DEVELOPMENT OF TOOL-USE BEHAVIOR IN A SOCIAL CONTEXT – NUT-CRACKING IN WILD BEARDED CAPUCHIN MONKEYS (*SAPAJUS LIBIDINOSUS*)

By

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(Under the Direction of Dorothy M. Fragaszy)

ABSTRACT

The habitual use of tools by wild capuchin monkeys presents a unique opportunity to study the maintenance and transmission of tradition. Here we study the development of tool-use in wild bearded capuchin monkeys (*Sapajus libidinosus*), and the social influence on this behavior. We followed a wild, habituated group in which most adults habitually crack nuts using anvils and hammer stones. We followed 16 infants and juveniles in five collection periods during 26 months, recording their behavior and the behavior of other individuals around them. Manipulation of nuts started at the age of few months, as single-object manipulation and object-to-surface actions. Combinatory actions appeared later, shortly after weaning. The juveniles adopted more efficient strategy for nut-cracking with age, and the rate of non-efficient actions decreased. Overall, infants and juveniles sustain a high level of interest in nuts and stones long before they can efficiently crack. We suggest that this interest is maintained with the help of social influence.

We show that the juveniles match the behavior of the adults in both time and space. The rate of manipulation of nuts by the juveniles was higher when others in the group cracked and ate nuts, and also when the juveniles themselves were near the anvils, where nut-cracking takes place. We suggest a model for the social influence on nut-cracking skill development that is based on two related processes: social facilitation from observing groupmates engaged in nut-cracking, and the opportunity for practice provided by the anvils, hammer stones and nut shells on and around the anvils.

Finally, we show that the rate of manipulation of nuts by infants and juveniles declines exponentially in the minutes following the end of nut-cracking activity around them, as does the time infants and juveniles spent near an anvil. The dynamics of social facilitation changed with the age of the juveniles, with the older juveniles showing a longer half-life for nut-related behavior.

This is the first study to provide such a broad and quantitative approach to the development of tool use, or indeed, any behavior thought to be traditional, in a wild population.

Key words: tool use; development; Sapajus, social learning; social facilitation; skill acquisition

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CHAPTER 1:

INTRODUCTION AND LITERARY REVIEW

The ability of animals to learn from each other, and the idea of tradition transmitted from generation to generation in animal societies, have long captured the imagination of researchers from various fields. In the last few decades this interest has blossomed to what Galef and Giraldeau called "an explosion of research", specifically in the area of social influence on foraging behavior (Galef and Giraldeau 2001).

This interest was partly driven by the discovery of tool use traditions in non-human primates, first in chimpanzees (Goodall 1964; Boesch and Boesch 1981; Sakura and Matsuzawa 1991), and later in orangutans (Van Schaik and Knott 2001), capuchin monkeys (Fragaszy, Izar et al. 2004) and recently, long-tailed macaques (Gumert and Malaivijitnond 2012). Together with the first detailed description of social transmission in a wild population (e.g., (Kawai 1965)), those discoveries led to heated discussions about the extent to which the term "culture" can be applied to non-human animals, and the relation between animals' traditions and the evolution of culture in our own species (e.g., (Galef 1992; Boesch 2003; Byrne, Barnard et al. 2004; Laland and Janik 2006; Whiten 2010) among many, many others).

The debate about animal culture is still raging, fueled in part by a lack of consensus as to what the definition of culture should be (Laland and Janik 2006). Although it is clear that any cultural practice that may exist in non-human animals is a far cry from the diversity and complexity of human culture, aspects of what characterizes our own culture – some forms of social learning, simple forms of tool use – can be seen in other animals, notably in other primates. Since behavior does not fossilize, in order to study the evolution of this universal phenomenon –

human culture – we can only look at the fossilized remains of culture – such as stone tools – or at the behavior of our extant relatives (Byrne 1995). By looking at the behaviors of extant primates, those which are closely related to us and those which are more distant, we can learn about the evolution of the traits underlining culture, and what are the conditions that support their evolution (Whiten 2010).

Here we review the behavior of extractive foraging, and especially tool-use – behaviors that are often seen as potential traditions. We then review the different mechanisms for social learning, and the methods to study them. We end by discussing the temporal aspects of social influence.

Extractive foraging

Primates as a rule are omnivores, but there are many differences in diet among the different species. Several genera of non-human primates (NHP) use an "omnivorous extractive foraging" strategy (Parker and Gibson 1977). Those species include chimpanzees, orangutans, capuchins, baboons and macaques, and to some extent squirrel monkeys and mangabeys. The diet of those species includes hard-to-access food items such as tubers, nuts with hard shells or invertebrate that are either embedded in a protective shell or reside inside branches, mounds etc., complementing the more easily obtained food such as fleshy fruits. (Yamakoshi 2004; Melin, Young et al. 2014). Species reliant on extractive foraging show greater frequency and variability of complex object manipulation compared to the non-extractive foragers. Specifically, in an experimental study with captive individuals, great apes performed more "secondary actions" (actions with two objects or object and a surface) followed by capuchins and then macaques, leaving the leaf-eaters behind (Parker 1974). In another study, captive capuchins and apes were shown to perform the most sophisticated manipulation, followed by the omnivores among the old world monkeys (Torigoe 1985)

