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ORIGINAL PAPER

Social learning strategies for nut-cracking by tufted capuchin monkeys (*Sapajus* spp.)

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Abstract The spontaneous use of stone tools for cracking nuts by tufted capuchin monkeys, now known to be habitual among wild populations in savanna environments, was first described in a semifree group living in the Tietê Ecological Park (SP, Brazil). Nut-cracking at TEP was first observed by our team in 1995 (Ottoni and Mannu in Int J Primatol 22(3):347–358, 2001), and its ontogeny and associated social dynamics, with inexperienced observers highly interested in the activities of proficient individuals, greatly tolerant to scrounging, support hypotheses about social biases on tool-use learning. Here we further analyze the social learning biases, better characterizing: the social context of nut-cracking in which observation by conspecifics occurs, the quality of the nut-cracking behavior itself and whether scrounging may be the motivation behind this behavior. We confirm that the choice of observational targets is an active one; monkeys do not simply observe those who they are socially close to. We investigate social learning strategies, describing how young capuchins choose to observe older, more proficient and dominant individuals during nut-cracking bouts. Monkeys with higher productivity rates were also more frequently targeted by observers, who were tolerated scroungers, further supporting the scrounging hypothesis. Finally, based on changes of the demographic patterns of tool use and observation, we set to retrace data from 14 years of continuous studies. We argue that we have followed the dissemination of the behavior (Transmission Phase) almost from its beginning, when juveniles were the most frequent nutcrackers, to a more common pattern where adults are the most active tool users (Tradition Phase).

Keywords Tool use · *Sapajus* · Social learning · Observational learning · Behavioral traditions

Introduction

Behavioral traditions in nonhuman animals have been the subject of intense debate in the last decade (Fragaszy and Perry 2003; Laland and Galef 2009). Here we adopt Fragaszy and Perry's (2003) definition of behavioral tradition as a shared behavioral practice amongst members of a group that is enduring over time and for which acquisition by new practitioners depends, to some extent, on social influences or mediation (Fragaszy and Visalberghi 2001). One of the means by which socially biased learning occurs is through observational learning, here defined as learning that is influenced by observing the actions of others.

Our first studies on the ontogenetic development of tool-aided nut-cracking by tufted capuchin monkeys (Resende et al. 2008) strongly suggested a socially biased learning process. Captive studies with capuchins have shown that these monkeys are capable of observational learning and that such capabilities can lead to the establishment of behavioral traditions (Custance et al. 1999; Dindo et al. 2009; Crast et al. 2010). Furthermore, studies of the variation in behavioral practices among groups in wild populations (Ottoni and Izar 2008) strongly support the hypothesis that these primates' variable behavioral repertoires may result, in part, from different behavioral traditions (Perry et al. 2003; Ottoni and Izar 2008; Crast et al. 2010).

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While many studies have focused on proximate questions of social learning mechanisms, fewer studies have questioned how individuals exploit information provided by others. Social learning strategies (Laland 2004; Kendal et al. 2005, 2009) pose questions about the rules that govern the use of social information such as "when to copy," "what to copy" and "whom to copy." In this paper, we address the latter—"whom to copy"—and investigate the choice of observational targets by naïve individuals in the context of stone tool use for cracking nuts.

The spontaneous use of stone tools for cracking open nuts by capuchin monkeys (*Sapajus* ssp.[1]) was first described systematically in a semifree-ranging group at Tietê Ecological Park (hereafter TEP) in Sao Paulo, Brazil (Ottoni and Mannu 2001)—the same capuchin group here studied. This behavior is now known to occur in many wild populations of *Sapajus libidinosus* (Fragaszy et al. 2004a; Moura and Lee 2005; Ferreira et al. 2010) as well as in at least some groups of *S. xanthosternos* (Canale et al. 2009) and *S. flavius* (Ferreira et al. 2009) that inhabit the Brazilian savannah (the *cerrado* and *caatinga*), but is absent in forest populations of other species of tufted capuchin monkeys (Ottoni and Izar 2008).

