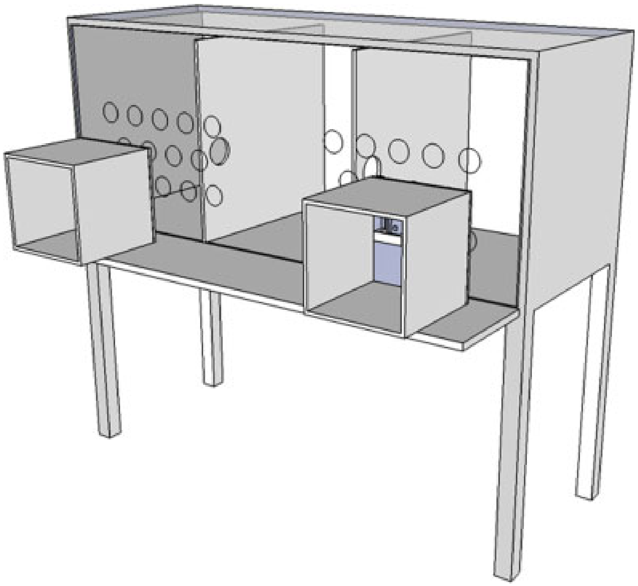

Fig. 1. The test chamber: Two identical boxes were presented in front of the left and right model sections.

Both colonies were housed in the same building, visually but not acoustically separated from each other, with indoor and outdoor enclosures measuring 25 m^2 (Colony A) and 31 m^2 (Colony B). Subjects had ad libitum access to monkey chow and water, and all testing occurred before the daily feeding of fresh produce and bread. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

Apparatus and Test Chamber

Tests were conducted in a mobile chamber (156 × 64 × 58 cm), which was located directly in front of the subjects' respective home area. Two opaque partitions, each with a 4 cm diameter viewing hole, separated the chamber into three sections of 52 × 64 × 58 cm (Fig. 1).

The foraging box measured 28 × 28 × 28 cm. The front panel of the box had two doors with horizontal handle bars. The door on the left could be pulled outward to reveal a cup with food in it (Fig. 2A). The door on the right could be lifted by sliding the handle bar upward to reveal a food cup with the same food reward as the left cup (Fig. 2B). The back panel of the box remained open so that the experimenter could bait the cups from behind the front panel (Fig. 3).

Two identical versions of this box were presented simultaneously to the high- and low-ranking female models. In colony A, the *pull* method was demonstrated by the *low*-ranking model (LO), whereas the *lift* method was demonstrated by the *high*-ranking model (HI). In colony B, the *pull* method was demonstrated by HI and the *lift* method was demonstrated by LO. This counterbalancing was done to ensure that if one method were more salient than the other, this would not be confused with a bias for HI or LO. The method was, however, linked

