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Semi-wild chimpanzees open hard-shelled fruits differently across communities

Bruce Rawlings · Marina Davila-Ross · Sarah T. Boysen

Abstract Researchers investigating the evolutionary roots of human culture have turned to comparing behaviours across nonhuman primate communities, with tool-based foraging in particular receiving much attention. This study examined whether natural extractive foraging behaviours other than tool selection differed across nonhuman primate colonies that had the same foods available. Specifically, the behaviours applied to open the hard-shelled fruits of *Strychnos* spp. were examined in three socially separate, semi-wild colonies of chimpanzees (*Pan troglodytes*) that lived under shared ecological conditions at Chimfunshi Wildlife Orphanage, and were comparable in their genetic makeup. The chimpanzees ($N = 56$) consistently applied six techniques to open these fruits. GLMM results revealed differences in the number of combined technique types to open fruits across the colonies. They also showed colony differences in the application of three specific techniques. Two techniques (full biting and fruit cracking) were entirely absent in some colonies. This study provides empirical evidence that natural hard-shelled fruit-opening behaviours are distinct across chimpanzee colonies, differences that most likely have not resulted from ecological and genetic reasons.

Keywords Chimpanzee · Extractive foraging · Hard-shelled fruits · Culture · Social learning

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Introduction

To augment the understanding of the origins of human culture, scientific research has paid particular attention to wild nonhuman primate communities and their extractive foraging behaviours, such as using tools for cracking nuts or harvesting insects (Whiten et al. 2001; Biro et al. 2003; Schoning et al. 2008). The traditional approach here has been the method of exclusion where specific behaviours present in one primate community, but absent in others, have led researchers to claim socially learned traditions in nonhuman primates (Whiten et al. 2001, 1999; Schoning, et al. 2008; van Schaik et al. 2003; van Schaik and Knott 2001). Critics, however, argue that such reports of population-specific foraging behaviours remain inconclusive because geographically distinct populations are likely to have different food resources and tools available, making it impossible to fully exclude ecological explanations (see Tennie et al. 2009; Galef 2004; Laland and Janik 2007). While a recent study has reported that chimpanzee communities living in the same area of the Taï Forest in the Ivory Coast selected tools of different materials to open nuts (Luncz et al. 2012), research is still needed to determine whether the actual behaviours underlying natural foraging, other than tool selection, differ across nonhuman primate communities that have the same food available. This study represents an attempt to do so by comparing a

range of techniques for opening the hard-shelled fruits of *Strychnos* spp. (commonly called monkey fruit or bush orange) in three socially separate chimpanzee colonies living in a shared environment.

Experimental studies investigating captive nonhuman primates have provided evidence that techniques used to obtain food from artificial feeding devices can be socially transmitted (e.g. Bonnie et al. 2006; Horner et al. 2006; Dindo et al. 2008). Novel techniques that are seeded into social groups have been found to spread with robust fidelity (Horner et al. 2006; Whiten et al. 2007; Hopper et al. 2011; Dindo et al. 2008; Crast et al. 2010; van de Waal et al. 2013). While such behaviours seem to be socially acquired, they may not be representative of foraging in the wild. Field experiments are a recent development, whereby experimental criteria are applied to attempt to control for ecological conditions when studying wild nonhuman primates. Biro et al. (2003) and Gruber et al. (2009) reported socially acquired tool-based foraging techniques in chimpanzee groups for experimentally induced nuts and honey traps, respectively. van de Waal et al. (2010, 2013) and Kendal et al. (2010) found that wild vervet monkeys and lemurs, respectively, showed socially learned solutions to 'two-action' puzzle tasks. While these findings show that neighbouring primate communities can differ in the methods applied to extract the same food, observational studies on semi-free-ranging nonhuman primates are still lacking.

An alternative factor often overlooked in social learning research is the impact of group demographics. Nonhuman primates of different age and sex groups may differ in tool use (Inoue-Nakamura and Matsuzawa 1997; Boesch and Boesch 1984; Lonsdorf 2005; Fessler 2002; Gruber et al. 2010). For example, immature chimpanzees often omit important stages of nut cracking with stones (Inoue-Nakamura and Matsuzawa 1997), and acquisition of expertise is a gradual process of adjusting techniques based on observing adult models (Inoue-Nakamura and Matsuzawa 1997; Lonsdorf et al. 2004; Corp and Byrne 2002; Boesch and Boesch 1984). Furthermore, several reports have documented that female chimpanzees use tools more often and that they forage more efficiently than males (McGrew 1979; Pruetz and Bertolani 2007; Lonsdorf et al. 2004; Gruber et al. 2010). Studies also suggest that primate sex-specific foraging behaviours may both be socially mediated (van de Waal et al. 2010; Agostini and Visalberghi 2005) and offer evolutionary advantages (McGrew 1979; Pruetz and Bertolani 2007; Fessler 2002). Such findings indicate that group demographics may play an important role in the social acquisition of foraging behaviours. Therefore, in the current study, group demographics received particular attention.