Capuchin monkeys (genera *Sapajus* and *Cebus*) show extractive foraging techniques in the wild (Fragaszy, Visalberghi et al. 2004), for example, Sapajus -(Gunst, Boinski et al. 2010), Cebus - (Panger, Perry et al. 2002). Their manipulative nature is readily seen in the lab. In captivity, capuchins (*Sapajus* spp.) start manipulating objects very early in life, at about 8-12 weeks. Concurrently with the first episodes of manipulation, they engage in percussive activity (Adams-Curtis and Fragaszy 1994). Those vigorous object-to-surface actions are a common characteristic of capuchin behavior, and previous researchers have noted their preference for "banging operation patterns" [(Yamakoshi 2004), pg. 161]. The rate of all manipulations increases rapidly through the first year of life, as does the proportion of more dexterous actions (Fragaszy and Adams-Curtis 1997).

Several studies explored the ontogeny of extractive foraging skills in wild capuchins. Perry (2009) studied handling of the Luehea fruit – hard shelled fruit that can be opened using pounding or rubbing - in several groups of white-faced capuchin (*Cebus capucinus*) in Costa Rica. (Perry 2009). Gunst (2010) looked at two different foraging tasks facing brown capuchins (*Sapajus apella*) in Suriname. In harvesting the maripa palm fruit, the limiting factor seemed to be the size and strength of the individuals (Gunst, Leca et al. 2010), while in preying on larvae enclosed in bamboo stalks, detection of the prey was the more complicated part of the task, and the last to be mastered by the juveniles (Gunst, Boinski et al. 2010).

These examples all show that capuchin monkeys face foraging tasks that take years to master efficiently. During this period the juveniles engage with the food items, even if they only get low payback for their efforts (and sometimes no payback at all). They also often engage in non- or less-efficient strategies, that they abandon when they become older and more efficient. Some skill development is directly related to body size, and other skills depend more on development of manual dexterity and/or cognition.

Tool-use – a special case of extractive foraging

Tool use was defined by Alcock [(Alcock 1972), pg. 464] as "the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the position or form of some separate object". In primates, most if not all habitual tool use is seen in the context of extractive foraging, and can be regarded as an extreme example of this behavior. All NHP that use tools also use other forms of extractive foraging, though the opposite is not true (Yamakoshi 2004).

As with other extractive foraging, too-use often takes years to master, and juveniles become gradually more efficient with time. We present here two well-studied examples from chimpanzees, which demonstrate this trajectory.

Termite fishing in chimpanzees

Termite fishing using sticks or grass blades was the first tool-use behavior in wild primates to be systematically studied (Goodall 1964). Soon after its discovery, the inefficient actions of infants with sticks and termite-mounds were also reported. Goodall (1968) described infants in a group in Gombe National Park, Tanzania using sticks that were far too short and often also too thick or too thin to be effective. Even when working with adequate tools, their techniques were clumsy and their attempts were very rarely successful (van Lawick-Goodall 1976). Lonsdorf (2005) looked more closely at the development of termite-fishing in young chimpanzees, in the same population (several generations later). Though all subjects could identify the hole and were seen manipulating a tool by 18 months, they start inserting the tool into the hole only at 2.5 years of age at the earliest, and successful extraction of termites was seen in some individuals only when they were 5.5 years old. In the years between the time their interest was first piqued by a termite mound and the time they could gain access to it, the young chimpanzees engage in a variety of behaviors: poking the mound and holes with their fingers, sniffing and looking into the holes, as well as picking up used tools, examining and manipulating them. Even after they were inserting the tool into the hole, they still had to refine their technique – to learn how deep to insert it and how long to leave it inside – before they became efficient tool users (Lonsdorf 2005).

Nut-cracking in chimpanzees

Nut-cracking using hammers and anvils was known for many years in several chimpanzee populations in West Africa, from Senegal to Côte d'Ivoire (Boesch, Marchesi et al. 1994), and in recent years was reported as far east as Cameroon (Morgan and Abwe 2006). The development of nut-cracking by young chimpanzees was studied in a habituated group in Bossou, Guinea. Inoue-Nakamura and Matsuzawa (1997) found that infants start interacting with nuts and stones in the first year of life, although they cannot open a nut by themselves until they are about 3.5-4 years old (and it takes them several more years to become efficient). The young chimps start with single manipulations of a single object, and then move on to connect nuts and stones with a surface – rolling, pressing and hitting. The frequency of object-to-surface actions increase with age, and by 3.5 years of age the chimps start to combine the nut and stone, and first nut-cracking is seen. Inefficient actions – such as raking the nuts or rolling them – are seen at age one and two but disappear by 3.5 years of age. Conversely, the frequency of actions that are part of efficient nut cracking increases with age (Inoue-Nakamura and Matsuzawa 1997).

Nut-cracking in capuchins

Together with chimpanzees, tool-use in capuchin monkeys is probably the best-studied examples of this behavior. Wild bearded capuchin monkeys, *Sapajus libidinosus*, of both sexes, use stone tools to crack palm nuts to obtain the kernel, and they do so on specific anvils composed of stone or wood (Fragaszy, Izar et al. 2004). Adult monkeys display variable efficiency, which correlates positively with body size (Fragaszy, Pickering et al. 2010). Tool users are highly selective of the stones, anvils and nuts they use, and how they use them (Visalberghi, Fragaszy et al. 2007; Visalberghi, Addessi et al. 2009; Fragaszy, Greenberg et al. 2010; Spagnoletti, Visalberghi et al. 2011; Fragaszy, Liu et al. 2013).

