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Inducing traditions in captive capuchin monkeys (*Cebus apella*)

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Potential foraging and social traditions have been identified in groups of wild capuchin monkeys (*Cebus* spp.). Verification of traditions requires documentation that socially mediated learning contributes to acquisition by new practitioners. We investigated the emergence and maintenance of a foraging tradition in two generations of infant tufted capuchins (*Cebus apella*) in captive social groups. In baseline, we provided the first cohort of infants with a foraging apparatus that dispensed juice via two methods inside a small enclosure away from adult interference (the crèche). Later in phase 1, we provided a second apparatus to all group members with only one method of solution available (in the group setting); the crèche apparatus, with both methods available, remained accessible to infants only. Two years later (phase 2), we replicated phase 1 with a new cohort of infants from the same social groups. As adult activity and expertise with the apparatus increased across baseline (no adult activity), phase 1 (initially unskilled) and phase 2 (initially skilled), the proportion of infants in each cohort that acquired the foraging skill increased and their latency to skill acquisition decreased. Despite ambiguous evidence that the infants conformed to the specific method of solution common in their group, the social context clearly contributed to the development and maintenance of a general foraging tradition. The results provide support for the existence of traditions in wild capuchin groups.

In many group-living species, specific behaviour patterns are shared among group members. A shared behaviour pattern is a tradition if adoption by new practitioners is facilitated by socially mediated learning and persists over time (Fragaszy & Perry 2003). Early suggestions that nonhuman species might have traditions came from observations that different populations of wild animals show behavioural differences that are not readily explained by genetic inheritance or ecological variation, but appear to be transmitted between individuals though nongenetic means; for example, song learning and migration-route learning in birds (e.g. Bonner 1980). The method of identifying potential traditions by tracking differences in behaviour between groups is referred to as the ethnographic approach (Rendell & Whitehead 2001; Leca et al. 2007) and group contrast method (Fragaszy & Perry 2003). Candidate traditions identified using this approach in wild populations include behaviours related to foraging, social interactions, tool use and vocal communication in species as diverse as birds (e.g. Hunt & Gray 2003), cetaceans (e.g. Rendell & Whitehead 2001) and nonhuman primates (e.g. Whiten et al. 1999, 2001; Panger et al. 2002; van Schaik et al. 2003). However, apparent traditions may reflect genetically predisposed behaviours (e.g. Kenward et al. 2005) and/or homogeneous but individually discovered solutions to shared ecological conditions (Galef 1980, 1992). For this reason, verifying that socially mediated learning supports an individual's acquisition of a behaviour is crucial to confirm that any behaviour is a tradition (Fragaszy & Visalberghi 2004).

Field studies investigating the behavioural ontogeny of potential traditions provide stronger evidence for the social contribution to skill acquisition and diffusion among group members (e.g. macaques: Huffman 1996; Leca et al. 2010; rats: Terkel 1996; chimpanzees: Biro et al. 2003; Humle et al. 2009; capuchins: Perry et al. 2003). To complement longitudinal field studies, controlled laboratory research can provide corroborating evidence that traditions can emerge and be sustained within captive groups of the species in question (see Whiten & Mesoudi 2008). A good example is provided by studies that have effectively induced traditions and arbitrary social conventions in groups of captive chimpanzees (e.g. Horner et al. 2006; Bonnie et al. 2007; Whiten

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et al. 2007). Providing empirical evidence for the role of socially mediated learning in the acquisition and maintenance of a behaviour pattern among group members strengthens the claims for traditions in wild populations of chimpanzees. In addition, controlled laboratory studies can clarify the social-learning mechanisms underlying behavioural transmission between individuals, which can help guide longitudinal field studies aimed at verifying traditions in natural settings.

The goal of the present study was to lend credence to claims of behavioural traditions in wild capuchin monkey populations by showing that traditions can develop and persist over time in groups of captive capuchins (*Cebus apella*). Interpopulation and within-group differences in various foraging and social behaviours have been identified as candidate traditions in groups of wild capuchins. For example, groups of capuchins vary in their use of specific food selection and processing behaviour and the social context appears to contribute to acquisition and maintenance of skills by new practitioners (e.g. Panger et al. 2002; Fragaszy et al. 2004; O'Malley & Fedigan 2005a; Ottoni & Izar 2008; Perry 2009). In addition, groups of white-faced capuchins, *Cebus capucinus*, at various sites in Costa Rica engage in idiosyncratic social behaviours ('games') that involve extracting items from one another's mouth and placing fingers inside one another's nose and/or mouth (Perry et al. 2003). Numerous field and captive studies suggest that capuchins experience a general support from the social context when learning a new behaviour pattern (e.g. Visalberghi & Fragaszy 1995; Bonnie & de Waal 2007; Meunier et al. 2008; Gunst et al. 2008). For example, mere proximity to others' foraging appears to influence acquisition of sex-typical foraging behaviour in black-capped capuchins, *Cebus nigritus* (Agostini & Visalberghi 2005). Stimulated by the social context to explore individually, capuchins may develop idiosyncratic ways of performing a particular behaviour or achieving a particular goal. Alternatively, capuchins may be influenced by particular groupmates to learn a specific form or technique of a behaviour pattern, one that is similar to that of others in their group (e.g. Perry 2009).

To determine whether traditions could be induced in captive capuchins, we provided a foraging apparatus to several socially housed groups of capuchins. Two different action sequences could be used to obtain juice from the apparatus (each action sequence will hereafter be referred to as a 'method of solution'). The behavioural tradition of interest was performance of the foraging skill, which was operationally defined as obtaining juice from the apparatus using at least one method of solution. We examined the acquisition of the foraging skill and subsequent use of the apparatus by infants (ages 7–18 months) of two cohorts (i.e. generations), first in a baseline phase and later in experimental phases separated by 2 years (phase 1 and phase 2). During baseline and the experimental phases, the foraging apparatus was provided inside a small wire-mesh enclosure within the group's outdoor enclosure (termed the 'crèche') that permitted entry only to infants and juveniles (see Fig. 1). Inside the crèche, infants could use both methods of solution to obtain juice; thus they had the opportunity to discover both methods of solution in an area that was within the group's enclosure (hereafter, the 'group setting') but removed from interference by adults. During phase 1 and 2 experimental sessions, all group members could access a second identical foraging apparatus in the group setting with only one method of solution baited with juice (one method of solution was pre-assigned to each group; Fig. 1). Thus, the first cohort of infants encountered the foraging apparatus without adult demonstrators (baseline sessions), and later encountered the apparatus in the presence of initially unskilled adults (phase 1 experimental sessions). In phase 2, the second cohort of infants first encountered the apparatus in the presence of skilled adults. This experimental design allowed us to disentangle the effects of experience with the foraging apparatus from the effects of the social context.