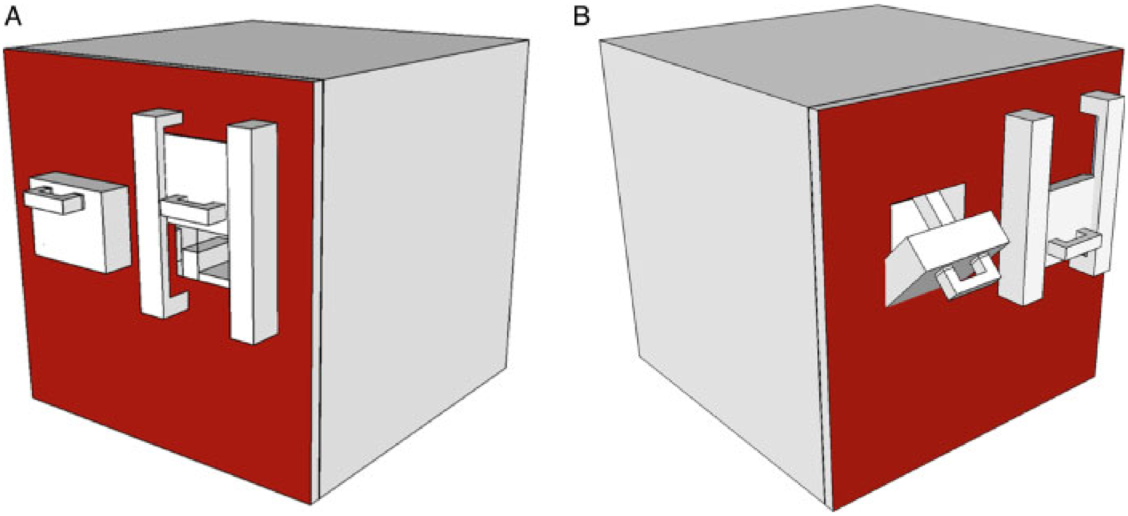

Fig. 2. The foraging box: (**A**) the left (pull) method open to reveal a cereal piece, (**B**) the right (lift) method open to reveal a cereal piece.

with a side of the test chamber. The left pull method was associated with the *right* side of the test chamber, as this allowed the subject to view it more closely, just as the right lift method was viewed from the *left* side of the test chamber for the same reason (Fig. 4A and B). To account for potential side biases in attention, we conducted baseline tests with the models present but without the boxes present, as is noted in the procedure section below.

Because the test condition presented two boxes simultaneously, it was necessary to have two experimenters for this study. Experimenter 1 was Marietta Dindo (MD) and Experimenter 2 was Kristin Leimgruber (KL).

Procedure

Model selection and training

Weekly 30 min ''food scans'' were collected by KL, in which subjects' order of access to a food tray was recorded. This method of ranking priority of access to the food trays was analyzed to assess the relative rank of group members (high, medium, or low ranking). This method has been used at the Living Links Capuchin Lab for more than 10 years and is generally a good indicator of group rankings [see de Waal, 1997]. Additionally, a ''perceived-rank questionnaire'' was also given to three researchers within the capuchin laboratory to confirm the ranks derived from the food scan data. Two individuals were considered higher ranking in the food scans than they were perceived to be by the researchers studying them. These two monkeys were overweight and tended to rush to the food trays and then run away, essentially ''cutting in line'' of higher ranked individuals. Because all ''perceived-rank questionnaires'' showed only these two individuals as lower ranking, their scores were reassigned to the lower ranked tier and noted with an asterisk in Table I.

Fig. 3. Experimental procedure: The observation condition of the test is shown here with Experimenter 2 (KL, left) and Experimenter 1 (MD, right) presenting the two models with the boxes. The subject (center) is observing the left model through the peephole. (Both experimenters stood for tests; here, Experimenter 1 has lowered her head so as not to obstruct the photograph.)

One high- and one low-ranking female from each colony served as models for their respective groups. The models were temporarily separated from their group and individually trained in the test chamber by MD to use one of the two possible methods. Training sessions consisted of the model collecting food 20 times by only using the trained method. All four models were able to perform the trained method consistently in the first session, but two more sessions on subsequent days were given in order to ensure their ability to model the behavior with fidelity for the trained method. On the fourth day of training, MD and KL performed a practice test where both models were presented with their respective box at the same time in the test chamber. This was done to ensure that they would not be distracted by the model at the opposite end of the test chamber.

Baseline observer preference

In order to determine if subjects had a preference for looking at one side more than the other or at one model over the other, each monkey was first given a 5 min baseline preference test. Subjects were