The ontogeny of this behavior was studied in a semi-free group in Tiête Ecological Park, Brazil. Resende (2008) showed that in this group, simple manipulations like picking up, biting and smelling nuts were seen at about the same time as the characteristic percussive actions, before the subjects reached six months of age. Combinatory actions with two objects (hitting one object with another) appeared at two years of age. Only two subjects were seen cracking nuts, and they first did so at age 25 and 29 months (Resende, Ottoni et al. 2008). These patterns are consistent with what has been found in captive capuchins (Fragaszy and Adams-Curtis 1997). A subsequent study with the Tiête capuchins showed that as the juveniles got older and gained more practice, their strikes became more efficient and they used fewer actions that were not essential for cracking (Resende, Nagy-Reis et al. 2014).

What motivates young animals to dedicate so much of their time to practice tool-use and other extractive foraging, when often they do not gain any food reward for their efforts? The answer might be found in social influence on this behavior.

Social learning

Social learning was defined by Heyes as "Learning that is facilitated by observation of, or interaction with, a conspecific, or its products'' ((Heyes 1994), pg. 207). Learning from others is common throughout the animal kingdom, and is found in fish, birds, mammals and insects (Galef 1996; Galef and Laland 2005; Leadbeater and Chittka 2007). When a behavior that is acquired, at least partly, through social influence persists over time, and is transmitted from generation to generation, it can be called a tradition (Fragaszy and Perry 2003; Whiten 2009).

Social learning can be achieved through different processes (for example, imitation, emulation, social or response facilitation and local enhancement). Imitation is broadly defined as "copying the form of an action" ((Whiten, McGuigan et al. 2009), pg. 2418), and in some cases, more narrowly, as copying the exact actions of an agent. Emulation, on the other hand, is defined as copying the end-state of an action – in this process, the learner observes the changes to the inanimate world that are the result of the behavior of another individual, and designs its own actions to achieve the same changes (Tomasello 1996). Response facilitation (sometimes called social facilitation) takes place when the mere presence of a demonstrator performing an action, or a set of actions, increases the probability of an animal observing it to engage in the same activity (Heyes 1994; Visalberghi and Addessi 2000). Local or stimulus enhancement is defined as a situation in which exposure to an individual's activity, or to the products of this activity, draws the observer’s attention towards the location of the activity and/or a specific object in this location involved in it (Heyes 1994; Hoppitt and Laland 2008). The observer then interacts with the object or explores the location, but not necessarily performs the same activity as the “demonstrator”.

Studies have shown that animals, while undoubtedly learning from their groupmates, rely on different mechanisms than those humans apply for the same end. Unlike humans, animals almost never engage in active teaching (although rare cases were reported, see (Boesch 1991; Thornton and Raihani 2008)). In addition, while humans imitate readily from a very young age, and do it without a need for external motivation (Meltzoff 1996), this is not the case for non-human animals. It is not yet clear to what extant true imitation - observing a demonstrator and faithfully copying its movements – exists in animals, and whether it can explain the spread of novel behaviors in a population. Several studies have shown that various animals are capable of at least some form of imitation (Akins and Zentall 1996; Moore 1996; Zentall, Sutton et al. 1996). However, when asking whether imitation plays a major role in the way non-human animals learn from each other, the answer seems to be a qualified “no”: there is very little evidence for imitative learning in the wild (e.g., (Tomasello 1994; Boyd and Richerson 2005; Rendell, Fogarty et al. 2011), although, see (Voelkl and Huber 2000)).

Instead, animals learn from each other mainly through emulation, local enhancement, and social facilitation (Tomasello 1994; Hoppitt and Laland 2008). Captive studies in various species, from graylag geese (Fritz, Bisenberger et al. 2000) to chimpanzees (Nagell, Olguin et al. 1993), show that animals can learn to perform a foraging task through local enhancement, without repeating the exact actions they are seeing.

It is important to note that social and asocial learning are not mutually exclusive. In learning a complex behavior, both social and asocial processes are likely to play complementary roles. This was termed “socially biased learning”: individual learning that is informed and influenced by social input (Galef 1995; Fragaszy and Visalberghi 2004).

Importance of artifacts

Social influence can be exerted not only through direct observation, but also from interactions with the artifacts left by a certain behavior. This is the often-neglected part of the Heyes’ definition of social learning, its last three words: “or its products”. Enduring artifacts associated with technical activities – such as open shells, broken branches, holes dug in the ground and more – can help individuals master the same tasks (Fragaszy, Biro et al. 2013). Artifacts provide opportunities for learning and practice, and can also be associated with the actions performed by the adults, and thus reinforce the lessons learned through observations.

The importance of artifacts was demonstrated in several studies, the most famous of which might be Aisner and Terkel’s study on the foraging behavior of the black rat (Aisner and Terkel 1992). In this species, pups learn the correct way to strip pine cones and eat their seeds while foraging with the mother. Careful experimentation on wild-caught rats showed that the cones themselves play a major role in this process. The authors suggest that wild rat pups learn to strip cones through stealing partially open cones from their mothers. They learn first how to continue to strip them, and then how to strip an intact cone.