In this study, individuals within each group could discover a novel behaviour pattern (i.e. operation of the foraging apparatus) without specific training by experimenters. In addition, the emergence of a 'group norm' for method of solution was facilitated by baiting only one method in the group setting. Accordingly, we tested the following hypotheses: (1) that adult presence and proficiency with a particular behaviour pattern supports learning by new practitioners and (2) that the particular form, or technique, used by proficient group members biases new practitioners

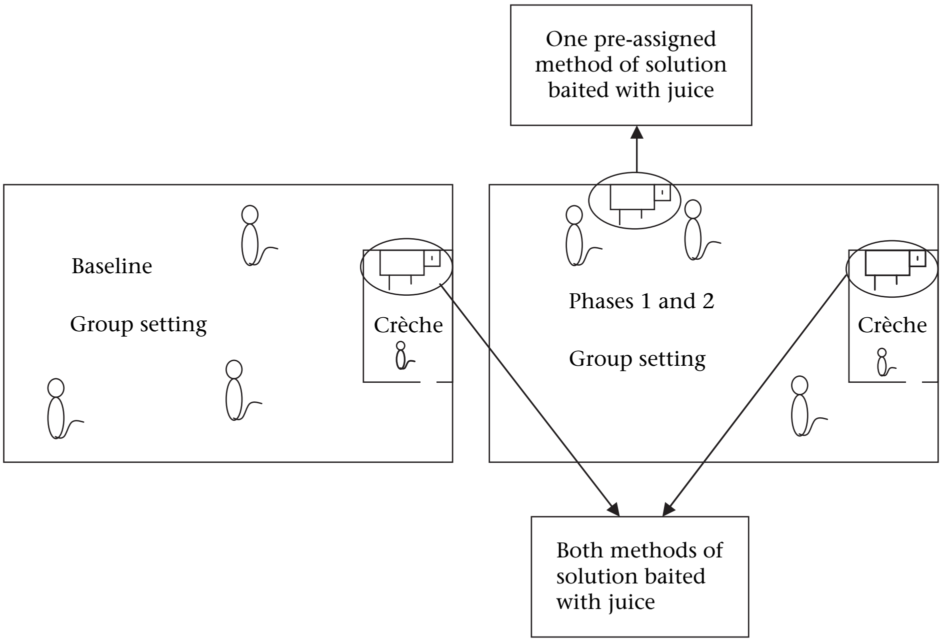

Figure 1. Generalized aerial view of the testing set-up (not drawn to scale; positions of crèche and apparatuses varied across groups). Baseline sessions: both methods available in the crèche; phases 1 and 2 experimental sessions: both methods available in the crèche and one method available in the group setting.

towards using the same technique. With regard to the first hypothesis, we predicted that a greater proportion of infants in the second cohort would acquire the foraging skill, and acquire it in fewer testing sessions, than infants in the first cohort. With regard to the second hypothesis, we predicted that when infants used the apparatus in the crèche, where both methods of solution were baited with juice, they would prefer the method of solution that was baited in the group setting (hereafter referred to as 'the group method of solution').

METHODS

Subjects and Housing

Focal subjects were 27 infant tufted capuchin monkeys (*Cebus apella*), 7–18 months of age, housed in social groups at LABS of Virginia (now Alpha Genesis, Inc., Yemassee, SC, U.S.A.). Table 1 presents details on the focal subjects and their social group. In baseline and phase 1, two social groups were tested, each housed in indoor–outdoor enclosures. In group 1 ($N = 14$) the outdoor area was 15.3 × 7.5 × 2.8 m (321.3 m^3); in group 2 ($N = 17$) the outdoor area was 15.3 × 15.2 × 2.8 m (651.2 m^3). During the 2-year interstice between phases, the two groups were rearranged into four smaller social groups housed in different indoor–outdoor enclosures. In group B ($N = 11$) and group D ($N = 9$) the outdoor areas were 3.2 × 5.8 × 3 m (55.7 m^3); in group F ($N = 10$) and group G ($N = 10$) the outdoor areas were 2.8 × 5.5 × 3 m (46.2 m^3). In the rearrangement of groups prior to phase 2, five adult females from phase 1 group 1 and one subject (Chunky) from phase 1 group 2 went to phase 2 group B. Four adult females and two subjects (Leo and Kitten) from phase 1 group 2 went to phase 2 Group F.

Table 1
Focal subjects' group (including group size and method of solution baited in the group setting), name, age in months at the start of testing, and description of other group members

Group	Subject	Age (mo.)	Other group members
Baseline and phase 1 (*N*=16 focal subjects)			
Group 1 (*N*=14)	Thor	14	One adult male (11 years)
Lever method	Dave	13	Seven adult females (8–18 years)
	Spider	12	One juvenile male (2.5 years)
	Fluffy	9	Two young infants (<1 month)
	Ken	9	
Group 2 (*N*=17)	Chunky*	18	One adult male (20 years)
Wheel method	Spaz	18	Four adult females (9–12 years)
	Cutie	18	One juvenile male (3 years)
	Sadie	18	Two young infants (2 months)
	Roger	18	
	Patch	15	
	Captain	15	
	Snake	15	
	Fred	12	
	Kitten*	9	
	Leo*	7	
Phase 2 (*N*=11 focal subjects)			
Group B (*N*=11)	Janis	14	One adult male (13 years)
Lever method	Stan	13	Five adult females (10–20 years)
	Elvis	13	One juvenile male (3.5 years)
	Buddy	11	
Group D (*N*=9)	Tonya	13	One adult male (8.5 years)
Lever method	Houdini	11	Five adult females (8.5–19 years)
			One juvenile male (2 years)
Group F (*N*=10)	Pel	11	Two adult males (15 and 6 years)
Wheel method	Tonto	11	Four adult females (11–14 years)
			Two juveniles (2.5 years)
Group G (*N*=10)	Mobe	15	Two adult males (18.5 and 13 years)
Wheel method	Cabuki	9	Three adult females (9–17 years)
	Gene	8	Two juveniles (3 and 2.5 years)

* These infants were juveniles in phase 2.

Materials

Crèche enclosure

The crèche was a welded-wire cage (122 × 74 × 91 cm) secured to the perimeter of the outdoor fencing approximately 1.33 m above the ground. Placement of the crèche within the group enclosure varied across groups to allow suitable filming of the infants' activity. A ramp led to an entryway wide enough to permit only juveniles and infants to pass through (juveniles were not considered as focal subjects but could enter the crèche). Hazelnuts and sticks were placed inside the crèche at the start of each testing session to encourage infants to enter and the crèche door was closed between testing sessions.