Since research on population-specific foraging has focused almost exclusively on tool use (Whiten et al. 2001; Schoning et al. 2008; van Schaik and Knott 2001), a range

of naturally challenging foraging tasks has been overlooked. Opening a hard-shelled fruit without a tool, for instance, is of special research interest. It is likely to be a challenging task for primates, as success here depends upon strategies that combine physicality and cognition, in this way sharing features with tool use (Stokes and Byrne 2001). Further, chimpanzee populations from West to East Africa process hard-shelled fruits, as do other wild primates throughout the world (e.g. aye-ayes, sakis, uakaris, capuchins, baboons, orangutans and bonobos: Koops et al. 2010; Matsumoto-Oda and Kasagula 2000; Lucas et al. 2011; van Lawick-Goodall et al. 1973; Mackinnon 2006; Sterling et al. 1994; Rosenberger and Hartwig 2011). This widespread consumption implies that comprehensive analyses of the opening techniques involving hard-shelled fruits can provide a valuable contribution to the literature spanning primate learning strategies alongside social and physical cognition.

The present study approach was to provide an overall analysis of the techniques chimpanzees use to open the hard-shelled *Strychnos* fruits and how they utilise these techniques, by comparing age and sex groups across three chimpanzee colonies at Chimfunshi Wildlife Orphanage, Zambia. *Strychnos* fruits are among the most shared fruits between female chimpanzees and their infants at some sites in the wild (Nishida and Turner 1996). The current study ruled out potential ecological influences by comparing socially separate colonies with the same specific foods available, living under equal ecological conditions. It is also important to note that the chimpanzee colonies were originally formed of orphans from different places in Africa, housed by arrival date, not (phylo)geographical background. Based on previous findings suggesting some forms of social learning for foraging (Luncz et al. 2012; Gruber et al. 2009; Horner et al. 2006; Whiten et al. 2007), we hypothesised that chimpanzees of different social colonies would apply different feeding behaviours that did not require tools, independent of available resources, group composition and phylogeny.

Methods

Subjects and colonies

Subjects were 56 chimpanzees at Chimfunshi Wildlife Orphanage (CWO), Zambia: 17 adult and adolescent males, 24 adult and adolescent females, 6 juvenile males (4–8 years of age) and 9 juvenile females (5–8 years of age). They were members of three stable, multimale–multifemale colonies with natural fission–fusion dynamics. Colonies 1, 2 and 3 included 27, 18 and 11 subjects, respectively. Table S1 shows the subject representation for

age and sex groups per colony, as well as overall colony composition (Colonies 1, 2 and 3 comprised 45–50, 24 and 13–14 chimpanzees, respectively, during the recording periods).

The largest colony (Colony 1) and middle-sized colony (Colony 2) lived in 77 and 65 ha enclosures, respectively. The smallest colony (Colony 3) lived in a 25 ha enclosure from August 2010 and in a 2 ha enclosure before that. Only one subject, an adult male, was recorded opening fruits (6 fruits) in the 2 ha enclosure. The enclosures contained naturally developed fruit groves, grasslands and forests in the miombo woodland. Walls, trees and fencing meant that the subjects could not observe chimpanzees that lived in the other colonies, at any times.

Colony formations took 2–5 years and ended 5–18 years before data collection. Each colony was composed of a mixture of wild-born chimpanzees and chimpanzees born at CWO (see Davila-Ross et al. 2011). The colonies were organised by the arrival dates of the wild-born chimpanzees, not by their (phylo)geographical background. Thirty-eight of the colony chimpanzees were presumably wild born and brought individually or in pairs to CWO, often from African countries that do not have wild chimpanzee populations. Twenty-four of them (Colony 1:13 chimpanzees; Colony 2:6; Colony 3:5) were brought from countries where wild chimpanzees live (e.g. Tanzania, Uganda and Rwanda). If they were born there, then the subspecies representation for these individuals would be 42–65 % for *Pan troglodytes schweinfurthii* and 31–42 % for *P. t. troglodytes* across the three colonies (Wilson et al. 2008; Tutin et al. 2008). As we do not know with certainty whether these chimpanzees were born in these countries, this estimation on subspecies representation was only presented to show that each colony very likely includes a mix of subspecies and that no apparent sign for phylogenetic differences could be found across the colonies.