Ottoni et al. (2005) studied the observational learning of nut-cracking in the capuchins at TEP. Their first enquiry with regard to the relatively frequent (23 %) observation of nut-cracking bouts by conspecifics was whether nut-cracking observation rates just reflected interindividual association rates. The monkeys were not simply observing individuals in close proximity, which indicated that nut-cracking observation involved some sort of target "preference." The authors then sought out other factors that could be affecting the observer's choice, but no significant correlation was found between observation and dominance rank or between observation and age rank. Next, a test for correlations between observer–target dyads and the nut-cracking performance of the observational target found a significant correlation between the proficiency of each tool user and the choice of observational targets by conspecific observers (Ottoni et al. 2005).

To account for the choice of more proficient observational targets, Ottoni et al. hypothesized that by observing the most skilled nutcracker, greater scrounging payoffs could be obtained and that this in itself could mediate the preference for watching the best nutcrackers. Evidently, this also allowed for opportunities of learning in social context, and hence, this mechanism could be contributing to the maintenance of this shared practice.

The present study was conducted with the aim of further investigating the choice of observational targets and the scrounging hypothesis. Data collection was specifically designed to: (i) better characterize the social context in which conspecifics observe each other cracking nuts, (ii) to quantify in more details the nutcrackers' performances, and (iii) the opportunities of observation and of scrounging. With social network analysis, we investigate how the choice of observational targets might reflect patterns of social association and interaction between group members. To address the social learning strategy "whom to copy," we build a model to investigating which individual attribute(s), such as sex, age, dominance, proficiency or productivity, might be predictive of the frequency with which monkey is chosen by conspecifics as an observational target.

Looking back to the demographic changes in nut-cracking behavior, we suspect we might have followed the dissemination of this behavior in the group from its early stages (Ottoni et al. 2009). We further reflect on how a change of strategy of whom to observe might have occurred, as the behavior gradually became established as a behavioral tradition.

Materials and methods

Subjects and study site

The capuchin monkeys (*Sapajus* spp.) here studied inhabit a 200,000 m^2 of reforested area, with restricted access to visitors, within the Tietê Ecological Park (TEP) in São Paulo, Brazil. During data collection, the mean group size was 25 individuals (6 adult females, 9 adult males, 3 female juveniles, 1 male juvenile and 6 infants), with variations due to the birth of three individuals, two deaths, and the migration of two adult males between the studied group and a peripheral group of males. For the demographic analysis, in order to be comparable with previous studies, we classified subjects as *infants* from birth up to 2 years of age, and *juveniles* as of the age of two until 5 years of age. All subjects over 5 years of age were categorized as *adults*.

The monkeys foraged on naturally available items (fruits, leaves, arthropods, small birds and mammals) (Ferreira et al. 2002) and received a daily supplement of food by the park staff. The capuchins also collected palm nuts fallen to the ground from the many specimens of the palm tree *Syagrus romanzoffiana* that grow at TEP. They crack the nuts open on top of "anvils" with the aid of stone "hammers", eating the inner kernel and the occasional beetle larvae (Ottoni and Mannu 2001).

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[1] Tufted (or "robust") capuchin monkeys, were previously included in the *Cebus apella* species. Later the subspecies were raised to species' level (*Cebus apella* [former *C. a. apella*], *C. libidinosus*, *C. nigritus*, *C. xanthosternos*, and *C. flavius*); see Chapter 1 in Fragaszy et al. (2004b) for a review. Recently, the "robust" and "gracile" species were separated into two genera, *Sapajus* and *Cebus*, based on molecular data (Lynch Alfaro et al. 2012). Under this revised taxonomy our study species will all be referred to here as *Sapajus* spp.—though in previous texts it was referred to as *Cebus* spp.

Data collection

During a 12-month period (beginning April 2006), the monkeys were followed by Coelho, 3 days a week from 7:00 to 17:00. Data regarding the social dynamics of the group were collected by means of two protocols: (1) 5-min-long focal scans, registering social activities (grooming, play and agonistic interactions) and social proximity (individuals in contact and up to one meter from the focal individual). The order in which focal individuals were followed was randomly predefined before each day of data collection; (2) All occurrences sampling of grooming, agonistic behavior (threat grins or physical aggression) and play (Altman 1974). The identity of individuals in association or of those interacting was noted as well as the direction of the behavior (i.e., who groomed whom). Each individual was sampled by focal scans a total of 40 times (200 min) over the course of a year. All occurrence sampling was required due to the rarity with which social interactions were captured by focal scan sampling. These data were used for building the association and interaction matrices used in the social network analysis.

