Anim Cogn (2016) 19:605–618
DOI 10.1007/s10071-016-0965-6

ORIGINAL PAPER

When and where to practice: social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*)

Y. Eshchar[1] · P. Izar[2] · E. Visalberghi[3] · B. Resende[2] · D. Fragaszy[1]

Received: 9 October 2015 / Revised: 6 February 2016 / Accepted: 10 February 2016 / Published online: 1 March 2016

Abstract The habitual use of tools by wild capuchin monkeys presents a unique opportunity to study the maintenance and transmission of traditions. Young capuchins spend several years interacting with nuts before cracking them efficiently with stone tools. Using a two-observer method, we quantified the magnitude of the social influences that sustain this long period of practice. During five collection periods (over 26 months), one observer recorded the behavior of 16 immature monkeys, and another observer concurrently recorded behavior of group members in the focal monkey's vicinity. The two-observer method provides a means to quantify distinct social influences. Data show that immatures match the behavior of the adults in time and especially in space. The rate of manipulation of nuts by the immatures quadrupled when others in the group cracked and ate nuts, and immatures were ten times more likely to handle nuts and 40 times more likely to strike a nut with a stone when they themselves were near the anvils. Moreover, immature monkeys were three times more likely to be near an anvil when others were cracking. We suggest a model for social influence on nut-cracking development, based on two related processes: (1) social facilitation from observing group members engaged in nut-cracking, and (2) opportunity for practice provided by the anvils, hammer stones and nut shells available on and around the anvils. Nut-cracking activities by others support learning by drawing immatures to the anvils, where extended practice can take place, and by providing materials for practice at these places.

Keywords Tool use · Social learning · Social facilitation · Skill acquisition · Artifacts · Culture

Electronic supplementary material The online version of this article (doi:10.1007/s10071-016-0965-6) contains supplementary material, which is available to authorized users.

✉ Y. Eshchar
eshcharyon@gmail.com

1 University of Georgia, Athens, GA, USA

2 University of São Paulo, São Paulo, SP, Brazil

3 Institute of Cognitive Sciences and Technologies, National Research Council, Rome, Italy

Introduction

In socially biased learning, learning is influenced by the present or past activities of social companions, or their products (Fragaszy and Visalberghi 2004; Galef 1995). Two of the most common processes that support socially biased learning are social facilitation and stimulus/local enhancement. Social facilitation occurs when the presence of a demonstrator performing an act increases the likelihood of the observer to perform the same act. Stimulus/local enhancement is when the interaction of a demonstrator with a specific object or place increases the likelihood of the observer to interact with the same object (Laland and Hoppitt 2013). Studies with captive individuals of various species, from graylag geese (Fritz et al. 2000) to capuchins (Dindo et al. 2009) and chimpanzees (Nagell et al. 1993), show that animals can learn to solve a foraging task with only local enhancement as a social input. Another form of social influence is exerted through providing an opportunity to learn: for example, in golden lion tamarins (*Leontopithecus rosalia*) adults preferentially provision their young with novel food items, thus facilitating the incorporation of new food items into the juveniles' diet (Rapaport and Brown 2008). Social influence can also be exerted via interactions with the artifacts left by another individual. Enduring artifacts associated with technical activities—such as open shells, broken branches or holes dug in the ground—provide opportunities for learning and practice and can also be associated with the actions performed by the adults, thus reinforcing the learning associated with observation (Aisner and Terkel 1992; Fragaszy et al. 2013a; Leca et al. 2010; Thornton and Hodge 2008).

Matthews et al. (2010) and Franz and Matthews (2010) modeled how social processes combined with operant learning (learning through rewards) predicted the mastery of a foraging task-learning to open baited boxes—in captive capuchins (*Sapajus* spp.—several species that were once lumped together under one name, *Cebus apella*). Their conclusion was that the monkeys' performance was best predicted by stimulus enhancement followed by operant learning. Similar results were obtained in wild meerkats (*Suricata suricatta*) which were presented with containers baited with food. Hoppitt et al. (2012) identified nine learning processes, six asocial and three social, that influenced the meerkats' learning of the task. Social processes included local enhancement: The rate of interaction with the baited container was positively associated with the number of previous observations of group members gaining access to it, and was higher in the period immediately after a group member interacted with the container. Importantly, seeing others gain access to the container correlated negatively with the rate at which the subjects abandoned the task—they were less likely to "give up" if they saw other meerkats accessing the box. Asocial processes such as reinforcement were also important: Rewarded interactions with the container (i.e., episodes in which the meerkat obtained food from the container) correlated positively with future rates of interactions with the container by the same individual.

Tool use

Once thought to be the exclusive realm of humans, it is now clear that animals from insects to primates use tools [for a review—(Bentley-Condit and Smith 2010)]. One of the best studied examples of tool use in wild animals is nut-cracking in bearded capuchin monkeys (*Sapajus libidinosus*) at the Fazenda Boa Vista and adjacent lands (hereafter, FBV), Piauí, Brazil. The monkeys in this population habitually crack several species of palm nuts using hard stones as hammers and boulders or logs as anvils (Fragaszy et al. 2004a; Visalberghi and Fragaszy 2013). Stone tool use also has been reported in other populations of tufted capuchins (genus *Sapajus*) (e.g., Canale et al. 2009; Ferreira et al. 2009; Ottoni and Izar 2008), and similar nut-cracking was described in several populations of chimpanzees (Boesch et al. 1994; Matsuzawa 1994; Visalberghi et al. 2015).

Several studies investigated the development of behavior in young individuals in capuchins and in chimpanzees [e.g., in chimpanzees—(Biro et al. 2003; Inoue-Nakamura and Matsuzawa 1997), in capuchins (Resende et al. 2008, 2014); for review, see (Lonsdorf and Bonnie 2010)]. In both species, infants interact with potential tools and food items years before they start using tools successfully. Specifically, young capuchins manipulate objects at much the same rate as do adults, but around the time of weaning (about 18 months) their rate of manipulation of hard-to-process items, including nuts, increases sharply to the adult level (Eshchar et al. In process). Several more years are required before the juveniles become efficient nut-crackers (Resende et al. 2014). It is not clear what keeps the immature monkeys (infant and juveniles) interested in nuts and stones throughout this period, and supports their repeated interactions with these objects. One possibility is that the observations of adult group members using tools, and the opportunities afforded by the adults' activities, such as discarded tools and cracked shells, play an important role in keeping the immatures' interest level high (Fragaszy et al. 2013a). This form of continuous, prolonged learning, involving repeated observation by the younger individual of the other performing a skilled action and repeated opportunities for practice provided by the proficient other to the younger individual, has been referred to as "master and apprenticeship" learning (de Waal 2008; Matsuzawa et al. 2001).

Social interactions in capuchin monkeys

Capuchins live in mixed-sex, mixed-age, matrilineal, cohesive groups (Fragaszy et al. 2004b) and exhibit a high level of tolerance to their group members while feeding, in some cases even sharing food (de Waal et al. 1993). Infant and young juvenile capuchins are highly tolerated (Coussi-Korbel and Fragaszy 1995; Fragaszy et al. 1997) and allowed to scrounge food from the adults (Coelho et al. 2015). Tolerance toward immatures decreases with age and immature monkeys older than 4 years are more often targets of aggression compared to their younger counterparts (Fragaszy et al. 1994; Izar 2004; Janson 1990).