Strychnos fruits, feeding sessions and data collection

The fruits from *Strychnos* spp. (Figure S1) weighed approximately 335 g (range 200–460 g) and had a diameter of 8.5 cm (range 7.0–9.7 cm), based on means calculated for five fruits. The *Strychnos* plants do not naturally grow in the chimpanzee enclosures (nor have they been planted there). Instead, the fruits were provided to the chimpanzees by their keepers. All fruits were bought from local farmers. Fruits were randomly distributed among the colonies, such that all three groups were provided with quantities of fruits proportional to group size, and were overall comparable in size, firmness, colour and ripeness (some ripe and some less ripe). It is, therefore, unlikely that the hard-shelled fruits differed in ways that could have explained differences in feeding behaviours across colonies. These fruits

were being given to the chimpanzees of CWO before the present study began, at least since 2005. To the authors' knowledge, no human had ever shown or taught the subjects how to open hard-shelled fruits on any prior occasions.

In each of the enclosures, feeding took place within an (approximately) 20 square metre area, close to the enclosure fences, which allowed unobstructed viewing from as close as 1–2 m to the chimpanzees. The feeding areas of Colonies 1 and 2 were roughly 200 m from each other, with the miombo woodland separating them, while the feeding area of Colony 3 was about 1.5 km further away. Each feeding area consisted of mainly dried ground, resulting in a hard surface with little grass and sporadic trees. The chimpanzees could, therefore, see their own colony members during feeding.

Feeding sessions were video-recorded with the objective of including as many subjects as possible. Recordings were made in 2007 (June–August) and in 2011 (August). Two subjects were video-recorded both as juveniles and as adolescents during the two recording periods. To avoid pseudoreplications, only the adolescent data were included, as this was the age group from which most data were obtained for both subjects. The chimpanzees were fed *Strychnos* fruits 2–7 times a week during the study period. Feeding sessions took place for all colonies between 11:30 a.m. and 1:30 p.m. each day, and video recordings were made from just outside the fence at the feeding sites.

Behavioural coding

A fruit-opening technique was defined as a distinct method applied by a chimpanzee to open a fruit using the mouth, hands and/or feet. Subjects may have used the same technique more than once, as well as combined a range of techniques for each fruit. Repeated as well as individually shown behaviours were tallied as fruit-opening events. For example, if a subject hit a fruit twice against the ground and then used a specific biting technique once, three fruit-opening events were counted. The study included a total of 939 fruit-opening events (mean = 17 events per individual) across 219 fruits (mean = 4 fruits per individual).

The behaviours were coded by one researcher using Windows Media Player. Intercoder reliability was evaluated with a second coder, based on 281 fruit-opening events (30 % of all events) for 29 subjects ($\kappa = 0.91$).

Data analysis

This study systematically examined fruit-opening behaviours by first conducting an overall analysis and then specifically compared chimpanzees across age groups, sex groups and the three colonies. As part of the overall

analysis, we assessed whether fruit-opening techniques were used in an organised manner. The applications of opening techniques were measured during four consecutive and mutually exclusive stages: initial opening (Stage 1), following initial opening, but before the first eating phase (Stage 2), further opening a partially opened fruit (Stage 3) and following the first further opening technique, but before additional eating phases (Stage 4). For descriptions and further details on the stages and eating phases, see Table S2.

Age, sex and colony comparisons were primarily conducted using generalised linear mixed models (GLMM). GLMM analysis examines the effects of predictor variables, while controlling for the potential nonindependence of response variables. Response variables were the mean number of combined technique types to completely open a fruit and the per cent number of fruits opened with a specific technique. The predictor variables were age groups, sex groups and colonies. Subject ID was included as a random effect. GLMM analyses were only performed on models where the improvement in the fit between the full and null models showed statistical significance. GLMM analyses were conducted using the programme R version 2.15 (R Development Core Team 2010) with the 'lme4' package (Bates et al. 2010).
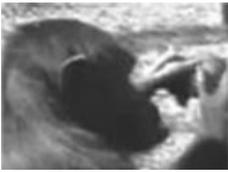
Results