A social dominance rank was determined using de Vries' et al. (2006) I&SI' index as run in SOCPROG (Whitehead 2008), based on agonistic interactions (Table 1). Only agonistic interactions in which (i) both individuals were identified and (ii) the reaction of individual B was submissive (moved away, submissive grin or vocalization) as a response to the action (threat, lunge, chase, physical aggression) of individual A were used.

For data collection on nut-cracking behavior, we adopted a protocol in which the focus was maintained on an ongoing event until it ended, simultaneous events being ignored. We named this method "Focal Event" as the focus was the activities surrounding a nut-cracking episode itself and not the monkey performing the behavior. A Focal Event began when a monkey approached an anvil and began to manipulate the elements there present and ended when it left the anvil or—in the event of a conspecific observer being present (after the capuchin manipulating the tool had left the anvil), when the observer also left the nut-cracking site. With this methodology, we could access not only observation and scrounging opportunities during a nut-cracking event but the subsequent actions of the conspecific observer, including delayed scrounging and manipulation of the elements within the nut-cracking site. The Focal Events were filmed and data-coded from video recordings. The choice of the next Focal Event was determined by the following rules: (1) If another event was beginning or in progress, we registered this event independent of the individual cracking nuts; (2) if two or more nut-cracking events were beginning or under way, we gave precedence to the episode with the least recently registered individual.

Video coding

From the video recordings, we registered 475 Focal Events (total of 26 h of video), 96 of which were characterized as being Exploratory events in which the monkey came to the nut-cracking site but only ate leftovers or examined the elements there present without attempting to crack open nuts. In the remaining Focal Events ($N = 379$) at least one monkey manipulated the hammer in a percussive manner, attempting to crack open nuts. These, henceforth, referred to as nut-cracking events, where further classified as: (1) Inept events, when there was improper use of the hammer and/or incorrect order of associating nut, hammer and anvil. This includes striking the anvil with the hammer without having positioned a nut on the anvil or positioning the nut on top of the hammer and subsequently striking the anvil with the hammer; (2) Adequate (but unsuccessful) events, when a monkey, having properly positioned a nut on the anvil and struck it with a hammer but nonetheless failed to crack it open, not gaining access to food; and (3) Successful events, in which the nut on the anvil was cracked open, giving access to the nutritious endosperm. The proficiency of each individual (Table 1) was calculated, as in Ottoni et al. (2005), by dividing the frequency of Successful events by the absolute frequency of nut-cracking events. This allowed us to compare the proficiency rates at present with that of the previous studies. For a more precise measure of scrounging opportunities, however, we adopted a measure of each individual's productivity.

Productivity was calculated as the average number of nuts they were able to crack per registered episode (Table 1). Furthermore, from the video recordings, we registered the frequency of nut-cracking events in which conspecific bystanders observed the tool-using behavior and whether scrounging occurred. We also computed the time spent in observation and the rate of scrounging, i.e., the sum of episodes in which the conspecific observer ate nuts (took hand to mouth and bit into nuts) in the presence of the nutcracker divided by the total amount of episodes observed by that conspecific. Thus, addressing whether scrounging was in fact occurring and how it might relate to the choice of observational targets by conspecifics.

A summary of the group composition and dominance ranks, as well as the results from nut-cracking events, such as proficiency and productivity, are presented in Table 1.

