

Research

Social traditions and social learning in capuchin monkeys (*Cebus*)

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Capuchin monkeys (genus *Cebus*) have evolutionarily converged with humans and chimpanzees in a number of ways, including large brain size, omnivory and extractive foraging, extensive cooperation and coalitionary behaviour and a reliance on social learning. Recent research has documented a richer repertoire of group-specific social conventions in the coalition-prone *Cebus capucinus* than in any other non-human primate species; these social rituals appear designed to test the strength of social bonds. Such diverse social conventions have not yet been noted in *Cebus apella*, despite extensive observation at multiple sites. The more robust and widely distributed *C. apella* is notable for the diversity of its tool-use repertoire, particularly in marginal habitats. Although *C. capucinus* does not often use tools, white-faced capuchins do specialize in foods requiring multi-step processing, and there are often multiple techniques used by different individuals within the same social group. Immatures preferentially observe foragers who are eating rare foods and hard-to-process foods. Young foragers, especially females, tend to adopt the same foraging techniques as their close associates.

Keywords: capuchins; social traditions; social conventions; *Cebus*; social learning

1. INTRODUCTION

The quest to explain the evolutionary roots of human culture requires detailed comparative data on behavioural variation in populations of wild non-human species, along with data on the mechanisms that could potentially give rise to this variation. The best comparative datasets on behavioural diversity in wild populations within the order Primates currently come from two ape genera: (chimpanzees, *Pan troglodytes* [1,2], and *Pongo*, orangutans [3,4]), one Old World monkey species (Japanese macaques, *Macaca fuscata* [5,6]), and one New World monkey genus (*Cebus*, capuchin monkeys: *Cebus capucinus* [7], and *Cebus apella* [8,9]). This article will focus on capuchin researchers' discoveries from the past two decades.

Capuchins are interesting for social-learning research because they exhibit many of the characteristics suggested as crucial for the emergence of material culture [10]: they are highly gregarious [9], and exhibit remarkable degrees of social tolerance while feeding [9,11], thereby enabling regular exposure of naive individuals to models. Capuchins are long-lived (up to 55 years in captivity [12]) and develop slowly, reaching maturity at 5.5–8 years in females and 6–10 years in males [9] (S. Perry 1990–2010, unpublished data); thus, they have much time to acquire and use socially

acquired information. *Cebus* has one of the largest brain sizes relative to body size of any primate [13] and generally excels at cognitive tasks [9]. Therefore, this genus is expected to be good at problem-solving, though opinions regarding the genus' capacity for imitation are mixed [9,14–16]. Capuchins are omnivores specializing in extractive foraging [9,17], so the foraging tasks they routinely need to solve are complex; therefore, it might be expected that they would benefit by having social cues to guide the acquisition of their foraging skills [18].

In this paper, I review and synthesize findings about two broad categories of traditions: (i) socially transmitted group- or dyad-specific forms of social interaction, and (ii) foraging (food choice and food processing) behaviours. Although the theoretical predictions regarding which species should exhibit material culture are fairly clear [10], it is less clear what factors should predict the emergence of social communicative rituals, and this is also a topic of great interest for researchers interested in explaining the emergence of human culture. It might be argued that group-specific communicative rituals would be expected in those species that rely extensively on coalitionary aid, and therefore need to communicate more about their position in a complex society of shifting alliances. In this case, *C. capucinus* (though possibly not *C. apella*) is a prime candidate to have social conventions, because these monkeys form coalitions in a wide variety of contexts and are highly dependent on allies in order to successfully migrate, acquire high rank and defend their offspring from infanticidal males [9,11].

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One contribution of 26 to a Discussion Meeting Issue 'Culture evolves'.

Whereas there are some questions regarding the mechanisms of social learning and the cognitive potential to learn in various ways that can only be investigated in a captive experimental setting, there are other issues regarding cultural evolution that can be addressed only by observing wild animal populations. For example, even if we know that animals are capable of acquiring traits socially, we still need to know to what extent this really happens in nature, and what factors in a species' natural range of circumstances promote a reliance on social learning and affect the choice of the demonstrator to attend to. In order to understand the population dynamics of culture change, it is also important to have empirical data on the speed and fidelity with which traits are transmitted within and between groups living in natural conditions, and how this varies according to ecology, demographics, social dynamics and the utility of the trait in question.

