



Scrounging facilitates social learning in common marmosets, *Callithrix jacchus*

CHRISTINE A. CALDWELL & ANDREW WHITEN

Centre for Social Learning and Cognitive Evolution and Scottish Primate Research Group, University of St Andrews

(Received 17 June 2002; initial acceptance 7 August 2002;
final acceptance 10 October 2002; MS. number: 7376)

We investigated the effect of close social interaction on the ability to learn a new behaviour via observation. The task chosen involved sliding a small door horizontally to gain access to a food reward. We divided 59 common marmosets into five groups that received different pretest experience: observation of a trained demonstrator through wire mesh (O); joint interaction with a trained demonstrator allowing the possibility of scrounging (S); individual interaction with the apparatus (I); joint interaction with another naïve individual (J); and no prior experience (control, C). Significantly more individuals from the scrounging group learned the new behaviour, compared with the group (O) that had purely observational experience. When animals from group O were later allowed to interact jointly with a trained demonstrator, the success rate of this group significantly increased. Social interaction with the demonstrator may have facilitated learning because it allowed subjects to understand the relation between the apparatus and the food or because social support facilitated interaction with the apparatus. However, results from the other conditions suggest that these factors alone do not account for the size of the effect. Thus, contrary to previous investigations of this phenomenon, scrounging facilitated social learning. This result probably depended on a complex interaction of a number of factors, including individual learning opportunities, social support and closer attention to the demonstrator.

© 2003 Published by Elsevier Ltd on behalf of The Association for the Study of Animal Behaviour

In the literature on social learning, contradictory predictions exist about the effect of social interaction on the tendency to learn a demonstrated behaviour. Although it is often assumed that information will spread in a non-random way through a population, mediated by social relationships that permit joint interaction (e.g. Kawai 1965), experimental research has instead tended to view close social interaction as a potential obstacle to social learning. The standard experimental paradigm therefore incorporates some kind of physical separation, such as wire mesh, between the skilled and naïve individual (e.g. Bugnyar & Huber 1997). This type of design is thought to facilitate the study of social learning, because allowing the two animals to interact could lead to scrounging by the naïve individual, which is generally considered to have an inhibiting effect on learning (e.g. Fragaszy & Visalberghi 1989; Beauchamp & Kacelnik 1991).

There are two main reasons why scrounging is thought to inhibit learning. The first is that the naïve individual is learning to scrounge, not learning the new skill. For

example, the naïve individual could use the presence of the skilled individual as a cue, rather than learn cues relevant to the task (e.g. Beauchamp & Kacelnik 1991), or may obtain reinforcement more reliably by following a skilled individual, instead of interacting with the task itself (e.g. Giraldeau & Lefebvre 1987). Second, scrounging and learning have been viewed as mutually exclusive strategic options determined by the relative payoffs involved (e.g. Barnard & Sibly 1981; Fritz & Kotrschal 1999a; Giraldeau & Caraco 2000).

Experimental tests that have explicitly compared pure observation of a trained demonstrator with scrounging from a trained demonstrator have tended to support this view. Nicol & Pope (1994), investigating social learning in chickens, *Gallus gallus domesticus*, compared a 'free' condition in which demonstrator and observers could interact, with a 'screen' condition in which they could not. They found that observers that had been separated from the demonstrator subsequently performed the task more successfully than those that had been able to interact. Giraldeau & Lefebvre (1987), studying pigeons, *Columba livia*, compared a condition that allowed observers to share the reward obtained by a demonstrator with a purely observational demonstration. Pigeons that had received the scrounging demonstration performed no

Correspondence and present address: C. Caldwell, School of Psychology, Washington Singer Laboratories, University of Exeter, Exeter EX4 4QG, U.K. A. Whiten is at the School of Psychology, University of St Andrews, St Andrews, Fife KY16 9JU, U.K.

better than a no-demonstration control group during subsequent tests.

However, being able to interact jointly with a skilled demonstrator might also facilitate a naïve observer's acquisition of the task. Social support may reduce neophobic responses, thereby facilitating interaction with and exploration of novel objects. Close social interaction with the demonstrator may also allow the observer to perceive in greater detail crucial skill-related actions. Finally, if scrounging itself entails some interaction with the object or apparatus involved, it may mediate a large degree of individual learning (e.g. learning the connection between the apparatus and reward).