Social networks

Based on the focal scans, we built an association matrix for social proximity using SOCPROG's simple ratio association index (Whitehead 2009). In this association matrix, the value shared between the individual in the column and

Table 1 Subjects and their individual attributes: sex, age group, dominance rank, frequency of nut-cracking, proficiency and productivity, frequency of being targeted by conspecifics and frequency of observing conspecifics cracking nuts

Subjects	Sex	Age group	Dominance rank	Nut-cracking episodes	Proficiency	Productivity	Target	Observer
Dav[a]	M	Adu	1	52	0.981	5.88	39	0
Fis	F	Adu	2	0	–	–	–	10
Cla	F	Juv	3	1	0	0	0	8
Cis	F	Adu	4	35	0.857	3.14	18	13
Med	M	Adu	5	48	0.958	6.92	13	5
Sus	M	Adu	6	38	0.974	5.15	11	5
Fil	F	Adu	7	22	0.522	1.5	4	9
Chu	M	Juv	8	24	0.074	0.25	11	25
Frd	F	Juv	9	2	0	–	0	16
Ana	F	Adu	10	16	0.765	3	6	0
Edu	M	Adu	11	4	1	4.5	0	0
Far	M	Inf	12	0	0	–	0	0
Vck	M	Inf	13.5	4	0	0	0	22
Jnt	F	Adu	13.5	10	0.9	7.1	3	6
Cac	F	Inf	15	0	0	–	0	4
Drw	M	Adu	16	20	0.8	4.5	6	2
Flu	M	Inf	17.5	0	0	–	0	4
Jqm	M	Adu	17.5	10	1	4.2	6	6
Amo	F	Inf	19	5	0	0	0	3
Vav	F	Adu	20.5	20	0.9	3.2	5	6
X	M	Adu	20.5	4	0	0	1	6
Jab	F	Inf	22.5	18	0.095	0.21	6	11
Ang	F	Juv	22.5	17	0.647	1.29	3	3
Ped	M	Adu	24	11	1	4.45	2	0
Z	M	Adu	25	18	0.944	4.33	4	2

[a] Dominant male

the individual in the row represents the ratio of the number of sampling periods (minutes) in which both individuals were registered within a 1 m radius of the focal individual, divided by the number of sampling periods in which at least one of these two individuals were registered within a 1 m radius. The value can vary between zero—where the dyad was never seen together—and one—where the dyad was always seen together over the total minutes sampled. Interaction matrices were built based on data collated from both Focal and All Occurrences' samplings. The values shared between individuals represent the frequency with which the dyad was seen interacting (grooming or playing with each other).

Two directed matrices were constructed based on the observation and scrounging activities during the nut-cracking events, in which the values represent, respectively, the total time over which the individual in the row observed the individual in the column and the rate of nut ingestion scrounged by the individual in the row, while the individual in the column was cracking nuts. These matrices were used to build the networks in Fig. 1 and for the regression analysis.

Analysis

First, we asked whether naïve individuals were simply observing the same conspecifics they would normally associate with or whether the choice of observational target reflected interaction relationships between group members. For this, we ran a multiple regression for networks (MR-QAP), modeling the dyadic dependent variable (observation network) using three independent networks (social proximity, grooming and play). The MR-QAP was carried out using the software UCINET 6 for Windows. This analysis conducts a multiple regression procedure between dyads. It then runs a repeated permutation of rows and columns of the dependent variable matrix (we ran 10,000 permutations), to control for biases due to autocorrelation (Borgatti et al. 2013).