2. SOCIAL CONVENTIONS

(a) *Social conventions in C. capucinus*

Most research on non-human animal traditions has focused on foraging skills rather than on group-specific communicative rituals [3,6,19]. However, human cultures are rich in social conventions, i.e. in social rituals that are unique to particular groups or cliques, and it is arguably the case that, relative to other species, humans devote a far greater portion of their cultural repertoire to these group-specific ways of conducting social interactions than to group-specific subsistence behaviours. Despite this, far less research has been devoted to social conventions than to foraging-related traditions in the animal literature, perhaps because the former are rarer in most species' repertoires.

White-faced capuchins are noteworthy for their innovative gestural repertoires. A comparative study was conducted of four populations of *C. capucinus* dwelling in tropical dry forest sites in Costa Rica, using the 'group contrasts' method [20]. In this study, social rituals were deemed to qualify as traditions if (i) they were common in some groups or sites (i.e. seen at a rate of at least once per 100 h) and never seen in other groups that had been studied for at least 250 h, (ii) the behaviour was observed to spread to additional group members over time, and (iii) it was durable, remaining in the behavioural repertoire for at least six months. According to these criteria, five behaviour patterns qualified as true traditions: (i) hand-sniffing (inserting one's fingers in or on the nostrils of the partner, often mutually, for prolonged periods of time), (ii) prolonged sucking of body parts, and (iii) three 'games', in which one partner bites firmly on something belonging to the other partner (a finger, a tuft of hair that has been bitten out of the face or shoulder or an inanimate non-edible object or 'toy') and the other partner works to retrieve the object, with the two partners frequently switching in the biting and retrieving roles. Since the publication of these results [20], another apparent bond-testing ritual, 'eye-poking' (the insertion of a partner's finger into one's own eye socket up to the first knuckle), has entered one group's repertoire and spread throughout

the group, persisting after the death of its innovator though at low frequencies.

Table 1 documents the occurrence of particular social conventions across groups. Table 1 makes two important points: (i) all of these odd behaviours have been invented in multiple groups, and (ii) none of these behaviours is seen in all groups: they are present and are common in 2–8 of the 18 study groups, and completely absent in 4–10 of the well-studied groups. Table 2 provides more detail on temporal variation in the frequency (occurrence/unit time) and popularity (number of performing individuals and dyads) of one illustrative tradition: hand-sniffing. For example, in the FF group in 2004, hand-sniffing was observed between five and six times per 100 h of observation, and was practised by 40 dyads that included a total of 18 individuals. Note that even in groups exhibiting hand-sniffing, it goes in and out of fashion. Further details on the methods, the dataset and the interpretation of the results are presented in the electronic supplementary material.

(b) *Hypothesized function of C. capucinus social conventions*

Whereas it is easy to understand how tool use and food choices impact fitness, it is less easy to understand exactly what is being accomplished by engaging in odd social rituals. Because non-participants seem uninterested in observing these rituals, and they typically occur on the periphery of the group, it seems unlikely that they function to display the quality of the performers' social relationship to third parties. Thus far, the available evidence best fits the hypothesis that these rituals function to test the quality of social bonds. Zahavi [21] has suggested that behaviours involving discomfort or risk can serve this function. In his verbal model, an actor imposes a small cost on a bond partner (the recipient). A tolerant or enthusiastic response from the recipient reliably signals the actor that s/he is in good standing with the recipient, whereas an aversive response reliably signals that the actor is in poor standing with the recipient. Thus, the same behaviour can elicit pleasurable or aversive responses, depending on the quality of their past interactions. The bond-testing hypothesis has been advanced to explain male–male greetings, including risky genital manipulation, in savannah baboons [22]. Sociologists have developed parallel arguments applicable to humans. For example, Collins [23] has argued that an important purpose of human conversations is for the interaction partners to convey to one another, via tone of voice, posture, eye contact and degree of enthusiasm, how committed they are to their relationship relative to relationships of other dyads in the coalitional structure of the community. So, the precise verbal content of the conversation is not necessarily as meaningful as the non-verbal components that convey affect, except in the way in which the text of the conversation meaningfully references aspects of their social relationship (e.g. by referring to knowledge that is specific to their friendship, or things they have done together). Some human rituals, such as Yanomamö greetings at the start of feasts, and