Current study

In this study, we examine the influence of seeing and being with other group members cracking nuts, as well as the presence of hammer stones used by others and nut debris from others' cracking, on immature capuchins' actions with nuts and stones. We followed 16 immature monkeys belonging to a wild, habituated group of bearded capuchins in FBV. We continuously recorded their location and behavior and concurrently recorded the location and behavior of others in the group. This method enabled us to examine quantitatively with fine temporal resolution the influences of other monkeys' presence and activity on the behavior of our focal subjects.

Following the studies of Matthews et al. (2010) and Hoppitt et al. (2012) described above, we tested several hypotheses linking social context to young monkeys' behavior with nuts and stones. Hoppitt et al. found that meerkats increased their interaction with baited containers after observing group members gaining access to them. Since there were only two containers, the subjects could not always interact freely with them at the same time as the demonstrator. In our study, nuts and nut shells were abundant around the anvils on which the adults crack them, and our subjects could interact with them, while other group members were cracking. Therefore, we expected that in our population the rate of immatures' interaction with nuts would be higher not only after, but also during the time at which adults cracked and ate nuts. We hypothesized that observing adult group members cracking would draw the juveniles toward the anvils and would be positively associated with the immature monkeys' rate of interacting with nuts and stones. These interactions are predicted to promote the juveniles' discovery of how to crack nuts themselves. Later studies with this same population will test that prediction. We further hypothesized that others' influence on immatures' actions with nuts and stones would wain as immatures aged, in accord with the decreasing tolerance of adults toward immatures' proximity during feeding, and/or the immature monkey's growing ability to crack nuts for itself.

Therefore, our specific predictions are as follows:

1. Immature monkeys manipulate stones, nuts and nut debris at a higher rate when they see and/or hear other individuals crack and eat nuts around them.
2. Immature monkeys manipulate stones, nuts and nut debris at a higher rate when they are within an arm's reach of an anvil.
3. Immature monkeys spend more time near anvils when other individuals crack and eat nuts around them.
4. The magnitude of social influence on young monkeys' activity with nuts and stones, and on time spent near anvils, diminishes with the immature monkey's age.

This study addresses the question of social transmission by examining social influences, exerted both by observation and by interaction with artifacts, on juveniles' practice of actions associated with nut-cracking. The model suggested here is applicable not only to nonhuman primates, and not only to tool-use tasks. We hope it can shed new light on the development of foraging skills across many taxa where young individuals forage in the company of others.

Methods

Study site

This study was conducted at Fazenda Boa Vista and adjacent lands (hereafter, FBV) in the southern Parnaíba Basin (9°39′S, 45°25′W) in Piauí, Brazil. FBV is a flat open woodland (altitude 420 m asl) punctuated by sandstone ridges, pinnacles, and mesas rising steeply 20–100 m. Rainfall in the region is highly seasonal, falling mainly between October and April (for further information, Visalberghi et al. 2008).

Nuts, stones and anvils

Palms are abundant in the area, and many produce fruit at ground level. Two species of palm nuts in particular were commonly cracked in this study: tucum (*Astrocaryum campestre*) and piassava (*Orbygnia* spp.). A tucum nut is on average 46 mm in length, weighs 15.5 g, and its shell is 4.1 mm thick, with peak-force-at-failure of 5.6 kN. An average piassava nut has a length of 61.3 mm, weighs 50.6 g, and has a thicker and more resistant shell than a tucum nut—6 mm with peak-force-at-failure of 11.5 kN (Visalberghi et al. 2008).

The hammer stones used to crack nuts weigh on average around 1 kg, though they range from 250 g to 2.5 kg. They are quartz, quartzite, siltstone or harder sandstone (Visalberghi et al. 2007). Quartz and quartzite stones are more resistant to fracture and thus longer enduring than sandstone or siltstone hammers, but they are also rarer in the landscape (Visalberghi et al. 2007). An anvil is defined as a flat, or nearly flat, horizontal or slightly sloping surface—a boulder, an exposed stone or a horizontal log—that presents at least two of the following three elements: (a) a potential hammer stone on the putative anvil or nearby, (b) distinctive shallow pitted depressions (1–2 cm deep) on the upper surface of the anvil that derive from cracking nuts with stones, and (c) the presence of cracked palm shells on or near the anvil (Visalberghi et al. 2007).

Subjects

At the beginning of the study, there were 11 immature monkeys in the group, aged from 3 months to 4.5 years. Five more infants were born during the study. At the beginning of the study, none of the subjects could crack open a whole nut of the more resistant species [piassava (*Orbygnia*)]. Monkeys ranged in age from 3 months to 6.4 years during data collection periods (see Table 1 in the Supplementary material). The two oldest juveniles, and to some extent two others, mastered this skill through the duration of the study. The group also included three adult males and five adult females. All but one female habitually cracked nuts. Body mass of each member of the group was recorded once annually, during the three dry season collection periods (Fragaszy et al. 2016) (see Table 1 of the supplemental material).

Data collection

Data were collected in five discrete collection periods, each lasting 6 to 9 weeks. Three of those collection periods took place during the dry season, and two during the rainy season. The time points were as follows: May–July 2011 (Dry season), January–February 2012 (Rainy season), May–July 2012 (Dry season), January–March 2013 (Rainy season) and June–July 2013 (Dry season). Observers were trained and reached an adequate level of reliability (see below) with the core observer (Yonat Eshchar) training the members of the dry season team and Michele Verderane, who was on the first team, training the new members of the rainy season teams (see below).

All observers used handheld devices with Pocket Observer© software by Noldus Information Technology. Observations were collected using two-person teams. One observer followed a focal subject to obtain a continuous record of its activities, including manipulation of nuts and of other objects, and locations, specifically if the subject was within an arm's length of an anvil (see supp. Material). Concurrently, the other member of the team recorded, as an instantaneous observation every minute, the identity, location and activity of other monkeys within 10 m of the focal monkey. All observations lasted 20 min, or until the focal subject went out of view and could not be followed, but not <5 min.

Observers first learned to identify all members of the group with the help of experienced field assistants. Subsequently, observers were trained on the ethogram by Eshchar. Reliability for focal observations was calculated using GSEQ: Generalized Sequential Querier© and URL: http://www2.gsu.edu/~psyrab/gseq/index.html. We used the time unit method, which compares the codes inserted by two observers and defines as a match any instant in which both observers used the same code within a time window of 5 s. For each observer–trainer pair, time unit kappa was at or above 0.7, which is considered highly reliable (Bakeman et al. 2005).