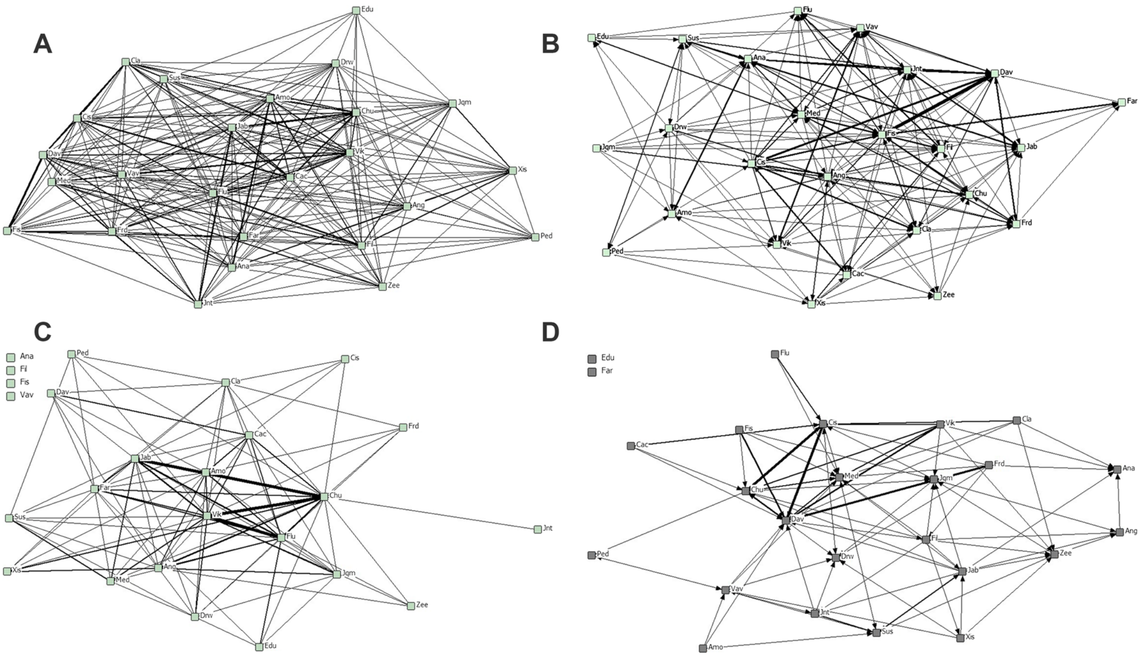

Fig. 1 Networks illustrating **a** social proximity, **b** grooming ($N = 852$), **c** play ($N = 390$) and **d** Observation ($N = 166$) of co specifics during nut-cracking events. The thickness of the ties (edges) portrays the strength of the association (in **a**), the frequency of the interactions (in **b**, **c**) and the duration of observational events (in **d**), between the nodes (individuals). *Arrows* in (**b**, **d**) indicate the direction of the interaction from the actor (groomer/observer) to the receiver (gromee/target)

Next, we questioned what possible factors (individual attributes) might be directing the social learning strategy of "whom to copy." We hypothesized that naïve monkeys could be targeting conspecifics that are (1) of a certain sex, (2) older (i.e., more experienced), (3) more dominant, (4) more proficient at nut-cracking or (5) who produce more cracked nuts. To address this question, we built a Generalized Linear Model, where the response value was the total *duration (minutes) an individual was targeted by conspecific observers*. The predictor variables were *sex*, *age* and *dominance rank* (as factors) and *proficiency* and *productivity* as (covariates). The *total frequency of nut-cracking* was used as an offset value in the model, to control for the fact that certain individuals might be more frequently targeted simply because they were more active. The GLM analysis was run with SPSS 16.

Given the nature of the data on nut-cracking, i.e., longitudinal repeated measures, we applied Generalized Estimating Equations (GEE) with SPSS 16 to control for unequal repetition of the same individuals over time when analyzing the frequency of activity by different sex and age groups (Norusis 2010).

Statement of animal rights

The monkeys are kept by the Centre for Rehabilitation of Wild Animals (CRAS—Centro de Reabilitação de Animais Silvestres) of the Tietê Ecological Park. The center provides food and veterinary care to the monkeys in full compliance with Brazilian Environmental law. Our study was of observational nature alone; the moneys were not handled in any way, nor did they suffer stress or any form of experimentation.

Results

Demographic pattern of nut-cracking behavior

Adults ($N = 14$) were responsible for the majority of nut-cracking episodes, with an absolute frequency of 308 episodes (81.3 %), while juveniles ($N = 5$) contributed with 65 episodes (17.2 %) and infants ($N = 6$) with only 6 Inept episodes (1.6 %). Overall, males ($N = 13$) performed 233 nut-cracking episodes (61.5 %), while females ($N = 12$) were responsible for 146 episodes (38.5 %). A significant effect of age group on frequency of nut-cracking episodes was found (GEE: Wald Chi square = 13.45, $df = 2$, $P = 0.001$), confirming the adults are more active at cracking nuts than juveniles and infants. The effect of sex on frequency of nut-cracking was not significant (GEE: Wald Chi square = 0.021, $df = 1$, $P = 0.884$), nor was there a significant interaction effect between age group and sex (GEE: Wald Chi square = 0.113, $df = 2$, $P = 0.945$).