In some cases where the demonstrator and observer have been allowed to interact, scrounging has not necessarily prevented the transmission of a new behaviour (e.g. Fritz & Kotrschal 1999b). Furthermore, Midford et al. (2000) explicitly compared a 'scrounging enabled' condition, where food could be shared by naïve observers, with a 'scrounging restricted' condition in which the demonstrator could monopolize the reward. Their scrub jay, *Aphelocoma coerulescens*, subjects showed more effective learning when scrounging was possible. However, Midford et al. noted that the manipulation (several small pieces of food versus one large piece) significantly altered the behaviour of demonstrators in such a way that they could not rule this out as the source of the variation between the groups. The single large reward tended to result in the demonstrators spending much less time performing the behaviour to be learned (digging in a specific target area).

Therefore, to date, there has been no conclusive evidence of the facilitating effect of social interaction, compared with pure observation, on social learning in any species. However, we predicted that this effect might be found if scrounging was studied within a population characterized by tolerant social interactions. Experiments on the social transmission of pine cone feeding between black rats, *Rattus rattus*, showed that rat pups would readily adopt the skill if their mother displayed it (Terkel 1996). Conversely, naïve rats housed with unrelated demonstrators, even for months at a time, failed to develop the behaviour. Learning to strip the pine cones required interaction with partially processed cones, and because rats do not generally tolerate the proximity of other rats during feeding, this was never possible when unrelated individuals were paired. Pups could learn from their mothers, however, because their presence, and thieving of partially stripped cones, was tolerated.

We studied common marmosets, a species that has already shown evidence of social learning (e.g. Bugnyar & Huber 1997; Caldwell et al. 1999; Voelkl & Huber 2000). We also predicted that this species would show the tolerant interactions necessary to observe a facilitative effect of scrounging. Common marmosets live in family groups in which typically one female breeds and other group members contribute to the care of infants (e.g. Rylands & de Faria 1993). Food sharing has been documented in several marmoset species, including common marmosets (e.g. Feistner & Price 1991).

We had two main aims. First we investigated whether social interaction with a skilled partner would facilitate learning compared with the standard dual-cage procedure. Second, we tested whether any such effect was related to the increased opportunity for individual learning about the apparatus, or to increased interaction with the apparatus caused by the social support of the presence of a conspecific.

METHODS

Subjects

We used 67 marmosets (38 females and 29 males). These included juvenile, subadult and adult animals (aged 6 months to 7 years). Of these animals, we used 59 as subjects and trained nine as demonstrators (one animal was first a subject then a demonstrator). The marmosets were from the breeding colony housed in the Medical Research Council facility at the University of Edinburgh. None had been subjected to any invasive research. They were housed in family groups of three to eight individuals with similar group structure to wild common marmosets. All the marmosets came from 19 of these family groups and all testing was done within the family group, so that subject and demonstrator (or partner in group J; Table 1) came from the same home cage (Fig. 1). All cages measured 1.1×1.2 m and 2.3 m high and were equipped with branches, ropes and platforms. All animals received fruit, commercial marmoset food, protein and vitamin supplements, and water ad libitum.

Apparatus

We used an 'artificial fruit' that had been designed for manipulation by marmosets. Whiten et al. (1996) designed an artificial fruit to test for imitation in chimpanzees, *Pan troglodytes*, which was a box with a hinged lid containing a food reward. A number of locks on the lid needed to be removed to lift the lid and reach the food reward. The logic behind the design was to produce an ecologically valid task, in that some manipulation was required before an edible core could be reached. We used a considerably simplified artificial fruit ($12 \times 6 \times 6$ cm), which was within marmoset manipulative capabilities, but the underlying logic was the same. The food reward could be reached through a hole in the centre of one of the horizontal faces of the box. This hole was concealed behind a sliding door, which could be pushed either left or right (Fig. 1, insert). The food reward was marshmallow (a highly preferred food), cut into pieces of about 0.5 cm^3 .