Reliability for instantaneous observations of other monkeys near the focal monkey was tested separately for each aspect (identity, proximity, activity and location) until agreement (sum agreement/agreement plus disagreement) was over 80 % for each of them for 20 consecutive samples. At each minute, ten individuals at the most could be coded. In some cases, the observers did not have the time to code all monkeys within 10 m in 1 min. In those cases, priority was given to individuals who were cracking or eating nuts and then to individuals who were closest to the focal monkey. In this paper, we pooled the number of group members within 5 m into three categories—whether the focal monkey had zero, one to three, or more than three group members within 5 m. Because of this pooling, the limitation of this method—the inability in some cases to code all monkeys in the area—does not affect the results presented here. We also noted whether any neighbor within 10 m was cracking or eating nuts.

At each collection period, a quarter to one half of the observations was collected in the field laboratory—an open area, about 12 m in diameter, that the monkeys visited habitually. There are many anvils on the site, and the monkeys were sometimes provisioned with nuts in that place as part of ongoing experiments (e.g., Fragaszy et al. 2010, 2013b; Massaro et al. 2012). Many nut shells and debris from years of nut-cracking can be found on and around the anvils, and all around the field laboratory.

The protocol was reviewed and approved by the Institutional Animal Care and Use Committee of the University of Georgia. The study adheres to the code of best practices for studies of nonhuman primates set by the International Primatological Society.

Data analysis

For each subject in each collection period, we collected between 19 and 53 observations which lasted cumulatively between 5.3 and 27.1 h (Table 3 in suppl. material). All observations for the same subject were collated for each season. Ten subjects appeared in all five collection periods.

The observations were exported from The Observer© to GSEQ© software to extract the frequency of different events (such as manipulation of nuts) under different conditions. General mixed linear models (GLM) and ratio *t* tests were used to evaluate the differences in activity under different conditions. The dependent variables were proportions of time spent in different locations, and rates of different actions (e.g., manipulation of nuts and of other objects). Rates were calculated as events divided by total time, and the proportion of time at a location as the number of seconds spent there divided by total time. In the models, we treated the variables as count variables and used total time and time devoted to manipulation of nuts as offsets. For variables that did not distribute normally (tested with Shapiro–Wilk), the Poisson distribution was used.

The independent variables [number of monkeys within 5 m of the focal monkey, the presence of nut-cracking activity in the group within 10 m (yes/no), and proximity within arm's reach of the focal monkey to an anvil (near/away)] were treated as fixed effects. Subjects' ID was used as a random factor.

Unless otherwise stated, the statistics are reported from general mixed linear models using a Poisson distribution. Randomization of residuals was used to compensate for over-dispersion. The estimates describe the difference in the dependent variable between the categories of the independent variable. SAS software was used for all analyses.

In order to understand the influence of group members on the activity of immature monkeys, we first looked at the amount of time the subjects spent with other group members in close proximity, and whether this amount changed when nut-cracking activity was taking place in the group. This helps us to understand the potential for juveniles to observe others cracking nuts.

We then determined the rate of manipulation of nuts and of other objects under different conditions—when other group members cracked and ate nuts in the immature monkey's vicinity and when there was no nut-cracking activity, when the subjects themselves were near an anvil and when they were not. Using general linear mixed models, we tested the difference in rate of manipulation among those conditions. The GLM method also enables us to determine whether adding any new variable has an effect on the model, and so, whether one of the additional variables has a significant effect when the first variable was already taken into account. Thus, we were able to determine the effect of the nut-cracking activity in the group on rate of manipulation regardless of the location of the subjects (near an anvil or away), and the effect of the subject's location on manipulation regardless of the concurrent occurrence or the absence of nut-cracking in the group. We examined the rate of striking a nut with a stone—the efficient action of nut-cracking—in the same manner. We then examined the relation between our main independent variables: We tested whether the percentage of time subjects spent near or far from an anvil is different when there was nut-cracking activity in the group compared to other times.

We postulated that the immature monkeys are drawn to anvils during nut-cracking episodes to collect food, even if just a few crumbs. To test that, we looked at events of scrounging—whether they were more common near an anvil and during nut-cracking activity. We also examined the tolerance extended toward immatures of different ages by looking at aggressive behaviors directed toward them and at the percentage of time they spent in the vicinity of other group members.

Finally, we looked at the development of those effects: Using a cross-sectional approach, we examined the effect of nut-cracking activity in the group and proximity to an anvil on the subjects' rate of manipulating nuts for monkeys of different ages.

Results

Time spent with other group members

Immature monkeys spent on average around 30 % of their time by themselves, with no other monkey within 5 m of them (SD = 13.9). They spent 40 % of their time with one to three other monkeys within 5 m (SD = 7.2), and 30 % with more than three monkeys in that range (SD = 12.2). When there was nut-cracking in the group—when group members cracked and ate nuts within a radius of 10 m from the subject, or nut-cracking could be heard—this picture changed, and the subjects tended to have more group members around them. In this latter situation, they spent on average 24 % of the time with no other monkeys within 5 m (SD = 19), 34 % with one to three monkeys around them (SD = 10) and 43 % with more than three monkeys within 5 m (SD = 25) (Fig. 1). When there was nut-cracking activity in the group, subjects were significantly more likely to be near three or more group members than alone ($P = 0.0003$, estimate = 1.3). That was not case when there was no nut-cracking activity nearby.

Influence of nut-cracking activity in the group on manipulation of nuts and other objects

The rate of manipulation of nuts by immatures was significantly higher when other group members were cracking or eating nuts in their vicinity (within 10 m), compared to other times (median (SD): 6.8 (18.9) vs. 3.8 (10.3) per 10 min, $P = 0.0009$, estimate = 4.1). Conversely, rate of manipulation of other objects was higher when there was *no* nut-related activity within 10 m, compared to when other group members were cracking and eating nuts within 10 m (median (SD): 10.8 (5.8) vs. 6.3 (5.7) per 10 min, $P = 0.0001$, estimate = 1.43, Fig. 2). Thus, the facilitatory effect of others cracking was specific to manipulation of nuts.

We also tested this social influence specifically in the place—and time—in which provisioning of nuts took place: the aforementioned field laboratory, during the dry seasons. The influence of group members cracking or eating nuts on the rate of manipulation of nuts by our subjects holds under those conditions as well ($P = 0.0406$, estimate = 2.33).

Influence of being within arm's reach of an anvil on manipulation of nuts and other objects

When on an anvil or within arm's reach from one, the subjects manipulated nuts at a higher rate compared to when they were farther from the anvil (median (SD): 19.7 (16.4) vs. 2 (2.2) per 10 min, $P < 0.0001$, estimates: 9.9).