Observation of nut-cracking behavior

Conspecifics observed 138 of the 379 nut-cracking events; however, in some of these events, more than one conspecific observer was present: a single observing bystander ($N = 102$), two observers ($N = 22$), three observers ($N = 4$) and four observers ($N = 2$). Hence, the total number of observational events ($N = 166$) is larger than the number of observed nut-cracking events.

Juveniles were the most active observers with an average of 10.4 observational events per individual, followed by infants, with 7.3 observational events per individual, and finally adults, with 5 observational events per individual. On occasion, juveniles would raise both hands, at shoulder or head height, and then bring them down together, toward the anvil, as if pounding an imaginary hammer on the anvil. These actions emulated that of the nutcracker and occurred rarely ($N = 7$, over 12 months and 379 episodes).

Scrounging

During a nut-cracking event, quite frequently (in 74.6 % of the observational events, $N = 125$), the bystander would feed on the endosperm of open nuts in the presence of the tool user. The rate of scrounging differed between individuals of different ages (GEE: Wald Chi square = 14.37, $df = 2$, $P = 0.001$). Infant monkeys scrounged cracked nuts in approximately 89 % of the nut-cracking events they watched, while older monkeys scrounged less frequently: juveniles (57.7 %) and adults (58.5 %). The scrounging rate, calculated as the frequency of ingesting (taking food to mouth) cracked nuts per minute spent at the nut-cracking site, was similar for both infants (2.75 bites per minute) and juveniles (2.84 bites per minute). The rate of food intake by the scroungers was not that much lower than the rate at which the monkey producing the cracked nuts (the “model”) ingested cracked nuts (3.30 bites per minute).

Choice of observational targets based on association and interaction networks

The multiple regression procedure (MR-QAP) had a significant model fit ($P = 0.001$), but the independent variables could only account for a fraction of the variation ($R^2 = 0.080$). Social proximity did not have a significant role in the model ($P = 0.093$) nor did play ($P = 0.383$). Grooming ($P = 0.006$) was the only factor related to observation in this network regression analysis—with a correlation of 27.7 % (Table 2).

Table 2 Results of the MR-QAP between observation network (dependent variable) and social proximity, grooming and play networks (independent variables)

Network	*P* value	The Pearson correlation
Social proximity	0.093	−0.009
Grooming	0.006	0.277
Play	0.383	0.035

Choice of observational target based on individual attributes

The Generalized Linear Model involved a regression of the *total duration (minutes) a monkey was the target of observation*, based on a normal distribution, and found a significant fit to the intercept-only model (likelihood ratio Chi-squared = 337.103, $df = 19$, $P = 0.000$). Sex, as a main effect, was not a significant predictor; however, the age, dominance rank, proficiency and productivity were found to be significant predictors of the dependent variable (*DurationObserved*) (Table 3). Therefore, naïve monkeys seem to be targeting conspecifics that are older, more dominant, more proficient and more productive at tool-aided nut-cracking.

Table 3 Results for the Generalized Linear Model for model effects on the response value *duration (minutes) an individual was targeted by conspecific observers* and predictor variables *sex*, *age, dominance rank, proficiency* and *productivity*

	Wald Chi square	*P* value
(Intercept)	59,648.076	0.000
Sex	2.773	0.096
Age	99.176	0.000
Dominance rank	72.414	0.000
Proficiency	11,480.585	0.000
Productivity	196,679.695	0.000

Dependent variable: *DurationObserved*

Model: (intercept), sex, age group, dominance, proficiency, productivity

We further ran a correlation analysis to verify how the individual attributes might be inter-correlated: Both proficiency and productivity were highly correlated to age and to each other but not to sex or dominance rank (Table 4).

Discussion

We corroborated the previous results of Ottoni et al. (2005) and confirm that the choice of observational targets is an active one—the tufted capuchin monkeys of TEP are not simply observing socially close partners during nut-cracking activities.