Training of Demonstrators

All nine trained demonstrators (five male, four female) were nonbreeding group members. We trained the demonstrators in the home cage, with the animal isolated from the rest of the group members. Training sessions took place over 3 weeks, during which each demonstrator

Table 1. Details of the testing sessions for the five groups of the experiment

| Group | Experience phase |
|--------------------------------------|--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| S, Scrounging (N=11) Condition 1 | Subjects could interact with a trained demonstrator. The artificial fruit was opened three times, with two pieces of food available each time As in O1 below |
| Condition 2 | |
| O, Observation (N=12) Condition 1 | Subjects could observe a trained demonstrator from behind wire mesh. The artificial fruit was opened three times, with one piece of food available each time As in S1 above |
| Condition 2 | |
| I, Individual learning (N=12) | Subjects interacted alone with the (open) artificial fruit. A single piece of food was visible through the open door. Food was replaced to a maximum of three items |
| J, Joint learning (N=12) | Subjects were paired and could interact with the (open) artificial fruit. Two pieces of food were visible through the open door. Food was replaced to a maximum of six items |
| C, Control (N=12) | This group received no prior experience |

After each phase, the subject was isolated with artificial fruit for 5 min.

received up to five sessions. We shaped the animals by initially allowing them to remove food from the outside of the artificial fruit, then from inside the artificial fruit but with the door open. Over subsequent sessions, the door was closed further until the demonstrator could reach the food reward from the artificial fruit with the door fully closed.

Procedure

We assigned subjects to five experimental groups (Table 1). Each test session consisted of an experience phase (except for individuals in the control group) followed by a trial. Individuals from groups I (individual learning), J (joint interaction with another naïve individual) and C (control group with no prior experience) received only one test session each. Because we were particularly interested in the effect of interaction and scrounging on learning, compared with pure observation, we gave groups S (scrounging) and O (observation) two sessions, counterbalancing the two types of experience. We designed the experiment in this way to investigate whether those from the group that performed more poorly could achieve the same level of performance as the more successful group if provided with the, apparently, more effective type of experience. We also wished to rule out the possibility that any difference in performance between the groups was due to individual differences (e.g. in motivation levels or neophobia). These two groups therefore gave rise to four conditions: S1 (joint interaction with a trained demonstrator, allowing scrounging), S2 (observation of a trained demonstrator through a wire-mesh divider), O1 (observation, as in S2) and O2 (scrounging, as in S1).

All testing was done in the animals' home cage (Fig. 1). Owing to the way in which the home cage could be divided into four equally sized sections, sessions

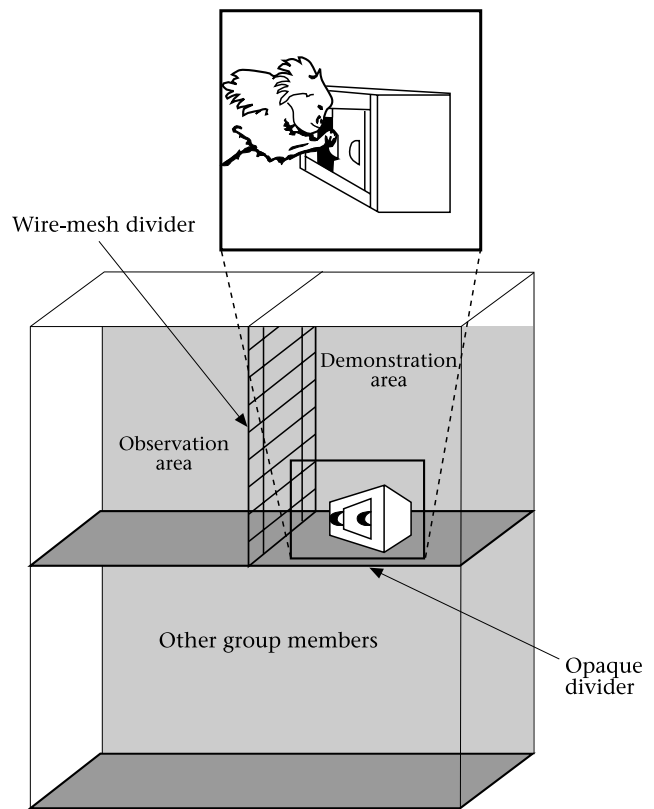


Figure 1. Schematic depiction of home cages (where testing was conducted). The cages could be divided into four sections (top left, top right, bottom left, bottom right). During testing, subjects and demonstrators were partitioned from their other group members by opaque plastic cage dividers. A wire-mesh divider separated demonstrator and subject during the observation (condition 1) and scrounging (condition 2) experience phases. During other phases, the wire-mesh divider was left in place, but opened so that the animals could move between the two upper sections (Table 1). Insert shows a marmoset opening the artificial fruit.