Thus, behavior can be transmitted socially and traditions can be maintained over time with processes such as local enhancement and social facilitation, processes that can at times take place even without direct observation.

Studying social learning

Establishing the role of social learning in the transmission of any specific behavior is not easy. Different studies apply different approaches to the problem. In the ethnographic method, researchers compare the pattern of variation in the behavioral repertoire of two or more groups, and can infer social transmission to be the cause of those variations, if genetic and ecological influences can be excluded (Laland and Hoppitt 2013). This method was used intensively in non-human primates' studies, including tool-use and other foraging traditions in chimpanzees (Whiten, Goodall et al. 1999) and orangutans (Van Schaik and Knott 2001). Other studies looked at the correlation between behavioral variations used by mothers and those used by their offspring (Perry 2009; Sargeant and Mann 2009; Holzhaider, Hunt et al. 2010). Both methods attempt to answer the question of the presence or absence of social influence on learning, but do not touch on the question of *how* this influence is exerted. Most studies that examined the processes of social learning are done on captive subjects (e.g., (Dindo, Thierry et al. 2008; Tennie, Call et al. 2010)), where all interactions with specific tasks, locations of all group members, observations of any activity etc. can be recorded. Those studies are invaluable for understanding the learning processes that different species are capable of, and which ones are likely to be used under different conditions.

Those studies, however, can only tell us how animal **can** learn, not how they **do** learn species-typical behaviors, under natural conditions. To answer that question, we need to turn to observational, developmental studies on wild populations. Several such studies were published (for a review - (Meulman, Seed et al. 2013). Biro et al. followed the ontogeny of nut cracking and leaf folding in chimpanzees, and detailed the possible social influences on the development of those behaviors (Biro, Inoue-Nakamura et al. 2003; Biro, Sousa et al. 2006). Lonsdorf studied termite-fishing in chimpanzees, and how the time a mother dedicates to fishing correlates with skill development of her offspring (Lonsdorf 2005). Coelho et al. studied nut-cracking capuchin monkeys, and showed that the juveniles preferentially observe nut-cracking sessions performed by dominant adults and proficient nut-crackers (Coelho, Falótico et al. 2015). This is the approach we take in this study.

Dynamic of social facilitation

As mentioned above, many studies have the importance of social facilitation and local enhancement in transmission of tradition. The effect is usually measured as the activity before observation compared to during or immediately after this observation. Most studies do not address the question of timing – how long after the observation the effect lasts. When this question is addressed, studies usually only check if the effect persists after some fixed interval (e.g., (McQuoid and Galef 1992)). As far as we know, the only paper that attempted to estimate the decay of this effect is Hoppitt et al (2012). In this study, wild meerkats were presented with baited boxes, and all interactions with the box, as well as the observations of conspecifics interacting with – and solving – the task, were recorded. The researchers found that individuals were more likely to interact with the box immediately after observing a conspecific interacting with it, and they also estimated the duration of this effect. When fitting an exponential model, the half-life of the effect – the time it takes it to halve in magnitude – was 20 seconds.

Since the literature on decay of social influence is, as mentioned, extremely scarce, we can turn to the literature on learning by reinforcement. When an animal receives an incentive – such as a food reward - its arousal state increases. This increase has the effect of increasing the activity of the animal. If the incentive was coupled previously with a specific response, the animal will be more likely to perform this behavior following the incentive. This arousal decays exponentially, so that at time t after delivery of the incentive,

$$A_t = A_0 * e^{-\beta t}$$

Where A_0 is the level of arousal at the time of delivery, and β is the rate by which the level declines with time (Killeen 1979; Killeen 1998).

This is the same equation Hoppitt et al. used to model the transient effect of observing a conspecific interacting with the box. In their model, A_0 denotes the strength of the social facilitation effect, and β denotes the rate by which the effect dies away. Therefore, the incentive in this case is not a reward, but an observation of others engaging in a specific behavior – which was shown time and again to indeed be a strong motivator. This seems to us to be an appropriate way to examine the decline in time of social influence.

Current study

In the first paper, we set out to study the developmental trajectory of nut-cracking behavior of wild bearded capuchins. We examine the appearance and trajectory of several behaviors: any manipulation of nuts, percussive actions with nuts, and combinatorial actions – combining nuts and stones. We compare those behaviors to other foraging activities, both with easy-to-access food items and other hard-to-access food. We link the development of tool use both to the weight of the infants and juveniles and to weaning. With comprehensive recording of activities and a wide range of ages of subjects, we could examine the long period of learning and practice before the juveniles start cracking nuts, and how their behavior changes afterwards.

In the second paper, we study the social influence on this period of practice. We consider two potential influences on infant and juveniles: direct observation of their groupmates cracking and eating nuts, and opportunity for individual learning and practice provided by nut debris, hammer stones and anvils. We studied those influences using a two-person data collection method, in which we record concurrently the behavior of a focal monkey – infant or juvenile – and the behavior of other monkeys in the group around them. We examine how the rate on nut-related activity – and other activities - by infants and juveniles changes when others crack and eat nuts around them, and when they are near an anvil – a location rich with nut debris. We also examine how these processes relate to each other, i.e., how observing others cracking nuts influence the likelihood of juveniles to spend time near an anvil. Finally, we consider those influences on infants and juveniles at different ages.