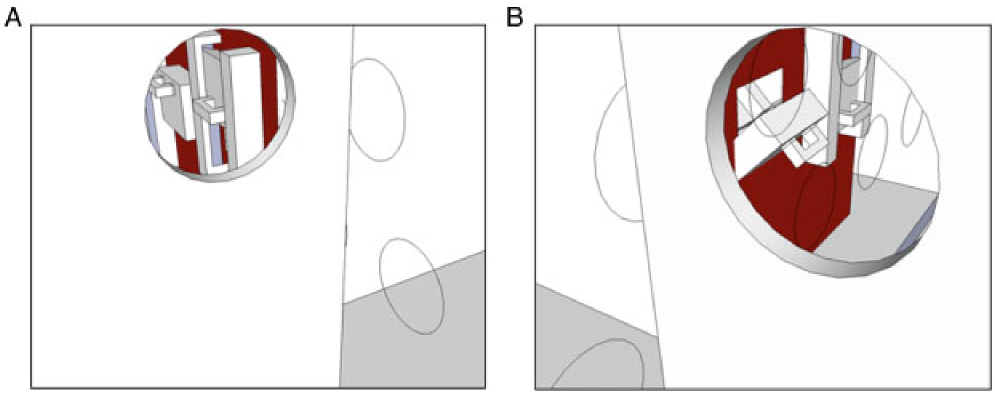

Fig. 4. The subject's views of the boxes: (**A**) the lift method and (**B**) the pull method as seen through the respective peepholes.

TABLE I. Subject Information—Data are Presented for Each Individual With Regards to Sex, Age, Rank, Observations Made, and Methods Performed

Subject	Colony	Sex	Age	Rank	Preferred model observed	Relatedness to preferred model	Preferred method observed	No. of looks per test		Preferred method used	Liftbias score
								HI	LO		
Ike (*IK*)	A	M	33	HIGH	X	X	X	18	20	PULL	0
Lancey (*LA*)	A	F	5	LOW	LOW	YES	PULL	7	18	LIFT	0.98
Lark (*LR*)	A	F	5	LOW	LOW	YES	PULL	7	28	PULL	0
Lucas (*LC*)	A	M	7	HIGH	X	X	X	26	23	PULL	0.03
Luther (*LH*)	A	M	2	HIGH	LOW	YES	PULL	8	22	PULL	0.13
Nate (*NT*)	A	M	3	HIGH	X	X	X	20	27	PULL	0
Nicole (*NI*)*	A	F	7	LOW	X	X	X	23	21	PULL	0.38
Wilma (*WL*)	A	F	9	LOW	X	X	X	17	19	PULL	0
Winnie (*WN*)	A	F	23	HIGH	LOW	NO	PULL	6	24	PULL	0.03
Winter (*WT*)	A	F	3	LOW	X	X	X	10	16	LIFT	0.85
Wookie (*WO*)	A	M	3	HIGH	X	X	X	12	24	PULL	0
Bailey (*BA*)	B	F	7	LOW	X	X	X	14	10	PULL	0.13
Benny (*BE*)	B	M	3	HIGH	X	X	X	12	11	PULL	0.03
Bias (*BI*)	B	F	20	HIGH	HIGH	NO	PULL	40	5	PULL	0
Bravo (*BR*)	B	M	13	HIGH	HIGH	NO	PULL	30	12	PULL	0
Goya (*GY*)	B	F	14	LOW	HIGH	NO	PULL	27	10	PULL	0
Gretal (*GR*)	B	F	3	LOW	LOW	YES	LIFT	0	8	LIFT	0.98
Mango (*MG*)	B	F	40	LOW	HIGH	NO	PULL	23	7	PULL	0
Mason (*MS*)	B	M	9	HIGH	X	X	X	9	10	LIFT	1
Sammie (*SM*)*	B	F	11	HIGH	HIGH	YES	PULL	23	3	PULL	0
Scarlett (*SL*)	B	F	2	HIGH	HIGH	YES	PULL	22	3	PULL	0
Snarf (*SN*)	B	M	3	HIGH	X	X	X	21	20	LIFT	0.88

The first letter of subject codes indicates relatedness, as each letter represents a respective matriline, e.g. LH and LC are related along the L-matriline. An "x" marks subjects with no significant model preference.

moved to the test chamber, and situated between two models, one high and one low ranking, from their social group. The foraging box was not present during this baseline phase, but each model was given a block of wood, a novel object to the subject, to control for interest in a novel object.