Table 2. Duration of contact (s , $\bar{X}\pm SE$) with artificial fruit during the experience phase, and the relation between duration of contact and later success during the trial

| Group | Duration of contact | Mean duration of contact | | t^* | df | P |
|-------------------------------|---------------------|--------------------------|---------|-------|------|-------|
| | | Succeeders | Failers | | | |
| Observation (Condition 2, O2) | 60.8±13.7 | 67.4 | 41.0 | 0.82 | 10 | NS |
| Scrounging (Condition 1, S1) | 61.0±17.7 | 79.8 | 10.7 | 3.25 | 7.88 | <0.05 |
| Individual learning (I) | 63.2±11.2 | 96.5 | 56.5 | 1.39 | 10 | NS |
| Joint learning (J) | 47.2±8.88 | 59.7 | 43.0 | 0.80 | 10 | NS |
| All groups ($N=47$) | 58.0±6.38 | 73.5 | 44.2 | 2.71 | 45 | <0.05 |

Values are given for each of groups O2, S1, I and J, and all groups together.

*Unpaired t test, succeeders versus failers.

commenced when the required combination of individuals from the group had entered the top two sections. During experience phases involving pure observation of the trained demonstrator (conditions O1 and S2), demonstrator and subject were separated by a wire-mesh divider (Fig. 1). During all other experience phases, the wire-mesh divider was opened, but not removed, such that the subjects (and the demonstrator in the scrounging conditions) could move freely around the top two sections of the enclosure.

The experience phase began when the artificial fruit was introduced. In sessions involving a trained demonstrator (S1, S2, O1, O2) we introduced the artificial fruit closed and containing food, and then allowed the demonstrator to open it three times. The experimenter reloaded the artificial fruit between openings by reaching into the cage, placing more food in the cavity and sliding the door back to the closed position. During the other experience phases (conditions I, J), the artificial fruit was introduced with the door open such that the food reward inside the cavity was visible. In these conditions we reloaded the artificial fruit up to two more times by replacing the food, but leaving the door in the open position. In each experience phase, the reward consisted of up to three food items per animal (six items in the scrounging and joint learning conditions).

Each experience phase took 5 min (including reloading time), after which the demonstrator (or partner in condition J) was released into another section of the cage to rejoin the rest of the group (Fig. 1). Trials followed immediately afterwards, during which subjects were isolated with the artificial fruit for 5 min. We videotaped all testing (both experience phase and test trials) for subsequent analysis.

Data Coding

For the experience phases, we coded videotapes for whether the subject interacted with, and took food from, the artificial fruit. We defined interaction with the artificial fruit as being within reaching distance of the apparatus, not necessarily touching it. Because the demonstration area was large (ca. 0.75 m^3), the artificial fruit could easily be out of the reach of the animal. We used the videotapes to identify the timings of onsets and

conclusions of bouts of interaction with the artificial fruit. Test trials were coded in a similar way. We defined success in opening the artificial fruit as the door opening fully such that food could be removed, regardless of the method used. This judgement of success was never ambiguous, however, as in all cases when the door was opened, it was opened fully and food was removed.

RESULTS

Behaviour of Groups During Experience

During the experience phase, subjects from group S did scrounge food. Only three of the 11 subjects never took any of the food during the experience phase. Most demonstrations involved some degree of scrounging. During each experience phase, the artificial fruit was opened three times, resulting in 33 demonstrations. In 15 (45%) of these, the demonstrator and subject each took one of the two food items; in five (15%) the subject took both pieces, and in 13 (39%) the demonstrator took both pieces.

Groups I and J also received an experience phase during which they could interact with, and take food from, the artificial fruit, so that we could investigate the relative roles of individual learning and social support. As predicted, conditions I and J resulted in levels of interaction with the artificial fruit during the experience phase that were equivalent to those of the scrounging individuals. There was no difference between these groups either in the time they spent in contact with the apparatus during the experience phase (ANOVA: $F_{3,43}=0.320$, NS; Table 2) or the number of food items taken ($F_{3,43}=0.182$, NS; Table 3).