Foraging apparatus

The foraging apparatus was a rectangular box (15 × 32 ×9 cm) with a smaller square box attached to the bottom right side (8.8 × 7.5 × 9 cm) manufactured from opaque PVC (see Fig. 2). Each of these portions of the apparatus housed a reservoir that could be filled with fruit juice, providing two separate juice dispensers (i.e. methods of solution). The larger part of the apparatus housed the 'lever method', which dispensed juice via pushing a lever up and down, releasing juice from a spout. The lever and spout projected perpendicularly from the front of the rectangular portion of the apparatus (each approximately 4 cm). The 'wheel method' was housed in the smaller part of the apparatus to the right of the lever method. Subjects could obtain juice by inserting a finger or tongue into an opening ('finger slot', 1.3 × 2.2 cm) and turning a scalloped wheel that brought the juice up to the opening. One or both reservoirs (depending on apparatus location) were filled from the back side of the apparatus prior to each testing session and emptied and flushed with water at the end of each session.

In the group setting, the foraging apparatus was secured to an exterior fence panel of the outdoor enclosure. In phase 1, the group apparatus was situated near the ground. In phase 2, the group apparatus was situated approximately 1.33 m above the ground along a horizontal platform. The group apparatus was always mounted within 3 m of the crèche. Both the group and crèche apparatuses were positioned in locations easily videotaped from outside of the enclosure, so their relative positions varied across

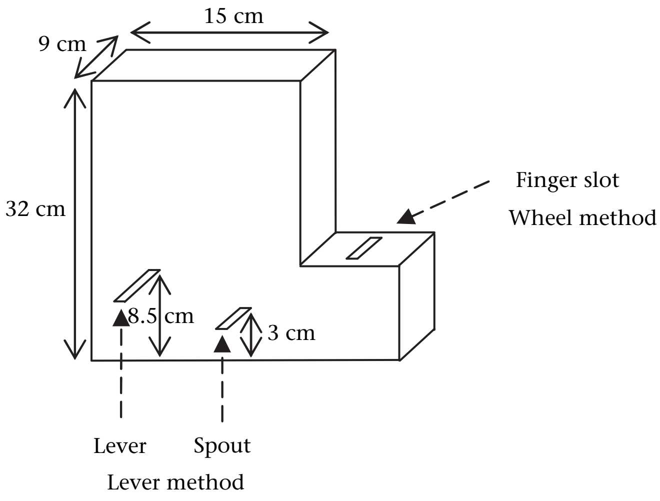

Figure 2. Foraging apparatus: juice dispenser with two methods of solution, lever method and wheel method.

groups. During experimental sessions, the crèche and group settings were filmed concurrently.

Experimental Design

The foraging apparatus was presented to six social groups of capuchin monkeys in testing phases separated by 2 years. Two groups were tested in baseline and phase 1, and four groups were tested in phase 2 (see Table 1). Testing consisted of the following sets of sessions in this sequence: habituation, baseline, phase 1 experimental, phase 2 habituation and phase 2 experimental.

Habituation

In each group, the subjects (the infants) were exposed to the crèche prior to baseline sessions. In each group, the crèche was opened and baited with food treats (such as peanuts and raisins) until each subject entered the crèche at least once.

Baseline

The foraging apparatus was provided in the crèche to subjects ($N = 16$) in groups 1 and 2 for 20 30-minute testing sessions to document the subjects' use of the apparatus when no adults could access it. In the crèche, both methods of solution were baited with juice at all times.

Phase 1 experimental

During experimental sessions, one apparatus was available in the crèche, where both methods of solution remained baited with juice, and a second identical apparatus was available in the group setting where all group members could access it. Groups 1 and 2 experienced 12 30-minute testing sessions. In the group setting, only one method of solution was baited with juice and was referred to as the 'group method' (GM); use of the alternative method of solution resulted in no juice. In the crèche, the alternative method of solution was referred to as the 'nongroup method' (NGM). Group 1 was assigned the lever method as the group method (i.e. only the lever reservoir was filled with juice); group 2 was assigned the wheel method as the group method (i.e. the wheel reservoir was filled with juice; see Table 1). The adults in phase 1 had no previous experience with the foraging apparatus prior to experimental sessions, whereas the infants in phase 1 had been provided with opportunities to investigate the apparatus and learn the foraging skill in the crèche during baseline sessions.

Phase 2 habituation/refamiliarization

As the groups had been separated into four new groups since the phase 1 experimental sessions ended (see Subjects and Housing, and Table 1), there were some adult and juvenile group members that had no prior experience with the foraging apparatus from phase 1. In addition, those with prior experience had not encountered the apparatus for 2 years. Thus, a habituation/refamiliarization phase was administered to the adults and juveniles in each group until at least three adults per group were skilled at obtaining juice from the apparatus using the method of solution assigned to their group. The infants born during the intervening 2 years (i.e. the second cohort of subjects) were kept inside without visual access to the outdoor enclosure during these sessions.

Phase 2 experimental

Groups D, F and G experienced 12 30-minute testing sessions. Group B experienced 11 30-minute testing sessions because of logistical issues. As in phase 1, both methods of solution could be used in the crèche and one method of solution was baited in the group setting and assigned as the group method of solution. In groups B and D, the lever method was assigned as the group method of solution; in groups F and G, the wheel method was assigned as the group method of solution.

The experimental design allowed us to disentangle the effects of experience from the effects of social context. That is, the baseline–phase 1 experimental comparison (comparison 1; see Fig. 3) allowed us to track changes in the same infants' behaviour initially in the absence and later in the presence of adults, but the change in social context was confounded by their increasing experience with the apparatus over the course of testing. The more powerful comparisons of phase 1 experimental–phase 2 experimental and, especially, baseline–phase 2 experimental (comparisons 2 and 3, respectively; see Fig. 3) allowed us to track changes in the behaviour of two different cohorts of infants that were exposed to different social contexts.

Testing Procedure

Baseline and phase 1 experimental sessions took place during June and July 2001. Phase 2 experimental sessions took place during April and May 2003. All testing sessions were videotaped. Testing sessions began in the morning, and one or two sessions were filmed each day, alternating between groups. To begin a testing session, all group members were moved to the indoor portion of their enclosure and the apparatuses were secured to the fencing in the outdoor area and/or in the crèche. A handful of hazelnuts and small sticks then were placed inside the crèche and the reservoirs for both methods of solution were filled with juice in the crèche. During experimental sessions, the apparatus reservoir corresponding to the assigned group method was filled with juice

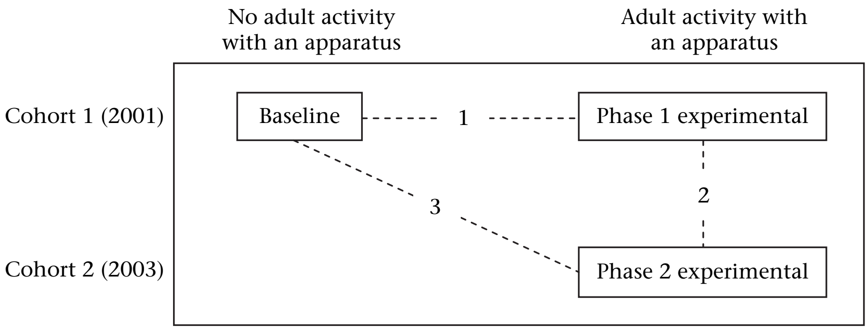

Figure 3. Schematic of experimental design and planned comparisons of dependent variables (comparisons 1–3). Cohort 1 (tested in 2001) experienced baseline and phase 1 experimental sessions. Cohort 2 (tested in 2003) experienced phase 2 experimental sessions. During baseline, there was no adult activity with a foraging apparatus. During phase 1 and 2 experimental sessions, adults had access to a foraging apparatus. Dependent variables included (1) the proportion of infants in each group that acquired the foraging skill and (2) the mean session number of their first solutions. These measures were compared between baseline and phase 1 (comparison 1), phase 1 and phase 2 (comparison 2), and baseline and phase 2 (comparison 3).