Observer preference tests

Immediately after the baseline period, the two experimenters (MD and KL) returned to the test area and began the test phase. Both experimenters were similar in age, general appearances, and both were very familiar to all subjects and models. In case any of the subjects had a bias toward or against one of the experimenters, the experimenters switched sides half way through every test, so that a method or model was not associated with any potential bias for an experimenter.

Tests began with MD and KL presenting the box to both models (Fig. 3). The experimenters coordinated their movements so that each demonstration occurred at nearly the exact same time. Each trial consisted of both models demonstrating their respective method once to collect a piece of cereal from the box. The boxes were then pulled away by the experimenters. Once the experimenters each stepped back, they then moved forward again for the next trial. After 20 trials, the experimenters switched sides (but not boxes) and proceeded with 20 more trials.

Method preference tests

After the demonstrations, the models were let out of the test chamber and back into their group enclosure. The subject remained in the test chamber and the partition panels were removed, giving the subject full access to all three sections of the test chamber.

The first experimenter presented the subject with the box on the left side of the test chamber for 20 trials. Immediately after, the second experimenter then presented the subject with 20 more trials on the right side of the test chamber. This was done in case a side was associated with the previous model. The order in which the experimenters first presented the box in the test condition was alternated so that 11 subjects were presented with MD first and 11 subjects were presented with KL first. Each trial consisted of the experimenter stepping forward with the box in hand and presenting it to the subject in front of the test chamber. Subjects were only allowed to collect food once, therefore only one method, pull or lift, could be used per trial. The results of Dindo et al. [2010] suggested that capuchin monkeys may perceive an opportunity for maximizing their food collection when they are aware that a second piece of food is present. Because subjects in this study had the opportunity to watch both methods and gain knowledge about foods available, the experimenters took a step back from the test chamber, thus moving the box out of reach, allowing the subject to consume the food before approaching again for the next trial.

Data coding and analysis

All tests were recorded using a Canon mini-DV recorder (Canon Elura 99, Tokyo, Japan). MD and RA coded all tests for the duration (in seconds) an individual spent observing either model, but were unable to get consistent scoring within 5 sec owing to the rapid switches some monkeys made per trial during the observation phase. Therefore, the frequency of looks left and/or right by the subject during baseline and during each of the 40 observer preference trials were coded, as well as the method performed during the method preference tests. for the agreement of watching per trial was 0.82 and for the method used was 1.0.

Data were recorded from video, and for each subject, the frequency and duration of looks made toward each model were coded, with *look* operationally defined as a subject peering through one of the two observation holes in the opaque panel. The observation holes were similar in size to the monkeys' faces, making it apparent during coding when a subject was looking, because the subject would press his or her face up to the hole.

RESULTS

Baseline Observer Preference

In the 5-min baseline condition in which the low- and high-ranking models on either side of the subject had a novel object (wooden block), only two high-ranking monkeys, the alpha male and the beta female of colony B (BI and BR), showed a significant preference in the frequency of looks toward one of the models, in both cases the high-ranking model (BI: $P<0.01$, B4: $P<0.03$, two-tailed binomial; Table I).

Observer Preference Tests

All but one subject observed both models during the observation period. Both the frequency of looks and duration (in seconds) spent observing each model were recorded (Table I). Subjects moved quickly back and forth between each observer peephole within each trial, so the frequency of looks was used to indicate observer preference. There was no overall preference for watching a high- or low-ranking model among the 22 subjects ($P = 1.17$, two-tailed binomial test). However, 11 of the 22 subjects did show a significant preference for which model they observed (Table I), with 10 out of the 11 preferring to watch the model of the *pull* method ($P<0.02$, two-tailed binomial test). These monkeys did not show a preference for watching the high- or low-ranked models, as five preferentially watched a low-ranking model and six watched a high-ranking model. Of the five who watched the low-ranking models, all five were related to the model, but only two of the six who watched the high-ranking models were related to the model; therefore, there was a significant preference in 7 of the 11 subjects for watching an individual related to themselves ($P = 0.05$, Fisher's exact test).