Table 1. Distribution of *C. capucinus* social conventions across study sites and social groups in Costa Rica. C, the behaviour is common (i.e. seen at a rate of >1/100 h) during at least 1 year the group was studied; R, the behaviour was seen anecdotally; X, the behaviour was never seen in >250 h of observation (see the table in the electronic supplementary material for number of hours each group was observed); ?, the behaviour was never seen, but the group was studied for <250 h. Site names: SR, Santa Rosa; LB, Lomas Barbudal; PV, Palo Verde; CU, Curú.

site name-group name	hand-sniffing	eye-poking	sucking	finger game	hair game	toy game
SR-SE	C	?	?	?	?	?
SR-CP	C	X	X	X	X	X
SR-LV	R	X	R	X	X	X
SR-NA	X	X	X	X	X	X
SR-CA	?	?	C	?	?	?
SR-CU	C	?	C	?	?	?
SR-BH	X	X	R	X	X	X
LB-AA	C	R	C	C	C	C
LB-FL	C	R	R	C	C	C
LB-RR	R	X	C	R	R	R
LB-MK	X	X	R	X	X	X
LB-CU	X	X	X	X	X	X
LB-FF	C	R	R	R ^a	X	X
LB-RF	C	R	X	X	X	X
LB-NM	?	?	?	?	?	?
PV-LT	?	?	?	?	?	?
PV-ST	C	X	R	X	X	X
CU-BE	X	X	R	X	X	C

^aRare variant using tail rather than finger.

Newfoundland ‘mumming’ rituals, in which one group feigns an attack on the other party, who remains deliberately vulnerable, have been explained as ‘rituals of trust’ [24] according to the logic of Zahavi’s bond-testing theory.

Why construct dyad-specific bond-testing behaviours? Other putative bond-testing behaviours do not involve innovative (and therefore easily misunderstood) behaviours—e.g. grooming, and non-conceptive sexual interactions, both of which are common throughout the order Primates. Like *C. capucinus* social conventions, these stereotyped signals (i) entail risk of injury as one party exposes vulnerable body parts to another individual whose actions s/he cannot necessarily visually monitor, and (ii) force individuals to signal partner preferences by allocating scarce social time [25]: if A is grooming B, s/he cannot simultaneously be grooming individual C. I speculate that dyad-specific rituals entail a ‘start-up’ time cost in addition to a risk cost and the time cost of each ritual performance, and are therefore more reliable signals than species-typical social behaviours such as grooming. The time costs (months, in some cases—S. Perry 1990–2010, unpublished data) required for partners to co-develop the particular elements of a social ritual are non-transferable to another dyadic relationship, and therefore strongly indicate degree of commitment to a particular relationship. Analogously, human romantic couples, friend dyads and parent–offspring dyads often devise dyadic-specific rituals (e.g. particular bedtime or mealtime rituals). If a couple breaks up and the two individuals go on to form new partnerships, they do not generally transfer these rituals to the new relationships, but rather, they form new rituals with the new partner. Further discussion of the probable function and design features of capuchin bond-testing signals can be found in Perry *et al.* [20].

Assuming that the apparent lack or at least rarity of social conventions for the purpose of bond-testing in most species is not an artefact of methods, but a true feature of their behavioural biology, why is it that white-faced capuchins have such a rich repertoire of such behaviours? It may be the case that coalitions are far more common, and also more important for maximizing fitness, in *C. capucinus* than in most species. Certainly, *C. capucinus* has one of the highest rates of coalitionary lethal aggression of conspecifics found in a mammal [11,26] and coalitions are employed in a wide range of contexts [11,27,28]. The greater importance of alliances may necessitate a richer source of information about whom to trust.