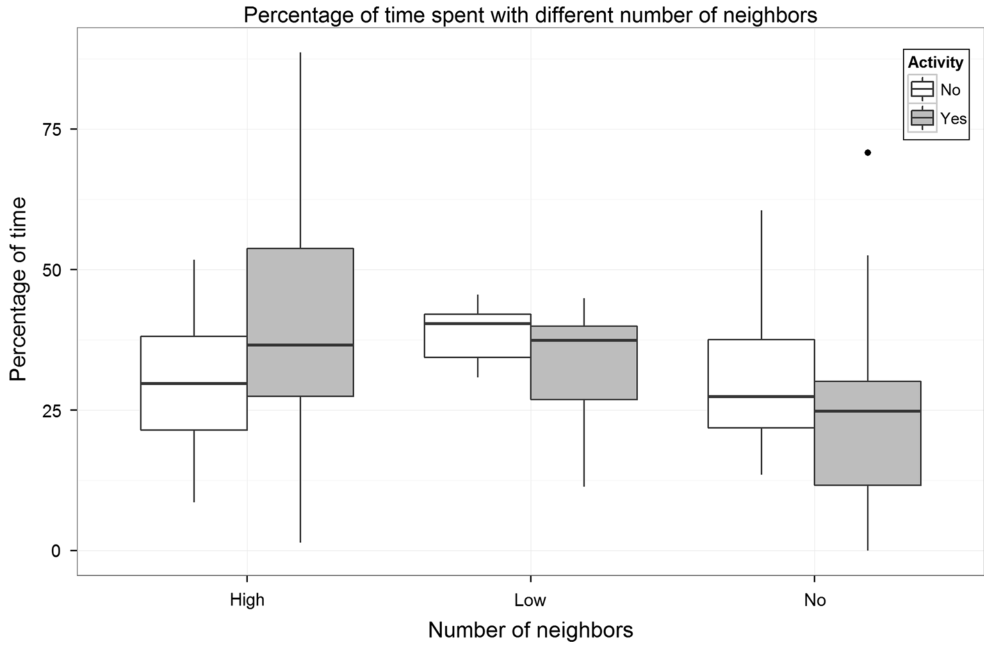

Fig. 1 Percentage of time spent by subject with no other groupmates within 5 m, with one to three groupmates within 5 m (*Low*) and with more than three groupmates within 5 m (*High*), at times of nut-cracking activity within 10 m of the focal subject (activity = yes) and no nut-cracking activity (activity = no)

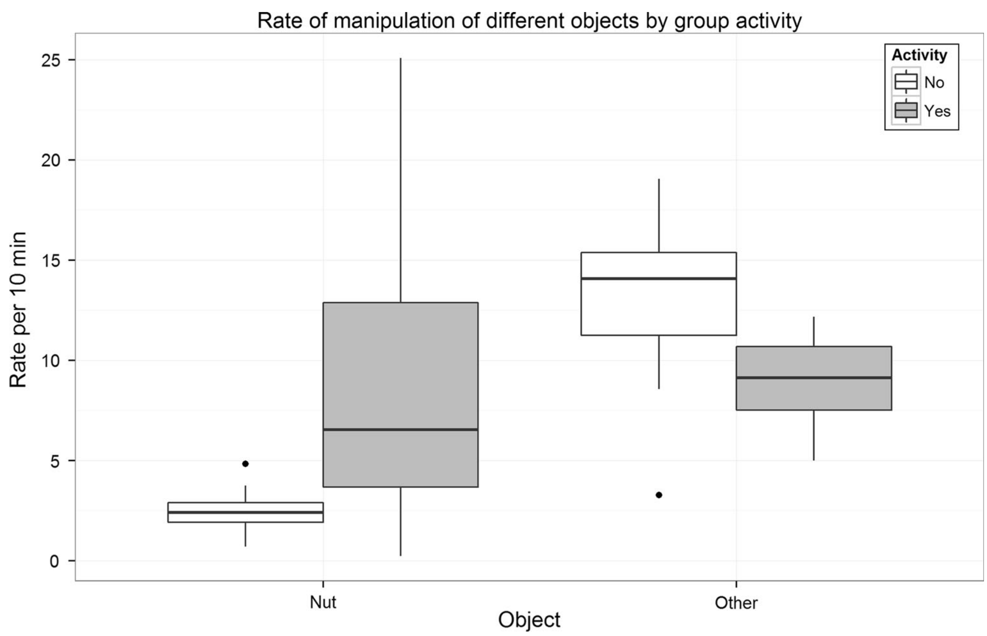

Fig. 2 Rate per 10 min of manipulation of nuts and of other objects, at times of nut-cracking activity within 10 m of the focal subject (activity = yes) and no nut-cracking activity (activity = no)

The rate of manipulation of other objects was higher when subjects were further away from an anvil, compared to when they were within arm's reach of one (median (SD): 11.5 (4.3) vs. 4.5 (5.8) per 10 min, $P < 0.0001$, estimate = 2.19, Fig. 3).

Relation between group activity and vicinity to anvils

Nut-related activity by group members affected subjects' manipulation of nuts even after vicinity to anvils is taken into account ($P < 0.0001$), and the effect of vicinity to anvils is significant when group activity is taken into account ($P < 0.0001$). The influence of group activity on manipulation of nuts was significant whether or not the subjects were near an anvil, and vice versa. As illustrated in Fig. 4 (see also Table 1), the rate of nut manipulation was lowest when the subjects were farther than an arm's reach of anvils and there was no nut-related activity in the group (median: 1.4 per 10 min, SD = 06), slightly higher when the subjects were away from anvils but others were cracking and eating nuts around them (median: 3.75 per

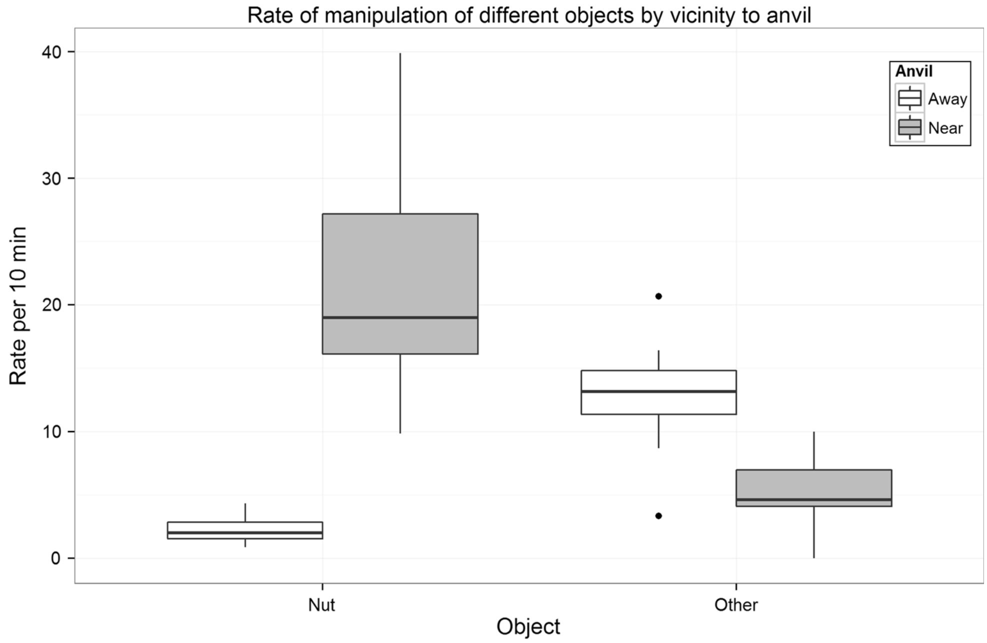

Fig. 3 Rate per 10 min of manipulation of nuts and of other objects, when the subject is on or within arm's length of an anvil, and at other times

10 min, SD = 2.6), higher still when the subjects were near (within an arm's reach of) an anvil, but there was no group activity (median: 16.3 per 10 min, SD = 9.4), and highest when the subjects where near an anvil and others were engaging in nut-related activity nearby (median: 28.8 per 10 min, SD = 19.7). In short, young monkeys coordinated their manipulative activity with nuts with the activity of others cracking nuts in time as well as in space, and these two forms of coordination were cumulative.