There was no significant relationship between the rank of the observer and the rank of the preferred model, with only 8 out of the 11 subjects being similarly ranked to the model they preferred to observe ($P = 0.23$, two-tailed binomial test). There was also no relationship between the sex of the subject and preferring a model; 2 out of 8 males had a model preference ($P = 0.29$, two-tailed binomial test) and 9 out of 14 females had a model preference ($P = 0.09$, Fisher exact test). Furthermore, there was no significant relationship between age and preferring a model, as 5 of the 11 subjects with a preference were youngsters under the age of 5 and 6 were adults over the age of 5; there was also no significant relationship between age and not preferring a model for the 11 subjects without a model preference, as 5 were youngsters and 6 were adults ($P = 0.67$, Fisher exact test). Finally, a lift-bias score was calculated for each subject for the number of lift actions performed out of the total number of trials (20). We looked at the lift-bias score for the first 20 and last 20 trials of each subject to distinguish an effect of the experimenter, and found that there was no effect of which experimenter (MD or KL) presented the box (Mann–Whitney U, $U = 252.0$, $z = -0.22$, $P = 0.83$).

Method Preference Tests

Immediately after the demonstration session, subjects were presented with the box in the absence of the models. Subjects had 40 trials in which to collect food from the box using either the lift or the pull method. There was no significant difference in which method was observed between the two colonies (A vs. B: two-tailed Mann–Whitney U, $U = 60.0$, $P = 0.97$, $N_A = 11$, $N_B = 11$). In both colonies, the lift-bias score for each subject revealed that the pull method was employed significantly more than the lift method, with 17 out of 22 individuals using it for 62.5–100% of the 40 trials (two-tailed Mann–Whitney U, $U = 67.0$, $z = 4.1$, $P<0.001$).

Although there was an effect of method on looking preference, there was no effect of rank on observer preference for a model. Ten of the 11 subjects that showed a significant preference in the observation phase preferred to watch the model who performed the pull method, whether the model was high or low ranking. Nine of those ten individuals used the pull method themselves during the method preference tests (two-tailed binomial test, $P<0.02$). Seven of those nine pulled for all 40 trials (100% pull), and the remaining two pulled for 87.5 and 97.5% of their trials, respectively. The one subject

(LA) who observed significantly more pulls but performed lift, lifted for 97.5% of her test trials. The one subject (GR) that watched the lift method significantly more during the observer preference test used the lift method for 97.5% of her trials. Thus, 10 out of the 11 subjects who had a significant model preference also matched the method they saw demonstrated during the method preference tests (two-tailed binomial test, $P<0.01$).

DISCUSSION

The model preference results indicate that individual preference and motivation for observing others are quite variable among capuchins, with no overall significant preference for one of the two foraging models available among the 22 subjects tested. All subjects, except one, chose to observe both models, but only half of the 22 subjects in this study showed a significant preference in which model they observed more. Coussi-Korbel and Fragaszy [1995] predicted that greater degrees of social tolerance would provide more opportunities for social learning to take place. The behavior of the capuchins, a socially tolerant species, in this study was consistent with this principle: they chose to watch both the low- and high-ranking models, regardless of their own rank. Among those with significant viewing preferences, there was a significant preference for watching a related model over a nonrelated model.

Thus, it seems in our study that rank does not play a strong role in an observer's selection of a model. However, rank may play a stronger role if the models are males instead of females. Our study was only able to provide female models to our observer subjects, and future research should take the sex of the model into further consideration. With regards to the models' performances on the task, Ottoni et al. [2005] suggest that capuchin monkeys prefer to watch the most proficient nut-crackers, basing their choice not on relatedness or rank order, but on an active assessment of the model's proficiency. In the case of our study, both models were given the same amount of training and both completed the foraging trials at the same time with the same end result of collecting one piece of cereal. We judged both models to be equally proficient demonstrators, and thus do not consider that this was an influential factor in this study.