In the third paper, we study the temporal aspect of social influence. We examine how the rate of manipulation of nuts – and specific activities with nuts – declines when other members of the group *stop* cracking nuts. This is an aspect of social influence that has received almost no consideration in the past.

Together, these three papers present a full picture of tool-use development, from ontogeny to social influence.

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CHAPTER 2

ONTOGENY OF NUT-CRACKING BEHAVIOR IN WILD BEARDED CAPUCHINS (*SAPAJUS LIBIDINOSUS*): LINKS TO GROWTH, WEANING AND FORAGING[1]

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1. Eshchar, Y., D. M. Fragaszy, et al. (In process).
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Abstract

Capuchin monkeys, like several species of primates, are extractive foragers – feeding, among other things, on hard-to-access or hard-to-process food. Young individuals need to learn how to handle those food items – a task that might take several years. Here we study the development of tool-use in wild bearded capuchin monkeys (*Sapajus libidinosus*). We followed a wild, habituated group in which most adults habitually crack nuts using anvils and hammer stones. We recorded the behavior of 16 infants and juveniles in five collection periods, six to eight weeks each, during 26 months. This enabled us to examine the long period of learning and practice leading the juveniles to eventually master nut-cracking, and follow the development of individual subjects through the years. We show that the frequency of foraging on hard-to-process items increased around the age of weaning, while foraging on more accessible food items did not. Manipulation of nuts started at the age of few months, as single-object manipulation and object-to-surface actions. Combinatory, two-object actions appeared later, shortly after weaning. The juveniles adopted more efficient strategies for nut-cracking with age, and the rate of non-efficient actions decreased. Overall, we found that infants and juveniles sustain a high level of interest in nuts and stones long before they can efficiently crack. The period of manipulation and practice is, we suggest, necessary for the development of this skill.

Key words: tool use, development, skill acquisition, *Sapajus*

Introduction

Few things influence the behavior, development and life history of an animal more than its diet and foraging habits. Primates as a rule are omnivores, but there are many differences in diet among the different species. Several genera of non-human primates (NHP) use an "omnivorous extractive foraging" strategy (Parker and Gibson 1977). Those species include chimpanzees, orangutans, capuchins, baboons and macaques, and to some extent squirrel monkeys, mangabeys and aye-ayes (the latter are the odd ones out in this list, both because they are the only prosimians and because their extractive behavior is highly specialized, as opposed to the more general manipulative behavior of the other species). The diet of these species includes hard-to-access food items such as tubers, nuts with hard shells or invertebrate that are either embedded in a protective shell or reside inside branches, mounds etc., complementing the more easily obtained food such as fleshy fruits. (Yamakoshi 2004; Melin, Young et al. 2014). Species reliant on extractive foraging show greater frequency and variability of complex object manipulation compared to the non-extractive foragers. Specifically, in an experimental study with captive individuals, great apes performed more "secondary actions" (actions with two objects or object and a surface) followed by capuchins and then macaques, leaving the leaf-eaters behind (Parker 1974). In another study, captive capuchins and apes were shown to perform the most sophisticated manipulation, followed by the omnivores among the old world monkeys (Torigoe 1985)

It is clear that extractive foraging requires sophisticated and varied manipulative skills, which suggested to many an association with intelligence. The "ecological hypothesis of intelligence" suggests that the cognitive skills of primates evolved to contend with the challenges of foraging on hard-to-access items (Parker and Gibson 1977). Although early studies did not show correlation between diet and indicators of intelligence, such as neocortex size (Dunbar 1992), recent studies present new evidence for it (MacLean, Hare et al. 2014; Parker 2015). A connection between diet and life history in primates has been suggested. Primates as a group have long life spans in relation to their body size (among mammals) and extended juvenescence, which may have evolved to enable juveniles to gain experience and develop various skills (Janson and Van Schaik 1993). Studies showed that omnivores and insectivores – for which those foraging skills can be especially important - tend to grow slowly as compared to folivores (Leigh 1994).

Capuchin monkeys (genera *Sapajus* and *Cebus*) show extractive foraging techniques in the wild (Fragaszy, Visalberghi et al. 2004), for example, Sapajus -(Gunst, Boinski et al. 2010), Cebus - (Panger, Perry et al. 2002). Their manipulative nature is readily seen in the lab. In captivity, capuchins (*Sapajus* spp.) start manipulating objects very early in life, at about 8-12 weeks. Concurrently with the first episodes of manipulation, they engage in percussive activity (Adams-Curtis and Fragaszy 1994). Those vigorous object-to-surface actions are a common characteristic of capuchin behavior, and previous researchers have noted their preference for “banging operation patterns” [(Yamakoshi 2004), pg. 161]. The rate of all manipulations increases rapidly through the first year of life, as does the proportion of more dexterous actions (Fragaszy and Adams-Curtis 1997).