Performance of Groups During Trials

There was an overall difference between the groups' success rates (chi-square test: $\chi^2_4=15.074$, $P<0.005$; Table 4). Residuals (Table 4) show that the only condition with an observed value significantly different from expected was group S, suggesting that the chi-square value is mainly accounted for by the higher success rate of this group compared with the other four groups. This suggests that the scrounging group's experience was in some way

Table 3. Number of food items ($\bar{X}\pm SE$) taken during the experience phase, and the relation between the number of food items taken and later success during the trial

| Group | Number of food items taken | Mean number of food items taken | | <i>t*</i> | <i>df</i> | <i>P</i> |
|-------------------------------|----------------------------|---------------------------------|---------|-----------|-----------|----------|
| | | Succeeders | Failers | | | |
| Observation (Condition 2, O2) | 2.50±0.42 | 2.78 | 1.67 | 1.17 | 10 | NS |
| Scrounging (Condition 1, S1) | 2.27±0.56 | 3.12 | 0.00 | 3.86 | 9 | <0.001 |
| Individual learning (I) | 2.58±0.26 | 3.00 | 2.50 | 0.70 | 10 | NS |
| Joint learning (J) | 2.75±0.55 | 4.33 | 2.22 | 1.82 | 10 | NS |
| All groups (<i>N</i> =47) | 2.53±0.22 | 3.14 | 2.00 | 2.33 | 33.92 | <0.01 |

Values are given for each of groups O2, S1, I and J, and all groups together.
 *Unpaired *t* test, succeeders versus failers.

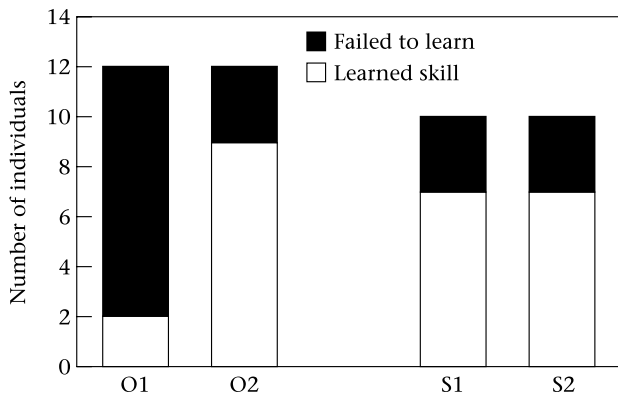


Figure 2. Number of individuals successfully obtaining food from the artificial fruit after interaction with, versus pure observation of, a trained demonstrator. The order of presentation of these conditions was counterbalanced for two groups. Group O received purely observational experience first (O1) followed by scrounging experience (O2). Group S received scrounging experience first (S1) followed by purely observational experience (S2).

more effective than that of the other groups, including those that had received with similar opportunities for individual learning and comparable levels of social support.

Because we were particularly interested in the efficacy of scrounging experience relative to purely observational experience, we compared these directly. More individuals from the group that were allowed to interact with a skilled demonstrator (S1) successfully reached food during the trial period, compared with those that had simply observed a skilled demonstrator from behind wire mesh (O1; $\chi^2_1=7.340$; Fisher's exact test: $P<0.02$; Fig. 2, Table 4).

The difference between the two groups could not be attributed to individual differences. When subjects in group O received subsequent scrounging experience, the success rate of this group improved significantly (binomial test: $P<0.01$; Fig 2). However, subjects in group S, when subsequently provided with the purely observational demonstration, showed no improvement (binomial test: NS; Fig. 2). One subject was lost from group S before the second condition because he was removed from his home cage for husbandry purposes. We therefore omitted him from this analysis.

Table 4. Success rates for all groups including standardized residuals (Siegel & Castellan 1988)

| Group | Failure | | Success | | Total |
|---------------------------|----------|----------|----------|----------|-------|
| | <i>N</i> | Residual | <i>N</i> | Residual | |
| Observation (Condition 1) | 10 | 0.246 | 2 | -0.663 | 12 |
| Scrounging (Condition 1) | 3 | -1.024 | 8 | 2.752* | 11 |
| Individual learning | 10 | 0.246 | 2 | -0.663 | 12 |
| Joint learning | 9 | 0.049 | 3 | -0.133 | 12 |
| Control | 11 | 0.443 | 1 | -1.194 | 12 |
| Total | 43 | | 16 | | 59 |

* $P<0.005$.