in the group setting. The video camera(s) were set up and a testing session began when the group was released into the outdoor enclosure. During data collection for phase 1, one narrator continuously described the activity at the group and crèche apparatuses and identified individuals. During data collection for phase 2, one narrator described the activity and identified individuals at the apparatus in the group setting and a second narrator described all crèche activity and identified individuals inside the crèche.

Coding and Analysis

Fifteen of 20 baseline sessions and all 12 phase 1 and 2 experimental sessions were coded from video (five baseline sessions from each group were lost or removed because of filming difficulties). For the current analysis, the behaviour of interest was referred to as 'solve' and was coded when subjects operated the functional parts of the apparatus and licked juice from the spout, finger slot or fingers. Each solve was identified as 'lever solve' or 'wheel solve' (see Table 2), then classified as a 'group method solve' or 'nongroup method solve', according to each subject's assigned group method (i.e. the method available in the group setting).

The occurrence of each solve was recorded during consecutive 10 s intervals (i.e. binary 1–0 sampling; Altmann 1974) spanning the duration of each testing session: 15 baseline, 12 experimental sessions focused on the group setting, and 12 experimental sessions focused on the crèche per group. This coding method yielded the frequency of 10 s intervals during which subjects solved in both the group and crèche settings, as the raw frequencies with which subjects solved were difficult to ascertain from the video footage. Two primary coders recorded the subjects' behaviour (the first two authors); one coder narrated the behaviour of infants in each interval and the other recorded the behaviour on a data sheet. Additionally, the two coders resolved any ambiguous solutions. When more than two coders were available for coding, the two primary coders headed up two coding teams and maintained a minimum of 80% agreement of the frequency of intervals during which subjects solved in each session. Upon completion of coding, the two coders rechecked all instances of solves in the crèche and group settings.

For the present analysis, we (1) counted the number of infants in each group that solved using either method of solution in either the group or crèche setting; (2) recorded the session number during which each subject first solved and which method was used in their first solution; and (3) we counted the frequency of 10 s intervals during which subjects solved using the crèche apparatus only during baseline and experimental sessions. For each group, there was a maximum of 2700 baseline intervals (15 30-minute sessions) and 2160 experimental intervals (12 30-minute sessions). Timing/camcorder errors caused a few sessions to end early, but never by more than 9 min. Across groups, the total number of coded intervals across sessions was never less than 92% of the maximum intended (range 92.0–99.9%; mean: 97.0% of maximum intervals).

To address the prediction that older group members' activity and proficiency with the apparatus would support learning a general skill by infants, we compared the proportion of subjects that solved across baseline, phase 1 and phase 2 using chi-square tests for goodness of fit, applying Yates' correction for small sample sizes (comparisons 1, 2 and 3; see Fig. 3). We also compared the subjects' latency to acquire the foraging skill (i.e. the average session number during which subjects first solved using either method of solution) across baseline, phase 1 and phase 2 using Mann–Whitney U tests. To verify the change in social context from phase 1 to phase 2, we made the same comparisons with the older group members (adults and juveniles).

To address the prediction that the subjects would develop a preference for solving using the method assigned to their group, we counted the frequency of coded intervals during which each subject solved using the group method (GM) and nongroup method (NGM) of solution. We then calculated the proportion of total intervals during which each subject solved using the group method of solution (GM/GM + NGM). This yielded a 'group method score' for each subject. If a subject's group method score was greater than 0.5 (chance), the subject was assigned a preference for solving using the group method of solution (i.e. GM preference); if a subject's group method score was less than 0.5, the subject was assigned a NGM preference. If a subject's group method score was 0.5, no preference was assigned. Statistically significant preferences were determined using binomial tests (where $p = q = 0.5$).

RESULTS

Influence of Social Context on Infant Learning

The proportion of older group members (adults and juveniles) that solved the foraging apparatus remained relatively constant across phases (approximately 0.75 in both phases); however, on average, the older group members in phase 2 began solving during earlier testing sessions than the older group members in phase 1 (first solutions in phase 1: mean + SE = session 6.4 + 1.0 of 12 sessions, $N = 15$, range sessions 2–12; first solutions in phase 2: mean + SE = session 1.6 + 0.20 of 12 sessions, $N = 29$, range sessions 1–4; Mann–Whitney U test: $U = 17$, $N_1 = 10$, $N_2 = 22$, $P < 0.001$). As the activity and expertise of adult group members with the foraging apparatus increased across baseline, phase 1 and phase 2 sessions, the proportion of subjects that learned to solve increased and their latency to acquire the skill decreased (refer to Table 3 and see Proportion of Solvers and Latency to Acquisition below).

Proportion of Solvers

The proportion of subjects that solved using either method in either the group or crèche setting increased significantly from baseline to phase 1, from phase 1 to phase 2 and from baseline to phase 2 (comparisons 1, 2 and 3, respectively; see Fig. 3). During baseline sessions, when no adults could access a foraging apparatus, just 2 of 16 subjects (12.5%) solved in the crèche. Both subjects were from group 1 and both used the wheel method

Table 2
Definitions of coded behaviour

Behaviour	Definition
Solve	Subject manipulates the functional parts of the apparatus in the correct sequence to obtain juice and drinks the juice
Lever solve	Subject pushes and releases lever with hand or foot and drinks the juice from the spout; a 10 s lag time between operating the apparatus and drinking was allowed
Wheel solve	Subject inserts finger or tongue into the finger slot and drinks the juice, by licking juice from the top of the finger slot or from the fingers after movement of the water wheel
Group method solve (GM solve)	Subject solves in the crèche using the same method of solution that is baited in the group setting
Nongroup method solve (NGM solve)	Subject solves in the crèche using the method of solution that is not baited in the group setting

Table 3
Proportion of subjects (infants ages 7–18 months) and adults (adults and juveniles over age 2 years) that solved (obtained juice from the apparatus) during each phase of testing, and latency to acquisition (mean + SE session number, numbered consecutively from session 1, during which each subject first solved using either method of solution in the group or crèche setting)

		Proportion of solvers	Latency to acquisition
Baseline	Infants	2 of 16 (12.5%)	11.5+3.5 sessions
Phase 1	Adults	11 of 15 (73%)	6.4+1.0 sessions
	Infants	9 of 16 (56%)[*]	6.6+0.75 sessions
Phase 2	Adults	22 of 29 (76%)	1.6+0.20[†] sessions
	Infants	11 of 11 (100%)[*]	1.8+0.33[†] sessions

[*] Significant increase from previous phase (chi-square tests: $P < 0.01$).
[†] Significant decrease from previous phase (Mann–Whitney *U* tests: $P < 0.01$).