Several studies explored the ontogeny of extractive foraging skills in wild capuchins. Perry (2009) studied handling of the Luehea fruit – hard shelled fruit that can be opened using pounding or rubbing - in several groups of white-faced capuchin (Cebus capucinus) in Costa Rica. She found that infants in their first Luehea season tried rubbing and pounding the fruit –

the two efficient techniques used by adults - only in about 30% percent of their handling attempts. Instead, both in their first and second year, individuals primarily used an array of inefficient methods, from juggling to scratching to bouncing on the fruits. In the following years, the juveniles gradually honed their technique and dropped the inefficient behaviors (Perry 2009).

Gunst (2010) looked at two different foraging tasks facing brown capuchins (*Sapajus apella*) in Suriname. In harvesting the maripa palm fruit, the limiting factor seemed to be the size and strength of the individuals. By age two, juveniles exhibited all the correct actions, but only at age three were they strong enough to reach adult-level efficiency. Infants and young juveniles spent more time than older individuals on harvesting attempts, and infants tried to compensate for their lack of success by using alternative strategies: gnawing on un-plucked fruits, and scrounging on fruits left by others (Gunst, Leca et al. 2010). In preying on larvae enclosed in bamboo stalks, detection of the prey was the more complicated part of the task, and the last to be mastered by the juveniles. The monkeys start sniffing and ripping the stalks at a very early age, but at this stage their behavior is only rarely directed towards an appropriate target (bamboo stalks likely to contain larvae). The frequency of targeting appropriate stalks increases gradually with age, and the monkeys reach full adult efficiency only around age 6 (Gunst, Boinski et al. 2010).

These examples all show that capuchin monkeys face foraging tasks that take years to master efficiently. During this period the juveniles engage with the food items, even if they only get low payback for their efforts (and sometimes no payback at all). They also often engage in non- or less-efficient strategies, that they abandon when they become older and more efficient. Some skill development is directly related to body size, and other skills depend more on development of manual dexterity and/or cognition.

Tool use in non-human primates

Tool use was defined by Alcock [(Alcock 1972), pg. 464]as "the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the position or form of some separate object". In primates, most if not all habitual tool use is seen in the context of extractive foraging, and can be regarded as an extreme example of this behavior. All NHP that use tools also use other forms of extractive foraging, though the opposite is not true (Yamakoshi 2004).

Capuchins are one of the best studied examples of nonhuman primates that use tools in the wild. Wild bearded capuchin monkeys, *Sapajus libidinosus*, of both sexes, use stone tools to crack palm nuts to obtain the kernel, and they do so on specific anvils composed of stone or wood (Fragaszy, Izar et al. 2004). Adult monkeys display variable efficiency, which correlates positively with body size (Fragaszy, Pickering et al. 2010). Tool users are highly selective of the stones, anvils and nuts they use, and how they use them (Visalberghi, Fragaszy et al. 2007; Visalberghi, Addessi et al. 2009; Fragaszy, Greenberg et al. 2010; Spagnoletti, Visalberghi et al. 2011; Fragaszy, Liu et al. 2013).

As with other tool users, the path to nut cracking from a naïve individual to an efficient adult capuchin is not yet clear, although we have a general picture. Resende (2008) studied tool-use development from birth to 3 years in nut-cracking tufted capuchins living in a semi-free group in Tiête Ecological Park, Brazil. In this group, simple manipulations like picking up, biting and smelling nuts were seen at about the same time as the characteristic percussive actions, before the subjects reached six months of age. Combinatory actions with two objects (hitting one object with another) appeared at two years of age. Only two subjects were seen cracking nuts, and they first did so at age 25 and 29 months (Resende, Ottoni et al. 2008). These patterns are consistent with what has been found in captive capuchins (Fragaszy and Adams-Curtis 1997). A subsequent study with the Tiête capuchins showed that as the juveniles got older and gained more practice, their strikes became more efficient and they used fewer actions that were not essential for cracking (Resende, Nagy-Reis et al. 2014).

Similar trajectories can be seen in the few studies that have looked at how young primates of other species develop tool use. We present here two examples from wild chimpanzees.

Termite fishing in chimpanzees

Termite fishing using sticks or grass bladed was the first tool-use behavior in wild primates to by systematically studied (Goodall 1964). Soon after its discovery, the inefficient actions of infants with sticks and termite-mounds were also reported. Goodall (1968) described infants in a group in Gombe National Park, Tanzania using sticks that were far too short and often also too thick or too thin to be effective. Even when working with adequate tools, their techniques were clumsy and their attempts were very rarely successful (van Lawick-Goodall 1976). Lonsdorf (2005) looked more closely at the development of termite-fishing in young chimpanzees, in the same population (several generations later). Though all subjects could identify the hole and were seen manipulating a tool by 18 months, they start inserting the tool into the hole only at 2.5 years of age at the earliest, and some individuals were not seen doing this until they were 4.5 years old. Successful extraction of termites was seen in some individuals only when they were 5.5 years old. In the years between the time their interest was first piqued by a termite mound and the time they could gain access to it, the young chimpanzees engage in a variety of behaviors: poking the mound and holes with their fingers, sniffing and looking into the holes, as well as picking up used tools, examining and manipulating them. By 3.5 years of age, they started modifying and creating their own tools, though most of them were not yet efficient in using them properly – they often pressed the tool to the mound or used it to swipe at the mound, instead of inserting it into the hole. Even after they were inserting the tool into the hole, they still had to refine their technique – to learn how deep to insert it and how long to leave it inside – before they became efficient tool users (Lonsdorf 2005).