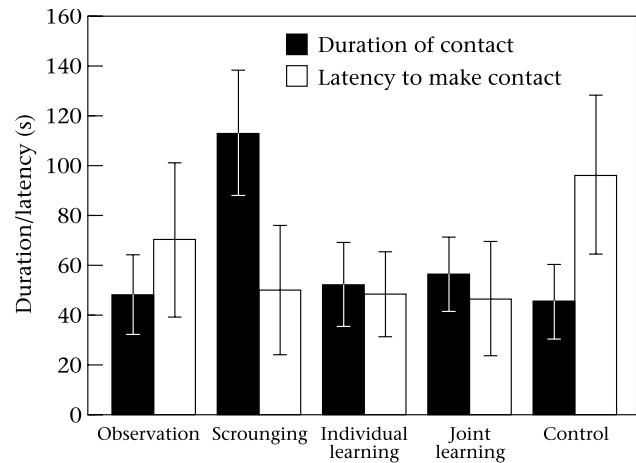


Figure 3. Duration of contact (s) and latency to make contact (s) with the apparatus during trials for the five groups ($\bar{X}\pm SE$).

We also looked at two other measures of performance in the trials, duration of interaction with the artificial fruit and latency to make contact with the artificial fruit (Fig. 3). There was a nonsignificant trend for the scrounging group to spend the most time in contact with the apparatus during the trial (ANOVA: $F_{4,54}=2.486$, $P=0.054$). There was also a nonsignificant trend for the control group to be slower than the other groups in their initial approach to the artificial fruit (Kruskal-Wallis test: $H_4=6.804$, $P=0.147$). Nonparametric statistics were used

for analysis involving latencies to approach, because of the skewed distribution of this measure. We used two-tailed statistical tests.

Predictors of Success

Judging by the differences between the groups, there was no apparent effect of amount of experience on later success. However, when individual performance was analysed, success during the trial appeared to be related to behaviour during the experience phase. We examined differences in performance during the experience phase between individuals that succeeded on the subsequent trial and those that failed. This has been done for the four conditions involving an experience phase during which the subject could interact with the apparatus (S1, O2, I and J), and all of those grouped together (Tables 2, 3). For three of the individual conditions there were no significant differences in performance, in either amount of food taken, or duration of contact with the apparatus. However, because in each case one of the groups being compared was extremely small (succeeders in groups I and J, and failers in group O2) this is not surprising. When we combined the performance of each of the groups, succeeders both took more food (unpaired t test: $t_{45}=2.710$, $P<0.01$) and spent longer in contact with the apparatus (unpaired t test: $t_{45}=2.404$, $P<0.05$) during the experience phase. The only group to show significant differences on either of these measures was the Scrounging group (Tables 2, 3). In this group the three subjects that did not open the artificial fruit during the trial had also spent very little time interacting with the apparatus during the experience phase and failed to take any food.

DISCUSSION

Why did Scrounging Facilitate Learning?

In our scrounging condition, in which subjects could closely interact and share rewards with a trained demonstrator, social learning was strongly facilitated. This result cannot be attributed to individual differences between our groups because subsequent scrounging experience allowed another group to reach the same level of performance on the trials.

This result cannot be explained simply in terms of individual learning of the object–reward association, or increased interaction with the apparatus caused by social support. In the individual and joint learning conditions, subjects received equivalent opportunities to form an association between the artificial fruit and the food reward, as they were allowed to remove food items from the open artificial fruit. Furthermore, the group in the joint learning condition benefited from the social support of a partner during the experience phase, another factor that might have contributed to the success of the scrounging group. However, although they interacted with the artificial fruit during the experience phase, and removed food rewards, these two groups none the less

failed to reach the level of success of the scrounging group when it came to opening the artificial fruit for themselves. In fact, the success rates of both of these groups were closer to that of the control group (which had received no pretrial experience) than to that of the scrounging group. Therefore, if the difference cannot be accounted for in terms of these two variables, other factors must be involved that made the scrounging condition more conducive to learning than the other conditions.

Performance during the experience phase was related to success in the trial. However, the results suggest that this was due principally to individual differences (e.g. in levels of neophobia), rather than to the amount of learning about the apparatus. There were unambiguous differences between the groups' success, despite their pretrial behaviour being virtually identical in amount of contact with the apparatus and number of food rewards obtained. We therefore conclude that the scrounging group must have had access to some extra information unavailable to the other groups.