An opposite pattern emerges with manipulation of objects other than nuts. Here, the highest rate occurs when the subjects are away from the anvil and there are no other group members cracking and eating nuts in the vicinity, and the lowest when the subjects are near an anvil and there is nut-cracking activity around them (Fig. 4; Table 2). The negative effect of nut-related activity by group members on the manipulation of other objects by the subjects was significant even when taking into account vicinity to anvils, and the negative effect of being near an anvil on manipulation of other objects was significant even after taking into account nut-cracking activity ($P < 0.0001$ in both cases).

Influence of activity in the group and proximity to an anvil on striking a nut with a stone

The efficient way to crack nuts involves striking the nut with a stone. This action first appeared in some subjects as early as age 15 months, but became frequent only during the fourth year of life (Eshchar et al. In process). This action showed the same pattern as overall manipulation with nuts. Striking a nut with a stone was seen

Table 1 Mean and median of rate of nut manipulation under different conditions

Activity	Anvil	Mean	Median	SD
No	Away	1.49	1.39	0.6
No	Near	17.15	16.26	9.4
Yes	Away	3.96	3.75	2.6
Yes	Near	29.4	28.84	19.7

almost exclusively near an anvil (median (SD): 0.04 (0.15) vs. 1.05 (8.9) per 10 min, $P < 0.0001$, estimates: 38.6, Fig. 5), and the rate was significantly higher when there was nut-cracking activity nearby compared to times when there were no activity nearby (median (SD): 0.09 (8.9) vs. 0.05 (3.1) per 10 min, $P = 0.0006$, estimates: 2.2). It should be noted that the stones used by juveniles—especially by the younger ones—were often not the hammer stones used by adults, but smaller ones found in the area. Often these stones were not hard/heavy enough to be effective tools.

Time spent near the anvils

Subjects spent more of their time within an arm's reach of an anvil while others in the group cracked and ate nuts around them, compared to when there was no nut-cracking activity (median (SD): 11.9 % (9.9) vs. 5.3 % (11.6), ratio t test $P = 0.0073$, Fig. 6). When looking only at the observations taken in the field laboratory during dry seasons, we again see that the subjects spent significantly more

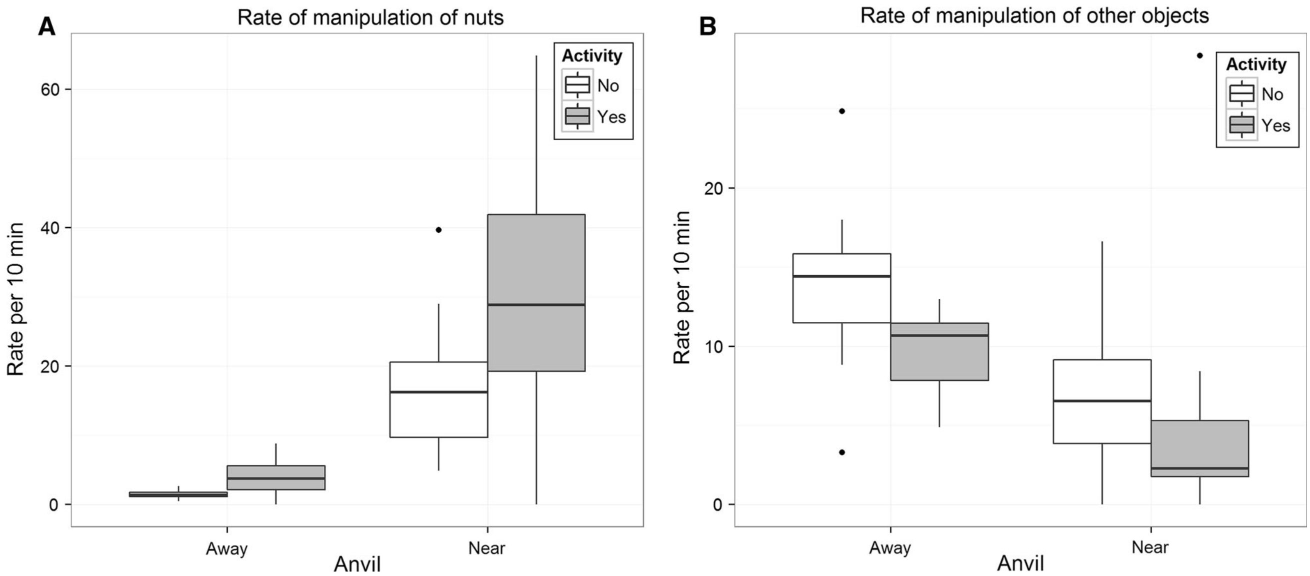

Fig. 4 Rate per 10 min of manipulation of nuts (**a**) and of other objects (**b**), at times of nut-cracking activity within 10 m of the focal subject (activity = yes) and no nut-cracking activity (activity = no), and when the subject is on or within arm's length of an anvil, and at other times

Table 2 Mean, median of rate of manipulation of other objects under different conditions

Activity	Anvil	Mean	Median	SD
No	Away	13.98	14.41	4.7
No	Near	6.82	6.55	4.6
Yes	Away	9.71	10.68	2.6
Yes	Near	4.54	2.28	6.7

of their time near an anvil when there was nut-cracking activity nearby ($P < 0.0001$).

Scrounging

Immature monkeys, especially those younger than 4 years, were highly tolerated and often stayed quite close to adults, while they were cracking and eating nuts. Immature monkeys maintained proximity not only with the mother, but also with other adults of both sexes. On occasion, immature monkeys scrounged (gained access to nut crumbs that were left from a nut-cracking episode), or licked the anvil after an adult cracked a nut there. Less frequently, immatures took cracked nuts or pieces of the kernel from the hands of others, in what is called "tolerated taking" (Fragaszy et al. 1997).

Scrounging can be done with any food item at any location. However, scrounging was much more likely to occur near an anvil (mean (SD): 0.27 (0.8) vs. 0.03 (0.1) per 10 min, $P < 0.0001$, estimate = 6.89) than farther away, and when there was nut-cracking activity nearby

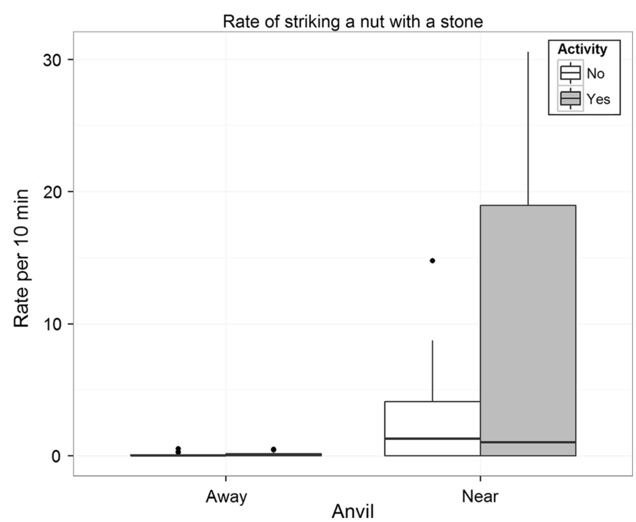

Fig. 5 Rate per 10 min of striking nuts with a stone, at times of nut-cracking activity within 10 m of the focal subject (activity = yes) and no nut-cracking activity (activity = no), and when the subject is on or within arm's length of an anvil, and at other times

than when there was not (mean (SD): 0.22 (0.6) vs. 0.08 (0.6) per 10 min, $P < 0.0001$, estimate = 6.95).