Overall analysis of fruit opening

We distinguished eight distinct fruit-opening techniques applied by subjects, including half biting, full biting, fruit cracking, hitting on object, hitting on ground, peeling, stomping and throwing (for further details on the techniques, see Table 1). The first six techniques were found consistently across all age and sex groups. Of the latter two techniques, only four instances of stomping and six instances of throwing were observed, performed by two and one individuals, respectively. It is important to note that fruit cracking was the only technique where fruits were used to open other fruits; specifically, fruits were used as 'hammers' to strike against other fruits (see Fig. 1 and Supplementary video).

In total, 19 subjects put fruits ($N = 26$) aside after applying a fruit-opening technique, to eat in the future (Supplementary video). For eight subjects, it was clearly visible that these fruits were cracked open, with the pulp visible (14 fruits).

Table S3 provides an overview of the six most common techniques applied throughout the four fruit-opening stages. The chimpanzees consistently used biting throughout Stages

Table 1 Fruit-opening techniques: names, number of opening events and definitions of fruit-opening techniques shown by subjects

Fruit-opening technique	Definition	Image
Half bite $n = 316$	Incomplete biting into the fruit, followed by breaking away part of the fruit with both the mouth and two hands (and sometimes the feet, see image)	
Full bite $n = 137$	Complete biting through part of the fruit while holding it in one hand. Full bites involve a bigger, more powerful bite than half bites	
Fruit crack $n = 151$	Using one fruit as a hammer to strike against another fruit. Fruit is held in one hand or placed on the ground, and another fruit is struck against it. See Fig. 1 and Supplementary video	
Hit on object $n = 164$	Striking a fruit against a rock or tree. The subjects always took the fruits to the rock or tree; rocks were never transported to fruit	
Hit on ground $n = 136$	Striking a fruit against the ground	
Peel $n = 25$	Using fingers to peel away the shell pieces of the fruit	
Stomp $n = 4$	Raising the foot above a fruit and powerfully bringing it down onto the fruit	
Throw $n = 6$	Throwing a fruit with force against the ground to crack	

Eight types of fruit-opening techniques were found in this study. Numbers refer to fruit-opening events

Fig. 1 Switching fruits while fruit cracking: an adult male chimpanzee used the fruit cracking technique, i.e., used one fruit as a 'hammer' to crack open another fruit (**a**, **b**), before visually inspecting it. Then, he put the latter fruit away (**c**), placed the 'hammer' fruit into his left hand (**d**), selected another fruit to use as a 'hammer' (**e**) and continued with the fruit cracking (**f**)

1–4 (mean = 2.6−69.3 % of techniques). Fruit cracking was present only in Stages 1–3 (mean = 13.2−19.9 %). Hitting was primarily applied before the first eating phase, in Stages 1–2 (mean = 15.8−21.3 %). In contrast, peeling was most frequently used after the first or any additional eating phase, in Stages 3–4 (mean = 9.7—18.3 %).

Fruit-opening techniques across age, sex and colonies

GLMM analyses were first conducted for combined techniques and then for specific technique types. For combined techniques, collinearity between all GLMM predictor variables was low; the maximum variance inflation factor (VIF) was 1.18. GLMM results showed that the chimpanzee colonies differed significantly in the mean number of technique types combined to completely open a fruit per subject (P < .001; see Table 2). Bonferroni-corrected pairwise comparisons revealed that chimpanzees in Colony 3 combined significantly more techniques than chimpanzees in Colony 1 (P < .001) and Colony 2 (P < .001). No differences between sex and age groups were found for combined techniques (P > .05; see Table 2).

For the GLMM analysis on specific techniques, Hommel–Hochberg corrections were applied for repeated comparisons and α levels were adjusted. Results for the

Table 2 Combined techniques: GLMM results for number of combined techniques to completely open a fruit, across age, sex and colony

Age	0.226	0.209	1.078	0.284
Sex	−0.119	0.164	−0.721	0.473
Colony	0.227	0.053	4.269	<0.001*
(Intercept)	0.712	0.307	2.323	