The most plausible interpretation lies in the close visual contact we observed between subject and demonstrator in the scrounging condition, which may have allowed the observer to learn the actions required more effectively. During the experience phase, the subject often came close to the demonstrator and may have acquired more task-relevant information than did subjects that observed through the wire mesh. This interpretation is also consistent with our other results. There were no significant differences between the five groups in latency to approach the artificial fruit (all except the control group behaved similarly, Fig. 3), suggesting that all individuals were equally motivated to gain the food reward. The nonsignificant trend for the scrounging group to spend longer in contact with the apparatus (Fig. 3) could indicate higher levels of motivation in this group. However, the difference in manipulation time may be more simply explained by the fact that succeeders (of which there were more in group S) were obtaining food, and therefore were less likely to cease their interactions with the apparatus. The only significant difference in performance between the groups was in the actual measure of trial success, suggesting that only the scrounging group was able to act effectively on this motivation.

This interpretation also suggests some potential explanations for the differences between our results and those in the literature. For example, there was no joint interaction between demonstrators and scroungers in Giraldeau & Lefebvre's (1987) study. Pigeons in the scrounging condition were separated from demonstrators and the food reward fell towards observers and demonstrators; in the nonscrounging condition, the food fell only towards the demonstrator. This could have led subjects to attend to the location of the food reward instead of the demonstration. In our study, however, subjects attended closely to the demonstration in the scrounging condition.

In other studies, the dominance interactions of individuals may have hampered the potentially facilitatory

effects of joint interaction. For example, when Nicol & Pope (1994) allowed observer chickens to interact with demonstrators, the demonstrator was often threatened by dominant observers, inhibiting the demonstrator's approach to the apparatus. Some dominant observers defended the apparatus, effectively preventing the demonstration. Thus, in Nicol & Pope's scrounging condition, there were fewer demonstrations. We found no such effect in our study and we attribute this to the generally tolerant nature of marmoset family groups.

When individuals are tested in groups, there will almost certainly be an economic interaction between producers and scroungers (Barnard & Sibly 1981). However, this should not necessarily mean that an individual that adopts the scrounger role has learned nothing from the experience. In Fragaszy & Visalberghi's (1989) study, for example, testing was done within the group, so there was little motivation for those individuals that had adopted a scrounging technique to switch to producing. In support of this suggestion, Lefebvre & Helder (1997) found that, although none of the birds from one of their scrounging conditions ever produced in the group setting, all seven performed the opening technique when tested alone.

Lefebvre & Helder (1997) reported another result that suggests why group testing has tended to result in low levels of social learning. Pigeons that scrounged in a group learned a task less effectively than pigeons that had scrounged singly. Lefebvre & Helder attributed their result to a confusion effect, in which attention was drawn away from the demonstrator to other individuals in the group. Therefore, in group studies of scrounging and social learning, it may not necessarily be the scrounging actions themselves that inhibit social learning, but the general distractions from the demonstration that are inherent to group testing.

Directed Social Learning

There are apparent contradictions in the literature, as to whether information is liable to be transmitted via socially tolerant relationships. Coussi-Korbel & Fragaszy (1995) referred to such identity-dependent effects as directed social learning. On the one hand, learners are more likely to pick up information from individuals with whom they interact closely, and on the other, this kind of joint interaction is liable to result in scrounging behaviour, which has generally been viewed as an inhibiting force in social transmission.

As noted by Fragaszy & Visalberghi (1989), social transmission of a suite of instrumental behaviours is generally assumed to occur in wild chimpanzees and there is now considerable support for this view (e.g. Whiten et al. 2001). However, as pointed out by Fragaszy & Visalberghi (1989), the behaviours typically proposed to have been socially transmitted are those learned by infants while they are still with their mothers, when the infant is free to interact with any of the same objects as the mother without threat or punishment. Furthermore, they can do this at the same time as the mother demonstrates the behaviour (referred to by Fragaszy & Visalberghi 1989 as

coaction). This type of joint interaction with a skilled individual (compared with individual practice, for example) may strongly benefit the learning of novel skills in nonhuman primates.

The marmosets in our experiment, all studied within their family group, showed the kind of tolerant interactions that we might expect to allow this kind of learning, and therefore were an apt species for studying the conditions under which scrounging facilitates social learning. We suggest that the inhibitory effects of scrounging on social learning may have been overstated, and that scrounging, within the context of joint interaction with a skilled demonstrator and the relevant materials, can under some conditions facilitate social learning. Directed social learning may therefore occur in many other species, with information transmitted preferentially via tolerant relationships.