3. SOCIAL LEARNING OF FOOD CHOICE: EXPERIMENTAL AND FIELD STUDIES

Capuchin foragers are unusually tolerant of frequent, close-range observations of other group members while they are eating, even permitting frequent scrounging. Perhaps because of this, *C. apella* is one of the best-studied primate species with regard to the issue of social learning about food (see [9] for a review). Experimental studies of captive animals indicate that the presence of foraging conspecifics facilitates sampling of novel foods, but that observers’ behaviour is not affected by the specific properties of the food eaten by the observed foragers [29,30]. Thus, it has been argued that capuchins do not pay close attention to the specific properties of foods eaten by others, but instead learn what to eat by coordinating their foraging in space and time (which, in the wild, would generally result in their eating the same items as group-mates). No analogous research has been done on *C. capucinus*, but the evidence from observational studies in the wild suggests a different view. For example, wild

Table 2. Temporal distribution of hand-sniffing in eight groups of monkeys at Lomas Barbudal. Cell values indicate (separated by commas) rate of hand-sniffing in ad libitum observation hours, number of individuals practising hand-sniffing and number of dyads practising hand-sniffing. ‘Dash’ indicates that no observations were conducted on that group in that year. For rate of hand-sniffing, 0, not observed, R, observed at a rate of <1 time/100 h and C means ‘common’, with the number after the C indicating the approximate rate. C1, seen at a rate of 1–2×/100 h; C2, seen at a rate of 2–3×/100 h, etc.

year	AA	FL	RR	MK	CU	FF	RF	NM
1990	0,0,0	—	—	—	—	—	—	—
1991	C1,4,3	—	—	—	—	—	—	—
1992	C5,10,13	—	—	—	—	—	—	—
1993	C4,12,12	—	—	—	—	—	—	—
1994	C1,1,1(?)	—	—	—	—	—	—	—
1995	C1,4,3	—	—	—	—	—	—	—
1996	?	—	—	—	—	—	—	—
1997	C1,7,6	—	0,0,0	—	—	—	—	—
1998	0,0,0	—	0,0,0	—	—	—	—	—
1999	0,0,0	—	0,0,0	—	—	—	—	—
2000	0,0,0	—	0,0,0	—	—	—	—	—
2001	0,0,0	—	0,0,0	—	—	—	—	—
2002	R,16,16	—	R,4,2	—	—	—	—	—
2003	R,14,15	0,0,0	R,2,1	—	—	C2,15,20	—	—
2004	R,7,6	C2,5,4	R,2,1	0,0,0	—	C5,18,40	—	—
2005	R,2,1	C1,5,4	R,2,1	0,0,0	—	C3,12,18	—	—
2006	R,2,1	C1,3,3	0,0,0	0,0,0	—	C3,13,21	—	—
2007	R,8,5	R,6,4	0,0,0	0,0,0	0,0,0	C3,11,17	R,2,1	—
2008	0,0,0	C1,8,6	R,2,1	0,0,0	0,0,0	C3,13,13	C2,4,3	0,0,0

white-faced capuchins are more likely to target a forager for close-range observation (‘peering’ at a range of less than 10 cm) if the forager is consuming an item that is rare in the diet, suggesting that they are more interested in watching the consumption of foods they do not already know about [17]. Captive *C. apella* infants were more prone to show close-range interest in a forager’s food if the food were novel rather than familiar, though they were just as likely to peer at others eating the novel food after trying it as they were before tasting it [31]. Thus, the function of close-range ‘food interest’ remains controversial (but see below).

4. SOCIAL LEARNING OF FOOD-PROCESSING TECHNIQUES: EXPERIMENTAL AND FIELD STUDIES

(a) What do capuchins learn from close-range observation of food processing?

Another hypothesis about food interest/peering is that the monkeys need to observe at close range in order to learn details of food-processing techniques. Wild *C. capucinus* preferentially target foragers for close-range observation when they are feeding on foods that require two or more steps to process [17], and this result is not accounted for by differences in handling time (and hence observation opportunity) between the types of foods. Free-ranging *C. apella* preferentially observe the most skilled nut-cracking individuals [32]¹, which could either indicate that they know who is best at nut-cracking and want to learn these skills, or that they have figured out that certain individuals obtain food more quickly and hence provide better scrounging opportunities. While these studies show that individuals are structuring their learning opportunities in a way that could

enhance their knowledge, they do not show what is actually learned.