Statistically significant differences are marked with '*'

frequently used techniques, with the exception of peeling, are presented in Table 3. Peeling showed a nonsignificant improved fit between the full and null models and thus was excluded from GLMM analysis. Collinearity between all GLMM predictor variables was low (maximum VIF = 3.22). GLMM analysis revealed statistically significant differences across age groups for hitting (P < .001) and tendencies of differences (Hommel–Hochberg corrections) in full biting (P = .048) and fruit cracking (P = .038), see Table 3. No age differences were found for half biting (P > .05). Bonferroni-corrected pairwise comparisons showed that juveniles used hitting on objects (P < .001) and hitting on the ground (P < .001) significantly more often than adults and adolescents. GLMM analysis (with Hommel–Hochberg corrections) revealed that the sex groups tended to show differences in

Table 3 Specific techniques: GLMM results for per cent number of fruits with technique events across age, sex and colony

Technique	Estimate	SE	t value	P value
Half bite				
Age	10.097	8.748	1.154	0.250
Sex	16.831	7.461	2.256	0.025
Colony	10.486	2.481	4.227	0.001*
(Intercept)	−4.317	22.154	−0.195	
Full bite				
Age	18.473	9.294	1.988	0.048
Sex	−15.975	8.216	−1.944	0.053
Colony	−11.635	2.750	4.231	<0.001*
(Intercept)	45.428	23.322	1.948	
Fruit crack				
Age	15.964	7.640	2.090	0.038
Sex	−12.611	6.792	−1.857	0.065
Colony	7.264	2.273	3.196	<0.001*
(Intercept)	−11.899	19.117	−0.622	
Hit on object				
Age	−40.873	7.459	−5.480	<0.001*
Sex	−0.067	6.661	−0.010	0.992
Colony	−0.303	2.233	−0.136	0.500
(Intercept)	85.486	18.609	4.594	
Hit on ground				
Age	−30.300	6.135	−4.939	<0.001*
Sex	2.312	5.479	−0.422	0.674
Colony	2.830	1.837	1.541	0.125
(Intercept)	51.695	15.304	3.378	

Statistically significant differences are marked with '*'

half biting ($P = .025$), see Table 3. No differences between sex groups were found for full biting, fruit cracking, hitting on ground or hitting on objects ($P > .05$). See Table S4 for the use of specific techniques across age and sex groups for each colony.

In addition, GLMM analysis showed that the colonies differed significantly from each other in the per cent number of fruits the chimpanzees opened by using half biting ($P = .001$), full biting ($P < .001$) and fruit cracking ($P < .001$), see Table 3 and Fig. 2. Two of these techniques were entirely absent in specific colonies. Full biting was not observed in Colony 3, but regularly occurred in Colonies 1 and 2 (produced by 11 and 13 subjects, respectively). Similarly, fruit cracking was absent in Colony 1, but was frequently observed in Colonies 2 and 3 (produced by five and six subjects, respectively). Furthermore, Bonferroni-corrected pairwise comparisons showed that the chimpanzees from Colony 1 opened significantly more fruits with half biting than chimpanzees from Colony 2 ($P = .019$).
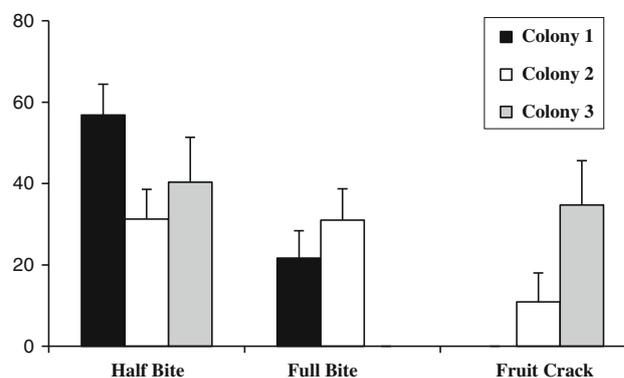
Mean & standard error of number of fruits with technique events [%]

Fig. 2 Fruit-opening across colonies: significant differences were found for the number of fruits opened with half biting ($P < .001$), full biting ($P < .001$) and fruit cracking ($P < .001$) events measured for every subject across the three colonies

Discussion

The present study represents a nonexperimental comparative assessment of the application of natural foraging behaviours for opening hard-shell fruits across three chimpanzee colonies. Analyses revealed fruit-opening differences across the three physically and socially separate chimpanzee colonies in the number of combined techniques and the occurrence of three specific techniques (half biting, full biting and fruit cracking). Most strikingly, full biting and fruit cracking were entirely absent in Colonies 3 and 1, respectively, yet present in the other colonies. This study provides empirical evidence that behaviours underlying natural extractive foraging, other than tool selection, can differ across primate colonies that have the same foods available. The current findings thus support previous findings on population-specific foraging behaviours obtained from wild nonhuman primate communities, where different resources were likely available (Whiten et al. 2001; van Schaik et al. 2003) and where foraging behaviours have been measured under experimental conditions (Gruber et al. 2009; Biro et al. 2003; van de Waal et al. 2010).