Nut-cracking in chimpanzees

Nut-cracking using hammers and anvils was known for many years in several chimpanzee populations in West Africa, from Senegal to Côte d'Ivoire (Boesch, Marchesi et al. 1994), and in recent years was reported as far east as Cameroon (Morgan and Abwe 2006). The development of nut-cracking by young chimpanzees was studied in a habituated group in Bossou, Guinea. Inoue-Nakamura and Matsuzawa (1997) found that infants start interacting with nuts and stones in the first year of life, although they cannot open a nut by themselves until they are about 3.5-4 years old (and it takes them several more years to become efficient). The young chimps start with single manipulations of a single object. By age 1.5 years they start to connect nuts and stones with a surface – rolling, pressing and hitting – though simpler manipulations still dominant. At this stage, all the basic actions required for nut cracking are present, but the individuals still do not combine them in the correct way. The frequency of object-to-surface actions increase with age, and by 3.5 years of age the chimps start to combine the nut and stone, and first nut-cracking is seen. Inefficient actions – such as raking the nuts or rolling them – are seen at age one and two but disappear by 3.5 years of age. Conversely, the frequency of actions that are part of efficient nut cracking increases with age (Inoue-Nakamura and Matsuzawa 1997).

Those studies are descriptive in nature, and do not place skill development within the context of the species' life history, physical growth curve, or age of weaning. Similarly, not much attention has been given to difference in development of skills between males and females. All those factors can be related to the timing of different milestones – when individuals start interacting with the tools and food items, when they start combining them, when they become efficient. Animals that grow more slowly and take longer to be weaned and to reach sexual maturity would be expected to start their interaction with food-related items later and perhaps also take a longer time to develop their foraging skills. Those skills depend on factors such as time spent on the ground, the propensity to forage and so on.

Therefore, our first prediction is that the frequency of foraging-related manipulations, and the time dedicated to foraging, increase rapidly around the time that the infants are weaned, and have to forage for themselves. Weaning is not a single point but a continuous process, and is often hard to estimate, especially in wild animals. Interbirth interval is sometimes used as a proxy for age of weaning, since females usually do not conceive when they are nursing an infant regularly. They might continue to nurse every now and then while cycling, but their offspring can been seen as "effectively weaned"; they get most of their nutrition from autonomous foraging. In our field site, the interbirth intervals were between 12 to 29 months (median 20.5 months) (Fragaszy, Izar et al. In process). Studies in related species (*Cebus capucinus* and species of *Sapajus)* present similar estimates: between 19.35 to 30.2 months (Fedigan 1995; Di Bitteti and Janson 2001; Izar, Stone et al. 2009). Tufted capuchins in captivity (*Sapajus Spp*.) showed an interbirth interval of about 19 months (Fragaszy and Bard 1997). When subtracting the time of gestation (around 5.5 months), those numbers seems to converge on an age of around a year and a half (18 months) as an average age of effective weaning (Fragaszy, Greenberg et al. 2010). It should be noted that in our field site, young capuchins were seen nursing daily as late as 17-19 months of age [Verderane, Fragaszy, Visalberghi, Izar, unpublished data], though it is impossible to know how much they relied on it as a source of nutrition. With this timeline in mind, we predict an increase in frequency of manipulation in the year following effective weaning (e.g., 18-30 months) compared to the first 18 months.

Looking at the trajectory of nut-cracking, we can see several common characteristics of tool use and other extractive foraging behaviors from the studies described above:

1. Primates start interacting with objects relevant to the foraging skill in question (food items and tools) very early in life. The frequency of those actions increases in the following months or years, and is sustained, sometimes for years, even when the juveniles do not yet gain any food reward from their activity.
2. Young individuals start with simple, single-object manipulation and object-on-surface actions, which mature into more complex actions and culminate, when applicable, in combinatorial, two-object actions.
3. The actions repertoire increases early in life, and variability decreases later.

Thus our second prediction is that in our population, infants start interacting with nuts and stones very early in life, increase both frequency of manipulation and variety of actions with age, and then decrease the variance when they concentrate on the more efficient actions.

This view of the development of tool use highlights the idea that tool use is a gradual achievement, dependent on growth and experience, rather than a conceptual achievement (Lockman 2000). Thus it can be studied using the same frameworks as other gradual developmental achievements, such as locomotion and other forms of foraging, and in relation to physical growth and life history.

Should we expect young capuchins to start cracking nuts around the time they are weaned? On the one hand, studies on white-faced capuchins showed that the diet of juveniles, from around the time of weaning, is not significantly different than that of adults (MacKinnon 2006). Studies on the same population as the current study showed that there were no significant differences, in term of toughness and elastic modulus, between the food consumed by adults and that consumed by juveniles after weaning (Chalk, Wright et al. In Process).