Early studies of the effects of observation opportunities on skill acquisition (reviewed in [9]) failed to produce much evidence that captive capuchins attend to the relevant details of observed food procurement tasks, even when allowed up to 75 observation opportunities of skilled demonstrators [33]. Later studies employed a two-action method in which an artificial fruit could be opened in one of two ways, and two groups of experimental subjects were exposed to a demonstrator who opened it in only one way. Custance *et al.*’s [14] study of human-reared capuchins and human demonstrators produced mixed results, whereas a more recent set of two-action studies, using a transmission chain design in which capuchins observed other capuchins, found much firmer evidence for faithful transmission [15,16]. These researchers drew on the idea that the quality of social relationship between the demonstrator and the observer will affect the fidelity of transmission, such that dyads with close affiliative relationships will have an inherent desire to behave similarly (i.e. the bonding- and identification-based observational learning model [34,35]). To facilitate tranquil, close-range observations of the demonstrations, demonstrator-observer pairs were restricted to those that had high rates of proximity and grooming and low tendencies to displace one another while co-feeding, and the demonstrator was slightly higher ranking, so that the observer would not disrupt demonstrations. The alpha male and alpha female were trained by humans in one of the two possible techniques for opening the fruit (lifting or sliding). Then they were allowed to demonstrate to another group member until satiated, at which point the observer had the opportunity to operate the apparatus. Monkeys were tested, pairwise, in this

fashion, until there were five links in the transmission chain for lifting and four links for sliding. At the end of the study, the sixth monkey in the 'lifting' transmission chain was using lifting 95 per cent of the time, and the fifth monkey in the 'sliding' chain was using sliding 90 per cent of the time, whereas there was 100 per cent fidelity in transmission up until the last link in both chains [15]. Another study [16] trained two alpha males in two different techniques for opening a fruit and then reintroduced these males to their groups as demonstrators. In both groups, the group members preferentially adopted the technique used by the alpha male, even though 81 per cent also discovered the alternative technique. The degree of conformity obtained in these studies is much higher than that seen in wild groups of *C. capucinus* (§4d), and this is most probably due to the care taken by Dindo *et al.* in choosing the demonstrator according to rank and tolerance of other group members in the two studies.

In a study conducted by de Waal & Bonnie [35] on *C. apella*, subjects first observed a model open one of three boxes, and then were given a chance to choose a box to open themselves. Dyads that had above-average 'relationship quality indices' (RQIs: relative hourly rates of exchanged grooming and resting in contact, divided by the relative hourly rate of dyadic agonism and aggression) were more prone to copy one another's choice of box to open than were dyads with below-average RQIs, at least in trials where the model's choice (but not the subject's) was rewarded [35].

It is likely that quality of social relationship also plays a factor in the desire of wild monkeys to copy one another, but in observational studies of wild animals, there is no way to control who has observational access to whom, or who demonstrates what techniques. So for most wild populations, the subset of practitioners of technique A will include both tolerant and intolerant dyads, as will the group consisting of practitioners of technique B.

(b) Interpopulation variation in food-processing techniques in the wild

Capuchin monkeys exhibit between-population variation in food-processing techniques. *Cebus apella* create tool kits, some quite elaborate, which vary between sites in their size and composition (§5). But even *C. capucinus*, which rarely employs tools, displays between-group differences in the specific techniques used to process those foods that are part of the diet at multiple sites not connected by forest corridors [36]. In our comparison of four white-faced capuchin sites, all in tropical dry forest, we found that 20 of the 61 foods that were common to the diet at multiple sites were processed differently at different sites. In 17 of the 20 cases, the difference simply involved the use of a species-typical action (pounding, scrubbing, tapping and, in rare cases, a fulcrum action) to a food type at one site but not at another. All these actions were seen at all four sites, but they were not employed in the same contexts everywhere. A few more elaborate foraging practices (e.g. following army ants to catch the prey they flush up) were seen at some sites but not others.