Infants began scrounging when they were a few months old, and the rate of scrounging peaked in the second year of life (average of 0.45 per 10 min, SD = 0.87). All subjects between 1 and 2 years old scrounged at least twice during that year, and one as many as 29 times. The rate of scrounging decreased with age (estimate = 0.64, $P = 0.008$) and was extremely rare in immatures 5 years and older. In fact, only one subject over 5 years was seen scrounging, and on just two occasions.

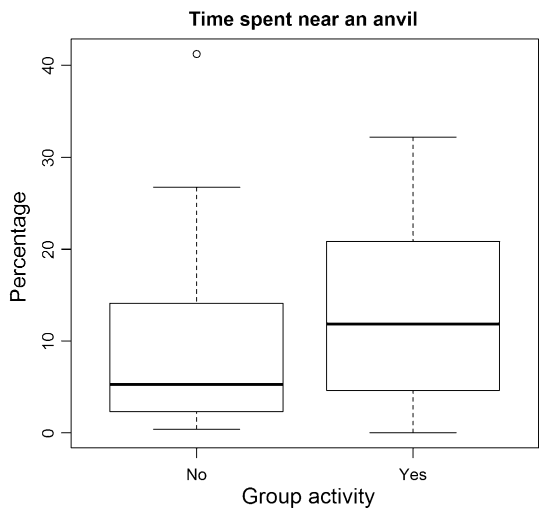

Fig. 6 Percentage of time spent on or within an arm's length from an anvil, at times of nut-cracking activity within 10 m of the focal subject (activity = yes) and no nut-cracking activity (activity = no)

Aggressive behavior and time spent with other group members

Aggressive behaviors—threats directed toward immatures or events in which immatures were displaced by others—were rather rare. The highest rate of threats that was recorded against one individual in one collection period was 0.3 events per 10 min, and the highest rate of displacements of one individual in one collection period was 0.05 events per 10 min. The threats and displacement were biased toward the older juveniles. Out of eight infants in the first year of their life, half were never threatened or displaced. However, of seven juveniles age four and older, all were seen threatened or displaced. The median of rate of aggression toward infants in their first year of life is 0.009 per 10 min (SD = 0.02), and this value peaked at age three to 4 years at a median of 0.17 aggressive events per 10 min (SD = 0.1). Juveniles aged 4 years and older received a median of 0.06 aggressive behaviors per 10 min (SD = 0.03).

Those results are even more striking because the younger juveniles had more opportunity to be the target of aggressive behavior—they spent more time with other group members. The time immatures spent alone—with no other group members within 5 m—increased significantly with age (estimate = 1.08, $P = 0.0367$). The median percentage of time infants in their first year of life spent alone was 20 % (SD = 10.3), while juveniles age four and older doubled that time, and spent a median of 42 % of their time with no other group member in the vicinity (SD = 14.7). This difference is even bigger if we look only times at which the immatures were within arm's length from an anvil. When infants in their first year of life were near an anvil, they were almost never alone (median percentage of time spent alone = 2 %, SD = 5.5). In contrast, the median percentage of time juveniles 4 year old and older spent alone while near an anvil was 31 % (SD = 23).

Influences of nut-cracking activity and proximity to anvil on different age groups

In all age groups, the rate of nut manipulation was significantly higher when subjects were near anvils, compared to times when they were far from an anvil ($P < 0.0001$ for all comparisons). Similarly, in all age groups, monkeys spent significantly more time near the anvils during nut-cracking activity in the group, compared to times with no group activity (Table 3).

Nut-cracking by others influenced immature monkeys' rate of manipulating nuts differently across age groups (see Fig. 7; Table 3). For monkeys less than 1 year old, the rate of nut manipulation was not significantly influenced by nut-related activity nearby. For monkeys from the second to the fifth year of life, the rate of nut manipulation was significantly higher when group members performed nut-related activity. In the sixth year of life, that was no longer the case.

Discussion

We present here quantitative indices of the magnitude of social facilitation and local enhancement in young capuchin monkeys with respect to activity with nuts and stones and time spent near anvils, where adults routinely crack nuts. We used a two-observer method that afforded detailed data about the activity of young monkeys in relation to the ongoing activity of others around them. Infants and juveniles interacted with nuts and hammer stones at a rate almost twice as high when others cracked and ate nuts around them compared to when others were not cracking nuts. When others were cracking nuts, the percentage of time young monkeys spent within an arm's reach of an anvil—a location rich with nut-cracking artifacts—increased almost threefold, compared to times when others in the group were not cracking nuts. While near an anvil, the immature monkeys were about ten times more likely to engage with nuts and hammer stones compared to when they were not near an anvil. We found that social influence was exerted both through others' actions while cracking nuts—which motivated the immatures to interact with nuts and stones—and through the presence of artifacts that provided opportunities for those interactions.

Importantly, these results were not simply a consequence of being with other group members. As stated before, the monkeys were sometime provisioned with nuts

Table 3 Medians and *P* value of rate of nut manipulation and time spent near an anvil at different age groups

Year	Median rate of nut manipulation per 10 min + SD		*P* value	Median percentage of time spent near and anvil + SD		*P* value
	At times of group activity	At times of no group activity		At times of group activity	At times of no group activity	
First	0.8 (2)	0.3 (0.2)	0.1860	3.3 % (3.3)	1.7 % (1.5)	0.0120
Second	8 (6.1)	2.9 (1.7)	0.0229	6.9 % (8.7)	3.4 % (2.3)	0.0086
Third	7.2 (5.1)	1.8 (2.6)	0.0192	30 % (12.1)	9 % (6.6)	0.0007
Fourth	9.3 (9.6)	3.7 (3.1)	0.0178	15.5 % (8.4)	5.6 % (3.4)	0.0001
Fifth	6 (9.2)	2 (5)	0.0304	6.5 % (7)	3.3 % (3)	0.0153
Sixth	12.2 (1.9)	5.7 (3.3)	0.2007	16.6 % (6.8)	5.9 % (3.4)	0.0064