Unlike that found by Ottoni et al. (2005), observation by conspecifics was, in this study, found to be correlated to dominance rank and age, with older and higher ranking individuals being more frequently watched by conspecifics

Table 4 Correlation analysis presenting Pearson's correlation (ρ) and significance (P value)

	Age group	Dominance rank	Proficiency	Productivity
Sex				
ρ	0.032	0.004	0.010	0.013
Sig.	0.237	0.346	0.138	0.071
Age group				
ρ		−0.015	0.266	0.272
Sig.		0.415	0.000*	0.000*
Dominance rank				
ρ			0.022	−0.099
Sig.			0.461	0.316
Proficiency				
ρ				0.921
Sig.				0.000*

* Attributes significantly correlated

while cracking open nuts. Similarly to that found in the previous study, the choice of observational targets is also partially explained by the target's proficiency at cracking open nuts, and hence, these observational targets yield good opportunities for learning. In summary, young capuchins (infants and juveniles) chose to observe older (adult) proficient and dominant individuals during nut-cracking bouts.

The distribution of nut-cracking episodes among age groups differed across several consecutive studies with the same population at the Tietê Ecological Park (TEP). Ottoni and Mannu's (2001) first study at TEP described marked individual and sex/age group differences in frequency of nut-cracking. Then, juveniles accounted for more than half the nut-cracking bouts ($N = 164$) followed by adult males ($N = 54$). Sex differences were less clear; however, adult males were found to be significantly more active than adult females. This pattern continued to be observed in the following ontogenetic study developed between 2000 and 2002 (Resende 2004; Resende et al. 2008). On average, juveniles showed a higher nut-cracking rate—frequency of nut-cracking episodes divided by months of activity—than that observed in adults; however, the marked individual variation between monkeys of similar ages led to the differences in the activity of the age classes being statistically insignificant. Figure 2 shows the mean frequency of nut-cracking episodes in each age group, for the three consecutive studies at TEP over a 10-year period. A change in the demography of nut-cracking can be seen, as in the two previous studies juveniles where the most active age group and in the third, and present study, adults are the most active.

At the time of Resende's study (Ottoni et al. 2005), the most proficient tool users—and who would yield greater scrounging opportunities—could not be sought out based on rules of thumb, such as "follow the dominant male" or "chose experienced older individuals." Nut-cracking behavior was still apparently spreading through the group, and most adults did not crack nuts. The most active stone tool manipulators were juveniles, but their performances varied greatly. Then, actual proficiency seemed to be the main variable directing the choice of conspecifics as observational targets (Ottoni et al. 2005).

The changes in the demography of tool use across the age classes throughout the several studies with the same population at TEP strongly conform to some of the patterns Huffman and colleagues (Huffman 1996; Huffman and Hirata 2003) described in (and generalized from) Japanese monkeys in their pioneering work on the dynamics of behavioral traditions in nonhuman primates. Hypothetically, one or a few tool users—whether as innovators, or as carriers of their natal groups' nut-cracking tradition—started cracking the available *Syagrus* nuts; the most interested—and most tolerated—observers of the activity, the juveniles became the most active nutcrackers during the "Transmission Phase" (Huffman 1996). As these individuals got older, the demographic pattern changed to what is usually found for already established traditions ("Tradition Phase"), where adults are the most proficient individuals, and the preferred observational targets (the alpha male in particular, in the case of capuchins). As the behavior goes into the Tradition Phase, the expected pattern, *young individuals learning from watching adults—which are usually also the more experienced and successful individuals*, becomes the predominant pattern. In fact, we see this in the present study, in which the observation of conspecifics during nut-cracking was significantly correlated not only with targets' proficiency, but with age and social hierarchy (making it harder to sort out the variables guiding the choices of observational target).