It is difficult to attribute between-group differences in food processing to social learning, because even

small ecological differences between sites could lead to differences in foraging behaviour (e.g. chimpanzees create longer ant-dipping sticks to forage on species of ants that are more aggressive or have more painful bites [37]). When there is homogeneity within groups and heterogeneity between groups, it is impossible to know whether members of the same group have converged owing to social-learning processes, or whether all group members are independently using trial-and-error learning to adapt to the same ecological constraints. It is easier to infer a role of social learning if there is within-group variation in a trait, and the patterning of variation can be compared with the association patterns within the group, to see whether closer associates are more likely to share techniques.

(c) Cross-sectional studies of association patterns and shared food-processing techniques in the wild

Several researchers have investigated whether those individuals who more frequently associate with one another are also more prone to share the same foraging techniques (see the electronic supplementary material for a table summarizing these results). At Palo Verde National Park, performers of rare techniques (e.g. rubbing mangoes, or pounding *Annona* or *Randia* fruits) had mean dyadic proximity scores that were significantly higher than the mean proximity scores for dyads that did not share the same food-processing technique [36]. The capuchins of Santa Rosa National Park who shared the trait of pounding *Luehea candida* fruits had significantly higher mean dyadic proximity indices than dyads that did not exhibit that technique [38]. At Lomas Barbudal, monkeys who spent more time associating were significantly more likely to share the same technique for processing *Sloanea terniflora* fruits [17]. A study of wild *Cebus albifrons* [39] yielded mixed evidence for a positive effect of association time on sharing of techniques, depending on the analytical technique used and the types of food-processing tasks included in the analysis. Indeed, several studies have found non-significant or marginally significant trends towards associations between capuchin proximity patterns and shared food-processing techniques [36,38,39] (S. Perry 2001–2010, unpublished data). These mixed results may be attributable to the studies' cross-sectional designs: the subjects may have acquired their food-processing techniques while young, before acquiring their current social networks. This is almost certainly true of adult males, who have emigrated from their natal groups. Thus, it would be surprising to find strong effects of adult proximity patterns on techniques employed. A longitudinal design, focusing on the early years of development, is better suited to capturing meaningful relationships between proximity (and hence social-learning opportunity) and techniques acquired.

(d) Longitudinal study of association patterns and shared food-processing techniques in the wild

Thus far, only one longitudinal study has examined the acquisition of foraging strategies in wild *Cebus* [40].

In this study, 48 immature individuals (21 females, 27 males) from three social groups were studied for a period of 7 years, covering the first 5 years of their development. The trait documented was the manner in which *L. candida* fruits were processed in order to extract the tiny seeds from the woody capsule in which they were embedded. *Luehea* is a food that is consumed at all three sites in Costa Rica where *C. capucinus* has been studied, and at all sites, the monkeys employ multiple techniques to obtain the seeds [17,38,41]. In their first year of life, infants simply pluck loose seeds from the end of the capsule. In their second year of life, they experiment with a variety of techniques, some efficient and some non-efficient. Gradually over the next few years, they narrow their range of techniques used until they settle on a single predominant technique, usually by age 5 years. There are two common techniques used by adults, pounding and scrubbing, which do not differ significantly in their efficiency. The proportions of pounding and scrubbing used vary according to social group. The main goal of this study was to examine the correspondence between the techniques observed by foraging individuals with the techniques they actually practised in any given *Luehea* season. Data on the techniques practised were collected on all group members, regardless of whether they were part of the developmental study, and information on gaze direction and proximity to other *Luehea* foragers was also noted.

The mother was presumed to be an important demonstrator for her young, and so observations of maternal technique were analysed both separately from, and jointly with, observations of other group members. The independent variable in the regression model was the proportion of *Luehea*-processing events observed that were pounding, as opposed to scrubbing. The outcome variable, 'practised technique', was the proportion of the focal animal's processing events that were pounding (i.e. the number of pounded fruits, divided by the sum total of fruits pounded plus fruits scrubbed). Regardless of whether the independent variable in the regression model was observations of maternal technique, non-maternal technique or both combined, females exhibited a highly significant impact of observed technique on practised technique for each of the first 5 years, showing the greatest impact (3.85% change in the proportion of pounding practised resulting from a 1% change in the observed technique, for maternal and non-maternal influence combined) during the second year of development. Males exhibited the same pattern, but to a far lesser extent, rarely attaining significance. With respect to maternal influence, males showed a significant impact ($p \leq 0.05$) of maternal technique observed upon male technique practised only in years 2 and 5. Overall, averaged across the 5 years of development, females exhibited a 2.79 per cent change in proportion of pounding practised resulting from a 1 per cent change in observed maternal and non-maternal techniques combined (s.d. = 0.49, $p < 0.0001$), whereas males exhibited only a 1.45 per cent change (s.d. = 0.34, $p < 0.0001$) [40].