(Fluffy used the wheel once and Dave used it twice in the same testing session). In phase 1, when the same subjects could access an apparatus in both the group and crèche settings and adults were active in the group setting, seven additional subjects (9 of 16; 56%) solved in either or both the crèche and group settings (three from group 1; six from group 2), a significant increase from baseline (Yates' corrected chi-square test: $\chi^2_1 = 24.1$, $P < 0.001$; odds ratio: 7.9). In phase 2, when subjects first encountered the apparatus in the group and crèche settings in the presence of skilled adults solving in the group setting, all 11 subjects solved in either or both settings (100%), a significant increase from phase 1 (Yates' corrected chi-square test: $\chi^2_1 = 8.4$, $P < 0.005$; odds ratio: 17.8) and baseline (Yates' corrected chi-square test: $\chi^2_1 = 69.7$, $P < 0.001$; odds ratio: 135.1).

Latency to Acquisition

On average, the phase 2 subjects first solved much sooner than the subjects in baseline and phase 1. During baseline, only two subjects solved in the crèche towards the end of baseline testing; Fluffy solved during the eighth and Dave solved during the 15th of 15 sessions (mean + SE = session 11.5 + 3.5, $N = 2$). During phase 1, the subjects' mean session of first solution was about halfway through phase 1 testing sessions during the sixth of 12 sessions (mean + SE = session 6.6 + 0.75, $N = 9$, range sessions 3–11). During phase 2, the subjects' mean session of first solution was towards the beginning of testing (mean + SE = session 1.8 + 0.33, $N = 11$, range sessions 1–4), a significant decrease from phase 1 (Mann–Whitney *U* test: $U = 4.5$, $N_1 = 9$, $N_2 = 11$, $P < 0.001$).

Preferences for a Particular Method of Solution

Most subjects in both experimental phases showed a preference for using the group method of solution in the crèche where both methods were baited with juice (i.e. the majority of solutions in the crèche corresponded to the method of solution baited in the group setting for most subjects; see Table 4). In phase 1, five of 16 subjects solved in the crèche. Four of those five subjects preferred to use the group method of solution, three of whom (Ken, Fred and Chunky) used the group method of solution significantly more often than expected by chance (binomial tests: $P < 0.01$; see Table 4). In phase 2, nine of 11 subjects solved in the crèche. Seven of those nine subjects preferred using the group method of solution, one of whom (Cabuki) used the group method of solution significantly more often than expected by chance (binomial test: $P < 0.0001$; see Table 4). Overall, a majority of subjects (11 of 14) that solved in the crèche used the group method of solution exclusively or in a majority of their solutions, and five of those 11 subjects demonstrated a statistically significant preference for the group method. The other three of the 14 subjects that solved in the crèche preferred the nongroup method of solution.

Method of First Solution

The location (group or crèche setting) and the method (GM or NGM) of each subject's first solution are both relevant to the development of the subjects' preferences for a particular method of solution in the crèche. Seven of the 14 subjects that solved in the crèche during experimental sessions first solved in the group setting, where only the group method of solution was available, and all seven of those subjects maintained a preference for the group method of solution when solving in the crèche (see Table 5). Three subjects maintained this preference despite discovering the nongroup method of solution in the crèche (Fred, Janis and Stan). The other seven subjects' first solutions occurred in the crèche. Five of these subjects maintained a preference for the method of solution they first used (see Table 5). Of these five subjects, Ken and Elvis first solved using the group method of solution during experimental sessions and used that method exclusively in subsequent solutions. Fluffy first solved in the crèche during baseline sessions using the wheel method. Fluffy's group was later assigned the lever method for phase 1 experimental sessions, but Fluffy continued to use the wheel method exclusively when solving in the crèche despite using the lever method in the group setting several times. Tonya and Houdini first solved using the nongroup method in the

Table 4
Frequency of intervals during which subjects solved using the group method of solution in the crèche during experimental testing

Subject	Phase, group	Total solve intervals (GM+NGM)	Frequency of GM solve intervals	GM score (GM/GM+NGM)	Assigned method preference	*P* (binomial tests)
Fluffy	1, 1	8	0	0	NGM	0.004*
Dave	1, 1	3	3	1	GM	0.125
Ken	1, 1	7	7	1	GM	0.008*
Fred	1, 2	18	15	0.83	GM	0.003*
Chunky	1, 2	8	8	1	GM	0.004*
Janis	2, B	8	6	0.75	GM	0.109
Stan	2, B	12	9	0.75	GM	0.054*
Elvis	2, B	2	2	1	GM	0.250
Houdini	2, D	18	3	0.16	NGM	0.003*
Tonya	2, D	5	1	0.20	NGM	0.156
Pel	2, F	6	4	0.67	GM	0.234
Tonto	2, F	2	2	1	GM	0.250
Mobe	2, G	1	1	1	GM	0.500
Cabuki	2, G	15	15	1	GM	<0.001*

Preferences for solving using the group method (GM) and nongroup method (NGM) of solution are noted.
[*] Denotes statistical significance at $\alpha = 0.05$ with a two-tailed binomial test where $p = q = 0.5$.

Table 5
List of subjects that solved the apparatus in the crèche, grouped by location of first solution (group setting or crèche)

Subject	Group, group method	Phase of first solution	Location of first solution, method used	Used both methods in crèche	Preference for group method in crèche	Preference corresponds to first solution?
Fred	2, W	Phase 1	Group, W	✓	✓*	✓
Chunky	2, W	Phase 1	Group, W		✓*	✓
Janis	B, L	Phase 2	Group, L	✓	✓	✓
Stan	B, L	Phase 2	Group, L	✓	✓*	✓
Tonto	F, W	Phase 2	Group, W		✓	✓
Mobe	G, W	Phase 2	Group, W		✓	✓
Cabuki	G, W	Phase 2	Group, W		✓*	✓
Fluffy	1, L	Baseline	Crèche, W			✓
Dave	1, L	Baseline	Crèche, W	✓	✓	
Ken	1, L	Phase 1	Crèche, L		✓*	✓
Elvis	B, L	Phase 2	Crèche, L		✓	✓
Houdini	D, L	Phase 2	Crèche, W	✓		✓
Tonya	D, L	Phase 2	Crèche, W	✓		✓
Pel	F, W	Phase 2	Crèche, W	✓	✓	

Columns from left to right: subject; subject's group and the assigned group method (L = lever method; W = wheel method); the testing phase during which each subject's first solution occurred; the location of each subject's first solution (group or crèche) and the method used in the first solution (L or W); whether each subject discovered both methods of solution in the crèche (check = yes); whether each subject preferred the group method of solution when solving in the crèche (an asterisk denotes a statistically significant preference; see Table 4); and whether each subject's preference corresponded to the method they used in their first solution.

crèche during experimental sessions and, despite later using the group method of solution in the group setting, both subjects preferred the nongroup method of solution when solving in the crèche throughout experimental sessions. Thus, 12 of the 14 subjects that solved in the crèche preferred the method of solution they first used (see Table 5).