Furthermore, the correlation between the frequency of being observed (observation) with the amount of nuts cracked open (productivity) by individuals indicates that the choice of observational target, as well as maximizing good opportunities to observationally learn how to use this stone tool technique, also maximizes scrounging opportunities. A mechanism, whereby scrounging reinforces observation (as suggested in Ottoni et al. 2005), might be especially important during the dissemination of the behavior (Transmission Phase—Huffman and Hirata 2003), with naïve individuals seeking the best chances of eating nuts and, incidentally, being exposed to situations conducive to learning. Once the behavior becomes established in a group (Tradition Phase), the discrimination of the most proficient nut crackers would be less important, as a simple "rule of thumb" such as "observe older individuals (i.e., more experienced) or high-ranking individuals (i.e., more successful)" would suffice for

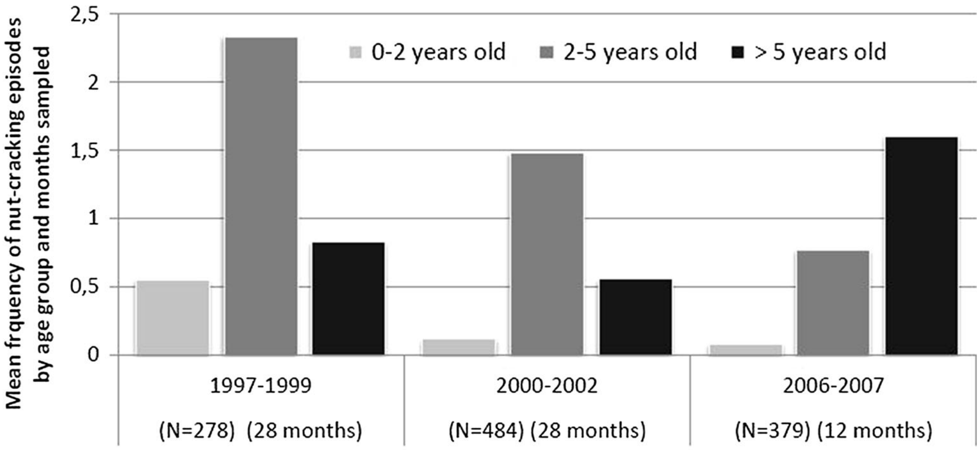

Fig. 2 Mean nut-cracking frequency for each age group, and relative to the duration (months) of sampling, in the three studies carried out at Tietê Ecological Park, 1997–1999 (Ottoni and Mannu 2001), 2000–2001 (Resende 2004; Resende et al. 2008) and present study (Coelho 2009; Coelho et al. 2008)

generating good opportunities for scrounging and also more conducive conditions for learning.

It is noteworthy that scrounging need not be the only mechanism mediating this acquisition. Capuchin monkeys are by nature inquisitive and motivated to observe manipulative behaviors of conspecifics, especially a noisy and conspicuous activity as cracking open nuts. They will persist in activities such as attempting to crack open nuts, sometimes in detriment to how unsuccessful they might be at the activity yet and often interspersed with play (Resende 2004); doing so, as well as observing others, seems to be rewarding in itself.

Nut-cracking sites function as an *atelier,* where the physical elements needed to apply stones as percussion tools to crack open nuts are available. Attracted by the opportunities to eat the remains of open nuts, monkeys are exposed to the local stimuli, the presence of stone “hammers,” hard surface of the anvil, nuts—both broken and intact—and the combination of these elements in the same space. Learning by trial and error, in this context, would still not configure individual learning devoid of social influences, since the elements present there have been brought together as a result of the actions of proficient individuals. This characterizes a case of “stimulus” or “local enhancement,” where enduring artifacts mediate social learning (Heyes and Galef 1996; Fragaszy et al. 2013).

Our data are consistent with directed social learning (Coussi-Korbel and Fragaszy 1995), where learning from other individuals depends on the identity or attributes of the individuals involved. This however means that biases of several types may be occurring simultaneously, such as “copy dominant individuals” and “copy older, more proficient individuals,” and that distinct biases may prevail at any given moment, according to the availability and attributes of the potential observation targets. As evidence of social learning strategies among nonhuman animals amounts, it is becoming clear that the strategies of *what*, *when* and *whom* to copy may be more context dependent than originally thought and that possibly multiple biases may be in action at the same time (Hoppitt and Laland 2013).

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