Acknowledgments

C.C. was supported by a University of St Andrews studentship. We thank all of the staff at the Medical Research Council Human Reproductive Sciences Unit, without whose help the data could not have been collected. We are also grateful to Johannes Fritz and an anonymous referee for very helpful comments on the manuscript.

References

- Barnard, C. J. & Sibly, R. M. 1981. Producers and scroungers: a general model and its application to captive flocks of house sparrows. *Animal Behaviour*, **29**, 543–550.
- Beauchamp, G. & Kacelnik, A. 1991. Effects of the knowledge of partners on learning rates in zebra finches, *Taeniopygia guttata*. *Animal Behaviour*, **41**, 247–253.
- Bugnyar, T. & Huber, L. 1997. Push or pull: an experimental study on imitation in marmosets. *Animal Behaviour*, **54**, 817–831.
- Caldwell, C. A., Whiten, A. & Morris, K. D. 1999. Observational learning in the marmoset monkey, *Callithrix jacchus*. In: *Proceedings of the AISB '99 Symposium on Imitation in Animals and Artifacts*, pp. 27–31. Edinburgh: The Society for the Study of Artificial Intelligence and Simulation of Behaviour.
- Coussi-Korbel, S. & Fragaszy, D. M. 1995. On the relation between social dynamics and social learning. *Animal Behaviour*, **50**, 1441–1453.
- Feistner, A. T. C. & Price, E. C. 1991. Food offering in New World primates: two species added. *Folia Primatologica*, **57**, 165–168.
- Fragaszy, D. M. & Visalberghi, E. 1989. Social influences on the acquisition of tool-using behaviours in tufted capuchin monkeys. *Journal of Comparative Psychology*, **103**, 159–170.
- Fritz, J. & Kotrschal, K. 1999a. Social constraints and profitability of scrounging affect social learning. In: *Proceedings of the AISB '99 Symposium on Imitation in Animals and Artifacts*, pp. 20–26. Edinburgh: The Society for the Study of Artificial Intelligence and the Simulation of Behaviour.
- Fritz, J. & Kotrschal, K. 1999b. Social learning in common ravens, *Corvus corax*. *Animal Behaviour*, **57**, 785–793.
- Giraldeau, L.-A. & Caraco, T. 2000. *Social Foraging Theory*. Princeton, New Jersey: Princeton University Press.

- Giraldeau, L.-A. & Lefebvre, L.** 1987. Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Animal Behaviour*, **35**, 387–394.
- Kawai, M.** 1965. Newly-acquired pre-cultural behavior of the natural troop of Japanese monkeys on Koshima Islet. *Primates*, **6**, 1–30.
- Lefebvre, L. & Helder, R.** 1997. Scrounger numbers and the inhibition of social learning in pigeons. *Behavioural Processes*, **40**, 201–207.
- Midford, P. E., Hailman, J. P. & Woolfenden, G. E.** 2000. Social learning of a novel foraging patch in families of free-living Florida scrub-jays. *Animal Behaviour*, **59**, 1999–2007.
- Nicol, C. J. & Pope, S. J.** 1994. Social learning in small flocks of laying hens. *Animal Behaviour*, **47**, 1289–1296.
- Rylands, A. B. & de Faria, D. S.** 1993. Habits, feeding ecology, and home range in the genus *Callithrix*. In: *Marmosets and Tamarins: Systematics, Behaviour and Ecology* (Ed. by A. B. Rylands), pp. 262–272. Oxford: Oxford University Press.
- Siegel, S. & Castellan, N. J., Jr.** 1988. *Nonparametric Statistics for the Behavioural Sciences*. Singapore: McGraw-Hill.
- Terkel, J.** 1996. Cultural transmission of feeding behaviour in the black rat (*Rattus rattus*). In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B. G. Galef, Jr), pp. 17–47. San Diego: Academic Press.
- Voelkl, B. & Huber, L.** 2000. True imitation in marmosets. *Animal Behaviour*, **60**, 195–202.
- Whiten, A., Custance, D. M., Gomez, J. C., Texidor, P. & Bard, K. A.** 1996. Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **110**, 3–14.
- Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C.** 2001. Charting cultural variation in chimpanzees. *Behaviour*, **138**, 1481–1516.