Establishing whether asocial or social acquisition has occurred remains difficult in field observations (Laland and Janik 2007). Here, the cross-colony differences in technique application could not easily be explained as a result of asocial learning. If such learning had occurred, then given the ecological similarity and comparable genetic composition, all colonies should have exhibited similar fruit-opening behaviours. It is also important to note that the three techniques which differed across colonies only involved the fruits and the subjects' strength and skill. Thus, it appears that ecological factors do not account for the cross-colony findings presented here.

Six opening techniques were used regularly by the chimpanzees. While *Strychnos* fruit-opening behaviours have been reported (Gruber et al. 2010; Nishida and Turner 1996; Boesch and Boesch 1990; McGrew 1999), the present work describes three techniques that, to the authors' knowledge, not been reported previously in chimpanzees, including fruit cracking, stomping and throwing. The latter two strategies appeared to be idiosyncratic techniques, observed only in three individuals (stomping by two and throwing by one). While the chimpanzees were fruit cracking, they were occasionally observed switching the 'hammer fruit' so that it became the fruit to crack open (see Fig. 1 and Supplementary video). Observations also revealed some indication of food preparations, where nineteen subjects put partially opened fruits aside, presumably to eat them later. These behaviours indicate further flexibility in utilising hard-shelled fruits to extract food.

Despite exhibiting a range of flexibility, some of the techniques applied by the subjects unfolded in an organised manner, with all techniques other than biting closely linked to specific stages of the fruit-opening process. Striking techniques (fruit cracking and hitting) were primarily used to penetrate the fruit's outer shell prior to the first eating phase. These powerful techniques gave way to peeling, a finer, dexterous behaviour used almost exclusively after the first eating phase, which seems appropriate for removing the last shell pieces. Previous field reports on primate feeding behaviours, including tool use, have described similarly sophisticated levels of dexterity and organisation (Inoue-Nakamura and Matsuzawa 1997; Russon 1998; Stokes and Byrne 2001; Byrne and Byrne 1991). Our results also suggest that chimpanzees were displaying hierarchical mental construction—the capacity to hold and integrate several cognitive, motoric or perceptual components to achieve the goal (Stokes and Byrne 2001)—when opening hard-shelled fruits.

Interestingly, across all colonies, juvenile chimpanzees opened more fruits with hitting techniques (i.e. on objects or the ground) than adolescent and adult subjects. Perhaps young chimpanzees develop their own feeding methods for these hard-to-process foods to compensate for the lack of adult/adolescent attributes, such as robust mandibular strength, before acquiring adult/adolescent techniques. These findings contribute to the current literature, where research on extractive foraging with tools has shown that immature chimpanzees acquire feeding behaviours based on observing adult models (Inoue-Nakamura and Matsuzawa 1997; Lonsdorf et al. 2004; Corp and Byrne 2002). Comparisons by sex revealed that females tended to display more half biting than males, especially among the adults and adolescents. These findings are consistent with field research showing sex differences in chimpanzee foraging behaviours (Goodall 1986; Lonsdorf 2005).

Consequently, it may be possible that such differences also extend to nontool use foraging conditions.

In summary, the current study examined natural, nontool extractive foraging across three separate chimpanzee colonies that had the same foods available and shared the same environment conditions, as well as comparable phylogenetic backgrounds. From these findings, we have concluded that chimpanzees may acquire their foraging behaviours from within their social communities. Chimpanzees, like humans, live in complex social systems, and thus, it is possible that learning specific foraging techniques and how to utilise them from within the social group may have had an important role in shaping human culture among early hominids. Previous field and captive studies have shown that primates are capable of socially mediated traditions (Dindo et al. 2008; Whiten et al. 2007; Reader and Biro 2010). While such findings are important for expanding our knowledge of primate tool use and social cognition, the current study, by observing large, semi-wild groups of chimpanzees, provided a unique interface between field research and captive studies. Further, we believe that studies of semi-wild primate groups are a valuable avenue of research to complement existing methods in attempting to understand animal social learning and the evolution of culture.

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