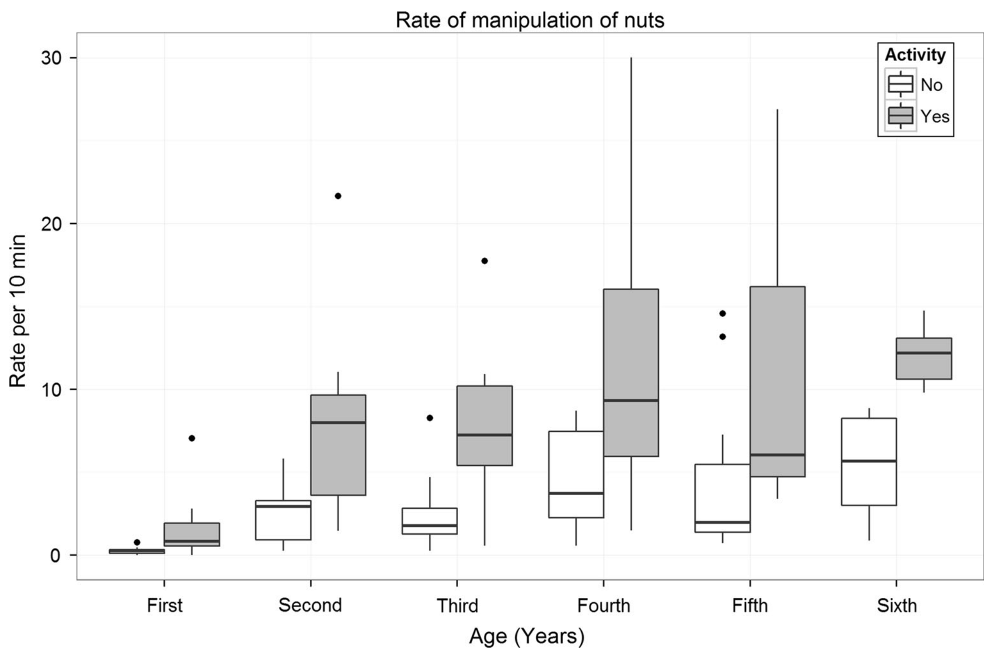

Fig. 7 Rate per 10 min of manipulation of nuts and of other objects, at times of nut-cracking activity within 10 m of the focal subject (activity = yes) and no nut-cracking activity (activity = no), by age

in the "field laboratory." There are several anvils in this area, and nut-cracking is very common there. The anvils in this area as well as the ground around them are covered with many broken nut shells. When the group is in the field laboratory, opportunities to interact with nut shells are extremely high. However, when looking only at data collected while the monkeys were in the field laboratory, the immature monkeys were still more likely to manipulate nuts when their group members cracked and ate nuts than when other group members were not cracking. Moreover, even when the subjects were already near an anvil (both in the field laboratory and elsewhere), the rate at which they manipulated nuts and stones was higher when others were cracking nuts nearby than when they were not.

Overall, our conclusion is that immature monkeys match the adults' interest and behavior with nuts and stones in time (manipulating and striking nuts when they saw others cracking) and even more strongly in space (manipulating nuts or stones near and on the anvils used for nut-cracking), both components of social influence as described by Coussi-Korbel and Fragaszy (1995). Below we examine the findings in more detail and in relation to what is known for other species, and discuss alternative interpretations.

First prediction: Immature monkeys manipulate nuts and nut debris at a higher rate when they can see and/or hear other individuals crack and eat nuts around them

This prediction was fully supported by our data. We defined "nut-cracking activity nearby" when other members in the group were cracking or eating nuts within 10 m from the focal subjects (immatures), or when the sound of nut-cracking could be heard. The rate of manipulation of nuts by our subjects under those circumstances was about four times higher compared with times when no nut-cracking activity took place nearby. This influence was also seen on the actions of striking a nut with a stone—the basic actions of efficient nut-cracking.

The findings were specific to interactions with nuts: The rate of manipulation of objects other than nuts and stones *decreases* when there is nut-cracking activity nearby. This indicates that the higher rate of manipulation of nuts and stones by immatures results from social facilitation and local enhancement: The presence of group members engaged in cracking and eating nuts motivates immature monkeys to interact with the same items in the same places.

As discussed above, there is plenty of evidence for the power of social facilitation to influence behavior in fish, birds and mammals (Clayton 1978). Hoppitt et al. (2012) showed specifically that in meerkats, the rate of engaging in a task is higher immediately after seeing a groupmate doing so, and the rate of abandoning the task is lower. The situation in Hoppitt et al.'s study is different from ours in one significant aspect: The meerkats had only two baited containers next to each other and could not easily engage in the task concurrently with another meerkat. The capuchins could interact with nuts while observing others cracking nuts around them. Therefore, we suggest that the higher rate of manipulation of nuts and stones *during* nut-cracking activity nearby stems from the same influence as that seen by Hoppitt et al. in meerkats immediately *after* observing others engaging in the task.

Second prediction: Immature monkeys manipulate stones, nuts and nut debris at a higher rate when they are next to an anvil

The second prediction was also fully supported by our data: The subjects did nearly all of their nut-related activity within arm's reach of an anvil site. It should be noted that nuts and nut shells were also found away from the anvils, and nut manipulation did occur at locations other than the anvils, albeit at a lower rate. Although other objects were found near the anvils (leaves, pieces of wood, etc.), our subjects preferably interacted with nuts and stones in those locations, and the rate of manipulation of other objects was lower near the anvils compared to other places.

These findings suggest that interacting with the artifacts made by nut-cracking, in the place where nut-cracking has taken place and in vicinity to the tools (hammer stones) used for it, is a key feature of practice for young monkeys. Other studies have shown the effect of interacting with artifacts created by specific activities on the learning of the same activities by nonhuman animals [e.g., see (Aisner and Terkel 1992; Gunst et al. 2008; Thornton and Hodge 2009)]. By interacting with nuts and stones near the anvil used by adults, our subjects increased the frequency of habitual actions combining nuts, anvils and stones, including the functional ones used by adults. The fact that monkeys use stones to hit nuts almost exclusively on an anvil supports this hypothesis.

Third prediction: Immature monkeys spend more time near anvils when other individuals crack and eat nuts

This prediction was also supported; immatures spent almost three times more of their time near an anvil when there was nut-cracking activity around them, than when others were not cracking nuts. We suggest that immatures were drawn to the anvils, while nut-cracking was taking place there partly by their interest in obtaining crumbs of nut kernels. Adults were very tolerant toward immatures less than 4 years old that approached the anvil, while they were cracking nuts. They did not prevent young juveniles from collecting crumbs from the anvil, and in a few cases, the juveniles even took a kernel directly from an adult's hand. Scrounging was performed by all young juveniles, and its rate peaked in one- to two-year-olds. Scrounging was more likely to take place near an anvil, when there was nut-cracking activity nearby. This is probably due to the nature of nut-cracking—it often creates crumbs, and discarded nut shells sometimes still contain pieces of kernels, so scrounging on nuts is more likely to be profitable than scrounging on other food items that are swallowed as a whole, or not fractured in pieces. Older immatures (4 years and older) scrounged much less often. They were sometimes threatened, but were never attacked, when approaching an adult while it was cracking nuts.