Examining only the data on the most recent year available for *Luehea* processing, for all 106 individuals

in the population for which maternity data were available, it was found that the 48 females were significantly likely to use the maternal technique, whereas the 58 males were not (Fisher's exact, $p = 0.002$ for females, $p = 0.18$ for males) [40].

It was not clear what factors caused the sex difference in tendency to conform. Males and females spent equal amounts of time in proximity to their mothers, and equal amounts of time alone, which suggests that their overall exposure to models did not differ [40]. The one available developmental study of chimpanzee terming [42] found that sex differences in conformity to maternal tool style were probably due to differences in visual attention to the mother, rather than to the amount of time in proximity to her. But male and female capuchins devoted equal amounts of time to actively observing the techniques of foraging neighbours, both when neighbours were foraging on *Luehea* and when they were foraging on other foods [40]. According to de Waal's BIOL model [34], individuals will have an intrinsic desire to copy the behaviour of individuals with whom they have strong social bonds.² It may be that females, being the philopatric sex in this species, are more motivated to copy group-mates than males are, since males migrate multiple times and hence do not form lifelong alliances with group-mates. Female-female dyads groom and affiliate at higher rates than do male-male dyads, with male-female dyads typically showing intermediate values [11,43]; these data, as well as data on the patterning of aggression in this species, indicate that females typically have more affiliative relationships and fewer conflictual relationships in their social groups than males do. Studies of captive brown capuchins have found that observing a model collect a reward does not influence the tendency to copy, nor is it necessary for the subject to obtain a reward in order to copy a model [44]. In the *Luehea*-processing study, subjects seemed capable of learning both techniques via trial-and-error learning, and there was no advantage to learning one technique over another, yet they still conformed to the technique they saw most [40].

5. EXPLAINING THE DIFFERENCES BETWEEN *C. CAPUCINUS* AND *C. APELLA* IN SOCIAL CONVENTIONS AND TOOL-USE TRADITIONS

In the past few years, there has been an explosion of research on the behavioural diversity of *C. apella* at numerous sites throughout South America (see [8] for a recent review of tool use at 29 sites, and [9] for a review of tool use in both captive and field settings for all capuchin species). Although there is currently no evidence for traditional bond-testing rituals at any of these *C. apella* sites (P. Izar 2010, personal communication), there are numerous reports of traditions involving tool use [8]. Monkeys at 10 of these sites exhibit no tool use, though they do engage in complex object manipulations while foraging. At 12 sites, tool use is reported anecdotally; at six, stone tool use for nut-cracking is customary, and the monkeys at one site (Serra de Capivara) use an elaborate tool kit including many types of stone tools as well as stick

tools [8,45,46]. *Cebus capucinus* has a far more impoverished tool-use repertoire, with no customary tool use reported for any site, and only scattered anecdotes from individual monkeys (e.g. use of a club to kill a snake [47]; wrapping of hairy fruits and caterpillars in leaves [36]). It is not yet entirely clear whether there is a species difference with regard to propensity to create tools and test social bonds, or whether the apparent differences between species in the frequency and types of traditions formed are due to differences in ecology. Tool use in *C. apella* is far more frequent in the arid savannah sites, where monkeys are often on the ground foraging on hard foods such as palm nuts and have ready access to stones. Although all of the well-studied sites for *C. capucinus* are in dry forest, most have ready access to water, and there are plenty of foods available that do not require tools to open. On the other hand, experiments done on captive *C. apella* and *C. capucinus* in equivalent housing conditions suggest that *C. apella* spontaneously engages in more complex object manipulations (combining an object with a substrate, or combining two objects together) and is less neophobic about handling new objects, relative to *C. capucinus* [48]. It may be the case that there are both ecological factors and evolved psychological dispositions contributing to the observed differences between species and populations of capuchins. Most studies of *C. apella* report that coalitionary aggression is less common than in *C. capucinus* [9,49], which could explain why there is a greater need to test the quality of social bonds in *C. capucinus*.