Of the 11 subjects who showed significant viewing preferences, instead of any overall trend to watch the high- or low-ranked model, a preference was seen for watching the pull method (10 out of 11). These method preference results contribute to the mounting evidence that capuchin monkeys are sensitive to the motions involved in the behaviors they observe [Custance et al., 1999; Dindo et al., 2008, 2010; Fredman & Whiten, 2008; Humle & Snowdon, 2008; Voelkl & Huber, 2000, 2007]. Of the ten who showed a preference for watching the pull method, nine preferred to perform that same method during the test condition. Furthermore, 17 of the 22 subjects preferred to perform the pull method, suggesting that this method was potentially a more distinguishable, and therefore a more salient, method to learn [Bandura, 1977]. These findings can be related to Range and Huber's [2007] study in which monkeys watched individuals more who engaged in manipulative behavior rather than simple searching behavior, perhaps suggesting that the kinds of motion involved in a behavior may influence the learning process more than previously thought.

While designing this study, we did not anticipate that subjects would be so motivated and able to watch both models in a single trial; however, the small section of the test chamber (52 cm wide) allowed subjects to quickly alternate between the two peepholes. Additionally, the opaque paneling may have provided the subject with a sense of security, knowing that the models could not reach through the partition except at the holes. In this sense, there was no apparent cost involved in observing one model over the other, because there was no potential for direct aggression or food sharing opportunities. This artificial context does not well reflect conditions that would occur in the wild, where all group members are free to observe whatever and whomever they choose. In this context, it may be possible to better investigate the kinds of opportunities naturally available to capuchins for social learning, as well as the processes by which behaviors are transmitted throughout a group. In order to further address the effects of rank on observer preference, future studies should employ less restricted experimental contexts and also control more stringently for the difficulty of the tasks involved.

ACKNOWLEDGMENTS

We are grateful to Andy Burnley of the University of St. Andrews for constructing the testing box and to Friedericke Range for helpful comments on an earlier version of the manuscript. M.D. was supported by an IPS research grant and a grant from the Russell Trust, A.W. by a Royal Society Leverhulme Trust Senior Research Fellowship, F.d.W. by NSF. The YNPC is fully accredited by the American Association for Accreditation of Laboratory Animal Care.

REFERENCES

Bandura A. 1977. Social learning theory. Englewood Cliffs, NJ: Prentice Hall.

Biro D, Inoue-Nakamura N, Tonooka R, Yamakoshi G, Sousa C, Matsuzawa T. 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. Animal Cognition 6:213–223.

Brosnan SF, de Waal FBM. 2003. Monkeys reject unequal pay. Nature 425:297–299.

Bugnyar T, Huber L. 1997. Push or pull: an experimental study on imitation in marmosets. Animal Behaviour 54: 817–831.

Buttelmann D, Carpenter M, Call J, Tomasello M. 2007. Enculturated chimpanzees imitate rationally. Developmental Science 10:F31–F38.

Cambefort JP. 1981. A comparative study of culturally transmitted patterns of feeding habits in the chacma baboon *Papio ursinus* and the vervet monkey *Cercopithecus aethiops*. Folia Primatologica 36:243–263.

Coussi-Korbel S, Fragaszy DM. 1995. On the relation between social dynamics and social learning. Animal Behaviour 50: 1441–1453.

Custance D, Whiten A, Fredman T. 1999. Social learning of an artificial fruit task in capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology 113:13–23.

Day RL, Coe RL, Kendal JR, Laland KN. 2003. Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. Animal Behaviour 65: 559–571.

de Waal FBM. 1997. Food transfers through mesh in brown capuchins. Journal of Comparative Psychology 111:370–378.

de Waal F. 2001. The ape and the sushi master: cultural reflections by a primatologist. London: Penguin Press. 433p.

de Waal FBM, Bonnie KE. 2011. In tune with others: the social side of primate culture. In: Laland KN, Galef BG, editors. The question of animal culture. Cambridge, MA: Harvard University Press.