These findings are in line with previous studies, which showed that immature capuchins scrounge readily from adults both in captivity (Fragaszy et al. 1997) and in the wild (Coelho et al. 2015). Transfer of food from adults to infants, including tolerating scrounging, has been seen in other nonhuman primates, though it is not very common [for review—(Brown et al. 2004)]. Specifically, it was reported in various species of callitrichids [e.g., (Rapaport 1999; Vitale and Queyras 1997)] and in great apes (e.g., Boesch and Boesch-Achermann 2000; Nishida and Turner 1996; Russon 2003). In those species, learning about foods that can be included in the diet might be aided by scrounging, as was suggested for callitrichids (Caldwell and Whiten 2003).

Fourth prediction: Social influence changes with the age of the subject

The data partly supported this prediction. Being near an anvil strongly affected the likelihood of interacting with nuts and stones at all ages considered—presumably because anvils provided opportunities for nut-related activity. Similarly, subjects of all ages spent more time near the anvil when there was nut-cracking activity nearby. This is somewhat surprising: Scrounging had all but disappeared by age five, and juveniles aged four and older were threatened and displaced more often compared to the younger juveniles. The data also showed that older juveniles (unlike the younger ones) spent a significant percentage of their time while near an anvil by themselves. Thus, the older juveniles may have been coming to the anvils during nut-cracking for different reasons than younger monkeys. Older juveniles did not scrounge for crumbs, but they might still have been attracted to others cracking nuts by intrinsic interest in this noisy activity. Some of them could crack nuts themselves, and when motivated to engage with nuts, they might have gone to a different anvil to try to crack nuts there.

Nut-cracking activity nearby influenced the young monkeys' rate of manipulating nuts in all age groups except the one-year-olds and the subjects older than 5 years. Infants interact with nuts opportunistically, whenever a nut or nut shell happens to be next to them. Thus, it is not surprising that we do not see any influence of others' nut-cracking on their behavior. Those 5 years old and older might not have been influenced by nut-cracking behavior nearby because they are less tolerated by the adults, and/or because they are already able to crack nuts with tools (Resende et al. 2014; Eshchar et al. In process). They were drawn to the anvils at times of nut-cracking in the group, but they did not spend their time there practicing and trying different actions with nuts, shells or stones, as the younger juveniles did.

Overall, the data show that social influence was most apparent between 12 and 48 months, when immatures were already independent feeders, interested in interacting with nuts and stones, and were still tolerated by the adults.

Model of social influence

We suggest a model for the social influence on nut-cracking skill development in young capuchin monkeys. The model is composed of two related processes:

1. Seeing group members cracking and eating nuts encourages infants and juveniles to interact with nuts and stones themselves. This influence is exerted in two ways:
    (a) Through social facilitation of action, as seen in previous studies [e.g., (Ferrari et al. 2005; Hoppitt et al. 2012; Matthews et al. 2010; Nagell et al. 1993)]. Seeing/hearing group members engage in a particular behavior, and getting a reward from it [which serves as vicarious reinforcement (Bandura et al. 1963)], motivates the observers to engage in the same activity.
    (b) Through local enhancement, i.e., drawing infants and juveniles toward the anvils, where nut-cracking has taken place. In those locations, there are usually many nut shells and debris, as well as a hammer stone. Infants and juveniles are probably drawn there by the presence of food, but when they are there, they have a lot of opportunity to interact with those artifacts (stimulus enhancement). Thus, capuchins are motivated to coordinate their behavior with others in both time and space.
2. Through interaction with artifacts created by nut-cracking. Previous studies have shown the importance of artifacts created by a specific behavior in learning the same behavior (Aisner and Terkel 1992; Gunst et al. 2008; Thornton and Hodge 2008). By interacting with nut shells on and around the anvils, the infants and juveniles can learn to associate nuts with food, and to learn the consequences of striking the nut on an anvil (vs. another surface) using a stone (vs. another object). This mechanism increases the breadth of social influence beyond the limited time in which others are cracking nuts (Fragaszy et al. 2013a).

Social influence is clearly not the only factor promoting acquisition of nut-cracking. We suggest that the processes described above provide repeated opportunities for the juveniles to manipulate nuts and stones in different ways, especially on the anvils, and motivate them to continue with this manipulation even in the absence of immediate tangible reward. Through this type of practice, which extends over years, they eventually master nut-cracking.

The same model can be applied to the mastery of other extractive foraging tasks by immature animals, especially those that take time to master. Such tasks were studied in capuchins [e.g., processing Maripa fruits (Gunst et al. 2010a), detecting larvae hidden in bamboo (Gunst et al. 2010b), processing Luehea fruits (Perry 2009)], as well as in chimpanzees [e.g., nut-cracking (Inoue-Nakamura and Matsuzawa 1997), termite fishing (Lonsdorf 2005), and harvesting Saba fruits (Corp and Byrne 2002)]. Outside the primate order, examples of development of extractive foraging include digging for prey in meerkats (Thornton and Hodge 2008) and extracting beetle larvae with probing tools in New-Caledonian crows (Holzhaider et al. 2010). All those studies describe a long period of learning and practice before juveniles reach adult-level efficiency. In several cases, studies have suggested that social influence motivates this long practice. The importance of artifacts was also noted in some studies (e.g., Carvalho et al. 2009).

This model presents an integrative perspective, combining two types of social influence—social facilitation and stimulus/local enhancement—with individual learning, and a major role for practice opportunity provided by artifacts. The method developed to obtain these data takes into consideration the behavior of both the focal monkey and other group members, and has proven to be extremely useful for evaluating quantitatively these different types of social influence on behavior. To our knowledge, other observational methods have not been able to support similar evaluations, particularly for group-living animals in natural settings. The method allowed us to carry out this sophisticated analysis of a complex behavior which is spontaneously acquired by wild capuchins, in a natural setting where many individuals are engaged in different activities concurrently. We suggest that similar examination of other extractive foraging behaviors in other species in natural settings will reveal a learning process not unlike the one described here. We hope that future studies will build on this method and this model, to elucidate the often-elusive role of social input in skill development, thereby strengthening our understanding of tradition in nonhuman taxa.

Acknowledgments We thank the people who helped collect the data: Kelly Laity, Jessica Tinker, Ani Popp, Carlos Carvalho, Michele Verderane, Natalie Schwob, Andrès B. Ardila; and especially Samara, Marcio, and Marcos Fonseca Oliveira, Marino Gomes de Oliveira and the entire Oliveira family, for their help and their permission to work on their land. Permits to EthoCebus research were given by IBAMA SISBIO: 28689-3 and CNPq: 002547/2011-2. The research was funded by the National Geographic Society, the University of Georgia, CAPES—Coordenadoria de Aperfeiçoamento de Pessoal de Nível Superior, FAPESP—São Paulo Research Foundation, and CNPq—The Brazilian National Council for Scientific and Technological Development (STREP Contr. No 029088). We thank the statistical consulting service at University of Georgia for their help in analyzing the data, and the University of Georgia Graduate School's Dean's award for the funding of this service.

Compliance with ethical standards

Conflict of interest We declare that we have no conflict of interest.

Ethical standard We declare that the study complies with Brazilian current laws regulating animal care and use, and with the guidelines for research with animals as outlined by the Association for the Study of Animal Behavior.

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