Two subjects' preferences in the crèche did not follow the method they first used: Dave (phase 1) and Pel (phase 2) preferred the group method of solution despite having first solved using the nongroup method in the crèche (see Table 5). Like Fluffy, Dave first solved in the crèche during baseline sessions using the wheel method, which later became the nongroup method during phase 1. Unlike Fluffy, however, Dave used the group method exclusively when solving in the crèche during experimental sessions. Pel first solved in the crèche using the nongroup method of solution during experimental sessions but used the group method more often than the nongroup method in subsequent crèche solutions. Also noteworthy, Chunky moved from a 'wheel group' in phase 1 to a 'lever group' in phase 2 and his method preferences in the crèche corresponded with the method baited in the group setting in each phase. In phase 1, Chunky, then a focal subject, used the wheel method exclusively when solving in the crèche (binomial test: $P = 0.004$; see Table 4). Later in phase 2, Chunky, no longer a focal subject but still fitting through the crèche entryway, demonstrated a significant preference for using the lever method to solve in the crèche (30 of 34 intervals: binomial test: $P < 0.001$). Altogether, 12 of 14 subjects that solved the crèche apparatus preferred to use the method of solution that they first performed.

DISCUSSION

Induction of Traditions

In the present study, the fundamental requirements of a behavioural tradition were met in captive tufted capuchin monkeys. Our first prediction, regarding the influence of adult presence and proficiency on the infants' acquisition of a general skill, was supported unequivocally: the social context contributed to acquisition of a skill by new practitioners and the skill was maintained over time in a new cohort of practitioners. During baseline, when infants had access to a foraging apparatus away from adult interference, only two of 16 infants learned a method of solution. Subsequently, during phase 1 experimental sessions, when adults had access to an apparatus in the group setting, seven additional infants learned a method of solution. Phase 2 was administered with a new cohort of infants to disentangle the effects of experience with the apparatus (i.e. during baseline sessions) from the effects of social context (namely, the presence of adults interacting with an apparatus). During phase 2, all 11 infants learned at least one method of solution, and they acquired the skill faster than the infants in phase 1, despite the latter infants' prior exposure to the apparatus during baseline sessions.

These results confirm the influence of adult presence and activity on the infants' acquisition of the foraging skill. It appeared that the mere presence of adults near and/or using an apparatus reduced the infants' neophobia and/or facilitated their interaction with an apparatus. Although we cannot yet confirm the social-learning mechanisms that supported the infants' learning, such a scenario is typical of capuchins learning about food (e.g. Visalberghi & Addessi 2003). Overall, this study, along with other laboratory investigations of social diffusion in capuchins (e.g. Dindo et al. 2007, 2009) provide support for the proposal that wild capuchin populations have traditions (e.g. Panger et al. 2002; Perry et al. 2003; O'Malley & Fedigan 2005b), although each case must be verified independently.

An important issue in studies of skill acquisition is the spatial proximity of group members. During the interstice between phases in the present study, the phase 1 groups were separated into four smaller groups and transferred into smaller enclosures (phase 1 mean space = 486 m^3; phase 2 mean space = 50 m^3). It is possible that the smaller enclosures in phase 2 contributed to the monkeys' increased activity with the apparatus compared to those in phase 1, as there was less room to move away and engage in other activities. A second, related possibility is that the smaller space may have provided phase 2 infants with increased social-learning opportunities if infants were necessarily in closer proximity to others interacting with the apparatus.

Data from phase 1 do not support these possibilities, as the individual space for monkeys in group 1 was 60% of that for monkeys in group 2 and there was no discernable difference in the infants' response to the apparatus between the groups, as presently measured (see Table 6). Furthermore, recent evidence suggests that capuchins' social interactions decrease in crowded conditions (van Wolkenten et al. 2006), as appears to be the case in other nonhuman primate species as well (e.g. Erwin 1979). This would suggest that the spatial change in housing between phases reduced social-learning opportunities for the phase 2 infants, in which case the effect of the social context observed in this study overrode any

Table 6

Comparing individual space of groups 1 and 2 of phase 1 and the two dependent variables examined in this study: the proportion (and percentage) of subjects in each group that solved the foraging apparatus and the mean session number during which subjects in each group first solved the foraging apparatus

	Group 1	Group 2
Individual space*	22.95 m^3/monkey	38.31 m^3/monkey
Proportion of solvers (%)	3 of 5 subjects (60%)	6 of 11 subjects (55%)
Mean session of first solution+SE	6.0+1.95	6.83+0.77

* Individual space (Erwin 1979): the average amount of space available to each individual in a group; calculated by dividing the space inside a group's enclosure (in m^2 or m^3) by the number of individuals in the group (N).

crowding effects. However, it is also possible that the smaller space in phase 2 was not sufficient to reduce social interactions, in which case the spatial change in housing between phases had no effect on the infants' learning opportunities. At this time we have no evidence to support an effect of spatial change between phases and further study is needed to evaluate the effects of spatial context on individual learning.

Method Bias

We have ambiguous support for the hypothesis that the particular form, or method, used by proficient group members would bias new practitioners towards using the same method. As predicted, most infants that solved in the crèche used the group method exclusively or for the majority of their solutions (11 of 14 infants). However, seven of those 11 infants first solved in the group setting, where only the group method of solution was available; and overall most infants that solved in the crèche preferred the method they used during their first solution (12 of 14 infants). These data suggest that the infants may have developed a response habit based on the reinforcement gained during their first solutions (e.g. see Pesendorfer et al. 2009). Although we cannot unambiguously attribute their bias for the group method of solution in the crèche to the social context, this issue does not detract from our primary finding that the social context supported the infants' learning a method of solution.

At this time, we cannot identify specific social-learning mechanisms that may have contributed to the infants' first solutions. Based on our observations during data collection, we hypothesize that stimulus enhancement, social facilitation of apparatus exploration and co-action with others at the apparatus all played a role in the method of solution the infants first used. For example, it is possible that other group members' activity with the group and/or crèche apparatuses drew the infants' attention towards specific features (i.e. the lever, spout, or wheel) prior to and following their first contact with the apparatus and their first solutions. Thus, the infants' preferences for a particular method of solution in the crèche over the period of the study was probably a product of both a supportive social context facilitating their continued interaction with the apparatus and the reinforcement (i.e. juice) gained during their first and subsequent solution(s).