Dindo M, de Waal FBM. 2007. Partner effects on food consumption in brown capuchin monkeys. American Journal of Primatology 69:448–456.

Dindo M, Thierry B, Whiten A. 2008. Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). Procedings of the Royal Society of London B: Biological Sciences 275:187–193.

Dindo M, Thierry B, de Waal FBM, Whiten A. 2010. Conditional copying fidelity in capuchin monkeys (*Cebus apella*). Journal of Comparative Psychology 124:29–37.

Fragaszy D, Visalberghi E. 2004. Socially biased learning in monkeys. Learning and Behavior 32:24–35.

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

Galef BG. 1990. Tradition in animals: field observations and laboratory analyses. In: Bekoff M, Jamieson D, editors. Interpretation and explanation in the study of animal behavior, vol 1: interpretation, intentionality, and communication. Boulder, CO: Westview Press. p 74–95.

Galef BG. 1992. The question of animal culture. Human Nature 3:157–178.

Gergely G, Bekkering H, Kiraly I. 2002. Rational imitation in preverbal infants. Nature 415:755.

Horner V, Whiten A. 2005. Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). Animal Cognition 8:164–181.

Huffman MA. 1984. Stone-play of *Macaca fuscata* in Arashiyama B troop: transmission of a non-adaptive behavior. Journal of Human Evolution 13:725–735.

Huffman MA. 1996. Acquisition of innovative cultural behaviors in nonhuman primates: a case study of stone handling, a socially transmitted behavior in Japanese macaques. In: Heyes CM, Galef BG, editors. Social learning in animals: the roots of culture. New York: Academic Press. p 267–289.

Huffman MA, Quiatt D. 1986. Stone handling by Japanese macaques (*Macaca fuscata*): implications for tool use of stone. Primates 27:413–423.

Humle T, Snowdon CT. 2008. Socially biased learning in the acquisition of a complex foraging task in juvenile cottontop tamarins, *Saguinus oedipus*. Animal Behaviour 75:267–277.

Imanishi K. 1957. Social behavior in Japanese monkeys, *Macaca fuscata*. Psychologia 1:47–54.

Laland KN. 1993. The mathematical-modeling of human culture and its implications for psychology and the human-sciences. British Journal of Psychology 84:145–169.

Lonsdorf EV. 2006. What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? Animal Cognition 9:36–46.

Ottoni EB, de Resende BD, Izar P. 2005. Watching the best nutcrackers: what capuchin monkeys (*Cebus apella*) know about others' tool-using skills. Animal Cognition 8:215–219.

Range F, Huber L. 2007. Attention in common marmosets: implications for social-learning experiments. Animal Behaviour 73:1033–1041.

Range F, Viranyi Z, Huber L. 2007. Selective imitation in domestic dogs. Current Biology 17:868–872.

Visalberghi E, Fragaszy DM. 2002. Do monkeys ape? Ten years after. In: Dautenhahn K, Nehaniv CL, editors. Imitation in animals and artifacts. Cambridge, MA: MIT Press. p 471–500.

Visalberghi E, Munkenbeck-Fragaszy D. 1990. Do monkeys ape? In: Parker TS, Gibson KR, editors. ''Language'' and intelligence in monkeys and apes: comparative developmental perspectives. Cambridge: Cambridge University Press. p 247–273.

Voelkl B, Huber L. 2000. True imitation in marmosets. Animal Behaviour 60:195–202.

Voelkl B, Huber L. 2007. Imitation as faithful copying of a novel technique in marmoset monkeys. PLoS One 2:e611. DOI: 10.1371/journal.pone.0000611.

Watanabe K. 1994. Precultural behavior of Japanese macaques: longitudinal studies of the Koshima troops. In: Gardner RA, Gardner BT, Chiarelli AB, Plooij FX, editors. The ethological roots of culture. The Netherlands: Kluver Academic Publishers. p 81–94.