6. EXPLAINING THE POPULATION DYNAMICS OF SOCIAL TRANSMISSION OF BOND-TESTING RITUALS AND FORAGING TRADITIONS

Useful foraging traditions (e.g. nut-cracking in chimpanzees [50] and brown capuchins [51]) persist in a fairly stable form for many generations, even long enough to leave an archaeological record. In contrast, capuchin social conventions are not transmitted with high fidelity and are fairly transient in group repertoires (table 2). They typically last no longer than 10 years and are rarely, if ever, transmitted beyond three links in a social transmission chain before going extinct [20]. In this way, they are similar to human fads, though the reason for the transience is somewhat different in the two cases. In both dyadic bond-testing rituals and human fads (in which multiple individuals conform to the same behaviour), the specific content (e.g. what specific motor patterns are used to inflict discomfort in capuchin bond-testing rituals, or what dances or clothing styles are currently fashionable) is to some extent arbitrary. It does not matter whether it is a finger or a toy that is extracted from the partner's mouth, any more than it matters whether people wear lace or ruffles on their dress hems. What matters is that some sort of cost (in time or money) is being expended in order to assert a particular role in the social structure. In the case of the dyadic bond-testing signals, part of what is being tracked is the mutual devotion to developing the dyad-specific ritual, and so it is important that each dyad exhibits somewhat different twists

on these general themes, and that it takes much time to construct a ritual that is mutually satisfying to both members of the dyad. This argument builds on Dunbar's [25] hypothesis that the preferential allocation of limited social (grooming) time reliably signals commitment to allies. So, whereas multiple dyads in the same group may be hand-sniffers, each dyad differs somewhat with regard to (i) where they insert their fingers (into the eye, mouth or nose), (ii) whether they grip one another's hands while they do it, and (iii) what postures they assume (with some partners clutching a particular body part with a free hand). In the case of human fashions, the purpose of adopting a fashion is not to test a dyadic relationship, but rather to advertise identification and/or membership in a group: it is important to be current in tracking what the high-prestige set of people is doing. High-status signals would lose their value if they remained static, because everyone would have time to conform; whereas if they shift constantly, only the wealthy and well-connected can rapidly conform [52,53]. In contrast, greater stability is expected for foraging traditions, because certain techniques or tool forms are more useful at obtaining high foraging returns than others, and so there will be selection for keeping useful variants in the repertoire.

The capuchin bond-testing rituals were practised chiefly by adults. Young animals typically became regular practitioners of hand-sniffing or eyeball-poking only when they reached adolescence at Lomas Barbudal. Game-playing started somewhat earlier, as early as age 1, but most often included one adult practitioner. New bond-testing rituals could be acquired in adults of any age, as individuals remained creative and flexible regarding their gestural repertoires for their entire lives. In contrast, foraging techniques in the Lomas Barbudal population were acquired at a young age, and the greatest social influence upon the acquisition of these techniques occurred during the first 3 years. For *Luehea* processing in *C. capucinus*, the technique that predominated at age 5 remained the dominant technique (i.e. the technique used more than 95% of the time) for the rest of the animal's life.

7. CONCLUSIONS

Research on social learning in capuchins has yielded ample evidence for traditions in wild populations as well as evidence for various social-learning mechanisms in captive *Cebus*. There appear to be species differences in the propensities to create different types of traditions, with *C. apella* showing a greater propensity for material culture (especially in marginal habitats) and the more coalition-oriented *C. capucinus* developing more social conventions, apparently for the purpose of testing social bonds. Capuchins selectively observe models best capable of conveying knowledge they lack. They converge behaviourally with those whom they observe, particularly if they have high-quality relationships with the models. Thus far, there is no evidence that capuchins exhibit complex cumulative culture, social norms or ethnic markers.

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ENDNOTES

¹There is a correlation between observation and proficiency of target, but not between nut-cracking frequency and proficiency.

²The reverse is also true: capuchins are more affiliative to humans who copy them [54].

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