Conformity to Group Norms

There is a growing interest in understanding whether conformity to group norms contributes to the maintenance of traditions within groups of animals (e.g. Whiten et al. 2005; Dindo et al. 2009; Pesendorfer et al. 2009). The development and maintenance of a tradition does not require that individuals discover all possible techniques before adopting a specific, group-common technique; rather, a tradition requires that new practitioners adopt a particular behaviour pattern due, in part, to social influences. Nevertheless, conformity may play a role in a tradition's spread and maintenance within a group. For example, Perry (2009) showed that some individuals in wild groups of white-faced capuchins in Costa Rica conform to (i.e. developed the same preferences as) other group members' preferred method of processing the *Luehea* fruit (i.e. the pounding and scrubbing methods), thus propagating the tradition in new practitioners. Similarly, in a study with captive capuchins, Dindo et al. (2009) showed that a majority of subjects preferred to use the foraging technique (one of two) that was demonstrated by a trained model. These studies imply that while many group members learn a specific behaviour pattern through a response habit formed following their initial reinforced action sequence(s), others might conform to the technique used by others. In this way, both processes may drive tradition maintenance in groups of animals.

In the present study, three subjects (Dave, Pel and Chunky) may have conformed to the group method of solution when solving in the crèche. Both Dave and Pel first solved using the nongroup method of solution in the crèche, but subsequently used the group method of solution more often in the crèche. Chunky shifted his solution preference in the crèche to match the current group method of solution (when he went from a wheel-baited group in phase 1 to a lever-baited group in phase 2). Further analysis is planned to determine how these subjects' individual and social experiences with the apparatus led to their method preferences in the crèche. Currently, however, their behaviour supports the notion that both conformity to group norms by some group members and the individuals' reinforcement histories contribute to tradition maintenance in groups of animals.

Conclusions

The present study demonstrates that social context powerfully affects young capuchins' acquisition of a foraging skill, in this case, obtaining juice from a dispensing apparatus. Results from this study support the implications from field research that wild groups of capuchin monkeys can develop behavioural traditions that are maintained over time. Furthermore, our results suggest that conformity to a single group-common technique, when more than one is available, is not likely to be the primary mechanism driving tradition maintenance in new practitioners. Rather, our results suggest that the formation of a response habit (e.g. an action sequence that is repeated because of its past reinforcement) can account for the development of most individuals' preferred technique. It seems likely that social influences (e.g. stimulus enhancement, social facilitation) contribute to an individual's development of a response habit, because they influence the occurrence of initial reinforcement. The results presented here cannot address this plausible inference, however, since our data do not account for each subject's social experiences and personal reinforcement history leading up to, and following, their first solutions.

The two-action task–two-group design is common in captive studies of traditions (see Whiten & Mesoudi 2008); however, ours is the first to track skill acquisition across two generations within social groups whose memberships stayed relatively stable over the course of the study. In addition, by employing an open diffusion paradigm, we simulated a naturalistic learning environment for young capuchins, in which youngsters explore and practise foraging skills relatively independently of their mothers. For example, young brown capuchin monkeys in Ralleighvallen, Suriname learn to harvest beetle larvae from bamboo stalks by investigating sites where larvae have been extracted by previous foragers (Gunst et al. 2008). Our experimental design differs from the commonly used observer–demonstrator paradigm, which is best employed with species that learn new skills directly through interaction with a skilled social partner, such as a parent (e.g. tamarins: Humle & Snowdon 2008; hamsters: Previde & Poli 1996; rats: Aisner & Terkel 1992; aye-ayes: Krakauer 2006; orang-utans: Jaeggi et al. 2010).

In the present study, a supportive social environment facilitated learning in young capuchins living in large, mixed-age social groups. Young individuals learned a foraging skill far more effectively in the company of proficient others than in any other circumstance. In this study, and in large social groups in general, the degree of social influence on an individual's acquisition and continued use of a particular behavioural pattern likely varies across group members and over time for each individual. How much the social context supports the acquisition and maintenance of a particular behaviour pattern depends on a variety of factors that are constantly in flux, including an individual's age, social rank, personality, the behaviour of those it associates with, and the extent to which they pay attention to what others are doing (Coussi-Korbel & Fragaszy 1995). In general, however, an individual's acquisition of a novel skill benefits from the social context through a variety of mechanisms (social facilitation, stimulus enhancement, etc.) coupled with experiences with the task at hand (e.g. Kenward et al. 2006; Humle & Snowdon 2008; Thornton & Malapert 2009).

To determine how the social context supported the infants' learning and level of proficiency at obtaining juice from the apparatus in the present study, we are currently analysing each infant's social interactions with various classes of other group members (including kin, nonkin adults and juveniles, and other infants), their individual reinforcement histories with the apparatus, and the extent to which each subject engaged in individual exploration and various types of social interactions at the apparatus (e.g. scrounging juice from others' use of the apparatus, simultaneously contacting and/or obtaining juice from the apparatus with others, and visual attention directed at others' actions with the apparatus). This analysis will help us to determine the processes underlying the infants' skill acquisition and method preferences in the crèche, and shed light on the process of tradition development and maintenance in wild capuchins.

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References

Agostini, I. & Visalberghi, E. 2005. Social influences on the acquisition of sex-typical foraging patterns by juveniles in a group of wild tufted capuchin monkeys (*Cebus nigritus*). *American Journal of Primatology*, **65**, 335–351.

Aisner, R. & Terkel, J. 1992. Ontogeny of pine cone opening behavior in the black rat, *Rattus rattus*. *Animal Behaviour*, **44**, 327–336.

Altmann, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, **49**, 227–265.

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.

Bonner, J. T. 1980. *The Evolution of Culture in Animals*. Princeton, New Jersey: Princeton University Press.

Bonnie, K. E. & de Waal, F. B. M. 2007. Copying without rewards: socially influenced foraging decisions among brown capuchin monkeys. *Animal Cognition*, **10**, 283–292.

Bonnie, K. E., Horner, V., Whiten, A. & de Waal, F. B. M. 2007. Spread of arbitrary conventions among chimpanzees: a controlled experiment. *Proceedings of the Royal Society B*, **274**, 367–372.

Coussi-Korbel, S. & Fragaszy, D. M. 1995. On the relation between social dynamics and social learning. *Animal behaviour*, **50**, 1441–1453.

Dindo, M., Thierry, B. & Whiten, A. 2007. Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proceedings of the Royal Society B*, **275**, 187–193.

Dindo, M., Whiten, A. & de Waal, F. M. B. 2009. In-group conformity sustains different foraging traditions in capuchin monkeys (*Cebus apella*). *PLoS ONE*, **4**, e7858.

Erwin, J. 1979. Aggression in captive macaques: interaction of social and spatial factors. In: *Captivity and Behavior* (Ed. by J. Erwin, T. Maple & G. Mitchell), pp. 139–171. New York: Van Nostrand Reinhold.

Fragaszy, D. M. & Perry, S. 2003. *The Biology of Traditions*. Cambridge: Cambridge University Press.

Fragaszy, D. & Visalberghi, E. 2004. Socially biased learning in monkeys. *Learning & Behaviour*, **32**, 24–35.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. & Gomes de Oliveira, M. 2004. Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, **64**, 359–366.

Galef, B. G., Jr. 1980. Diving for food: analysis of a possible case of social learning in wild rats (*Rattus norvegicus*). *Journal of Comparative and Physiological Psychology*, **94**, 416–425.

Galef, B. G., Jr. 1992. The question of animal culture. *Human Nature*, **3**, 157–178.

Gunst, N., Boinski, S. & Fragaszy, D. M. 2008. Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour*, **145**, 195–229.

Horner, V., Whiten, A., Flynn, E. & de Waal, F. B. M. 2006. Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children. *Proceedings of the National Academy of Sciences, U.S.A.*, **103**, 13878–13883.

Huffman, M. A. 1996. Acquisition of innovative cultural behaviours in nonhuman primates: a case study of stone handling, a socially transmitted behaviour in Japanese macaques. In: *Social Learning in Animals: the Roots of Culture* (Ed. by C. M. Heyes & B. G. Galef, Jr), pp. 267–289. San Diego: Academic Press.

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

Humle, T., Snowdon, C. T. & Matsuzawa, T. 2009. Social influences on ant-dipping acquisition in the wild chimpanzees (*Pan troglodytes verus*) of Bossou, Guinea, West Africa. *Animal Cognition, Supplement 1*, **12**, S37–S48.

Hunt, G. R. & Gray, R. D. 2003. Diversification and cumulative evolution in New Caledonian crow tool manufacture. *Proceedings of the Royal Society B, Supplement*, **271**, S88–S90.

Jaeggi, A. V., Dunkel, L. P., van Noordwijk, M. A., Wich, S. A., Sura, A. A. L. & van Schaik, C. P. 2010. Social learning of diet and foraging skills by wild immature Bornean orangutans: implications for culture. *American Journal of Primatology*, **72**, 62–71.

Kenward, B., Weir, A. A. S., Rutz, C. & Kacelnik, A. 2005. Tool manufacture by naïve juvenile crows. *Nature*, **433**, 121.

Kenward, B., Rutz, C., Weir, A. A. S. & Kacelnik, A. 2006. Development of tool use in New Caledonian crows: inherited action patterns and social influences. *Animal Behaviour*, **72**, 1329–1343.

Krakauer, E. B. 2006. Development of aye-aye (*Daubentonia madagascariensis*) foraging skills: independent exploration and social learning. Ph.D. thesis, Duke University.

Leca, J. B., Gunst, N. & Huffman, M. A. 2007. Japanese macaque cultures: inter- and intra-troop behavioural variability of stone handling patterns across 10 troops. *Behaviour*, **144**, 251–281.

Leca, J. B., Gunst, N. & Huffman, M. A. 2010. Indirect social influence in the maintenance of the stone handling tradition in Japanese macaques (*Macaca fuscata*). *Animal Behaviour*, **79**, 117–126.

Meunier, H., Petit, O. & Deneubourg, J. L. 2008. Social facilitation of fur rubbing behaviour in white-faced capuchins. *American Journal of Primatology*, **70**, 161–168.

O'Malley, R. C. & Fedigan, L. M. 2005a. Evaluating social influences on food-processing behaviour in white-faced capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, **127**, 481–491.

O'Malley, R. C. & Fedigan, L. M. 2005b. Variability in food-processing behavior among white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. *American Journal of Physical Anthropology*, **128**, 63–73.

Ottoni, E. B. & Izar, P. 2008. Capuchin monkey tool use: overview and implications. *Evolutionary Anthropology*, **17**, 171–178.

Panger, M. A., Perry, S., Rose, L., Gros-Louis, J., Vogel, E., MacKinnon, K. C. & Baker, M. 2002. Cross-site differences in foraging behaviour of white-faced capuchins (*Cebus capucinus*). *American Journal of Physical Anthropology*, **119**, 52–66.

Perry, S. 2009. Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). *Animal Cognition*, **12**, 705–716.

Perry, S., Baker, M., Fedigan, L., Gros-Louis, J., Jack, K., MacKinnon, K. C., Manson, J. H., Panger, M., Pyle, K. & Rose, L. 2003. Social conventions in wild white-faced capuchin monkeys: evidence for traditions in a Neotropical primate. *Current Anthropology*, **44**, 241–268.

Pesendorfer, M. B., Gunhold, T., Schiel, N., Souto, A., Huber, L. & Range, F. 2009. The maintenance of traditions in marmosets: individual habit, not social conformity? A field experiment. *PLoS ONE*, **4**, e4472.

Previde, E. P. & Poli, M. D. 1996. Social learning in the golden hamster (*Mesocricetus auratus*). *Journal of Comparative Psychology*, **110**, 203–208.

Rendell, L. & Whitehead, H. 2001. Culture in whales and dolphins. *Behavioural and Brain Sciences*, **24**, 309–382.

van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M. 2003. Orangutan cultures and the evolution of material culture. *Science*, **299**, 102–105.

Terkel, J. 1996. Cultural transmission of feeding behavior 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.

Thornton, A. & Malapert, A. 2009. The rise and fall of an arbitrary tradition: an experiment with wild meerkats. *Proceedings of the Royal Society B*, **276**, 1269–1276.

Visalberghi, E. & Addessi, E. 2003. Food for thought: social learning about food in capuchin monkeys. In: *The Biology of Traditions* (Ed. by D. M. Fragaszy & S. Perry), pp. 187–212. Cambridge: Cambridge University Press.

Visalberghi, E. & Fragaszy, D. 1995. The behaviour of capuchin monkeys, *Cebus apella*, with novel food: the role of social context. *Animal Behaviour*, **49**, 1089–1095.

Whiten, A. & Mesoudi, A. 2008. Establishing an experimental science of culture: animal social diffusion experiments. *Philosophical Transactions of the Royal Society of London, Series B*, **363**, 3477–3488.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E. G., Wrangham, R. W. & Boesch, C. 1999. Culture in chimpanzees. *Nature*, **399**, 682–685.

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.

Whiten, A., Horner, V. & de Waal, F. B. M. 2005. Conformity to cultural norms of tool use in chimpanzees. *Nature*, **437**, 737–740.

Whiten, A., Spiteri, A., Horner, V., Bonnie, K. E., Lambeth, S. P., Schapiro, S. J. & de Waal, F. B. M. 2007. Transmission of multiple traditions within and between chimpanzee groups. *Current Biology*, **17**, 1038–1043.

van Wolkenten, M. L., Davis, J. M., Gong, M. L. & de Waal, F. B. M. 2006. Coping with acute crowding by *Cebus apella*. *International Journal of Primatology*, **27**, 1241–1256.