On the other hand, nut-cracking can be seen as a more sophisticated task than most, as it requires coordinated actions with a surface and two objects. The monkeys must learn how to position the nut on the anvil effectively, select the right stones, use the stone effectively and more. All these aspects of performance might require practice. In chimps, termite fishing (another activity that involves coordination between object and a surface) is seen in some juveniles only at age 5.5 years, a couple of years after weaning, although some individuals start as early as 2.5 years, before weaning (Lonsdorf 2005). Young chimpanzees in Bossou start cracking nuts at around 3.5- 4 years, which is around the time of weaning (but the novice juveniles are not as efficient as adults) (Inoue-Nakamura and Matsuzawa 1997). It should be noted that the longer nursing period of chimpanzees gives them absolutely more time to practice these behaviors before weaning. In addition, contrary to chimpanzees’ tool use, capuchins’ nut cracking requires considerable strength: the stones used as hammers weigh an average of about 1kg (Visalberghi, Fragaszy et al. 2007), and can reach 2kg (Spagnoletti, Visalberghi et al. 2011), which is more than the mass of some adult females. The two most common nuts that were cracked in this study, Tucum and Piassava, have hard, thick shells (4.12mm and 6.01mm, respectively) with peak-force-at-failure of 5.57 kN for Tucum and 11.5 kN for Piassava (Visalberghi, Sabbatini et al. 2008). Therefore, lifting the stones and using them with enough force to crack the nuts requires strength that young juveniles might not yet possess. Another extractive foraging behavior that was described above, the harvesting of maripa fruits, demonstrate that strength and body mass can be limiting factors – the juveniles performed all the correct actions by age two, but only at age three did they reach the efficiency level of adults (Gunst, Leca et al. 2010).

Our third prediction is that <u>around the time of weaning the actions needed for nut cracking – putting a nut on an anvil and hitting it using another object - will start to appear</u>. However, efficient cracking itself will appear later, when the juveniles had more time to learn the task, and also to gain mass and become stronger.

Even after the juvenile period, body mass has been shown to be related to nut cracking efficiency. Among adults, the number of strikes needed to crack open a nut is correlated with body mass (Fragaszy, Pickering et al. 2010). The stones used as hammers weigh an average of about 1kg (Visalberghi, Fragaszy et al. 2007), and can reach 2kg (Spagnoletti, Visalberghi et al. 2011) Bearded capuchins reach 1kg at around 400 days (1.1 years). After the first year their growth rate slows significantly, and they reach their adult size only in their eighth to tenth year

(Fragaszy, Izar et al. In process). Mass and strength limit when juveniles can crack nuts, even when they perform the correct actions.

This leads to our fourth prediction: <u>body mass affects the frequency with which different actions are performed.</u> Specifically, we predict that combinatory actions, and especially actions involving hammer stones, will increase in frequency with body mass. However, the influence of mass may be difficult to assess, given the strong correlation between weight and age in infants and juveniles.

When looking at weight, we have to also consider sexual dimorphism. Adult male bearded capuchins weigh substantially more than females, and there is no overlap between the two sexes. In our field site, males weigh on average 3.5kg, and females – 2.1 kg. We observe a sex difference in the rate of growth from the second year of life on: males increase in mass at a faster rate than females. In addition, from the second year on the variance in weight among males is much higher than the variance among females (Fragaszy, Izar et al. In process).

When the juveniles are old enough to start cracking nuts, the difference between the sexes in body size can be significant. Thus, our fifth prediction is that t<u>he frequency of nut cracking and related actions – especially combinatory actions with nuts - differs between males and females after weaning, mediated by differences in body mass</u>. We might also expect to see greater variability among males compared to females, since they show greater variance in mass.

Current study

In this paper we describe the manipulative behavior of young capuchin monkeys in a wild, nut-cracking population, with a specific focus on extractive foraging activities involving nuts, stones and anvils. We view tool use as a foraging skill, and relate it to growth and experience. Our data were collected in five different periods during both dry and wet seasons, over 24 months. We followed 16 infants and juveniles (10 in all five collection periods) ranging in age from several months to over six years. Using these data we track the ontogeny of nut-related activities, and examine the four predictions made above. We start by looking at the locations in which young capuchins spend their time. Most nut manipulation, and all nut-cracking, is done on the ground, and the objects related to nut-cracking are all found on the ground. Thus, the time spent on the ground influences their opportunities to practice the activities associated with nut-cracking. Next, we look at the age when different actions first appear in the young capuchins' repertoire, and at how the rate of performing different actions changes with age. We examine the relation between foraging-related manipulation and weaning (prediction 1). We differentiate between two categories of food: embedded food, which includes both nuts and other food items that require processing prior to consuming, and non-embedded food that can be consumed directly. Later we focus on one type of embedded food, nuts, which require the help of tools to be processed, and examine how nut-related activities change with age (prediction 2). We look at the relation of nut manipulation to weaning (prediction 3), as well as its relation to mass and to sex (predictions 4 and 5). All this enables us to place the development of nut cracking in this species within the bigger picture of extractive foraging and life history.

Methods

Study site

Our site is located 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 masl) punctuated by sandstone ridges, pinnacles, and mesas rising steeply to 20–100 m above it. The climate in the region is seasonally dry. At our site, annual rainfall in 2006 – 2008 averaged 1290 mm per year. From May to September rainfall averaged 25 mm and from October to April 1266 mm.

Anvils

An anvil is defined as a flat, or nearly flat, horizontal 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 (hard stone weighing 150 g or more) 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.

Study duration

Data were collected in 5 discrete collection periods; each consisted of 6-9 weeks of observations. Three of those collection periods took place during the dry season, and two during the rainy season. The time points were: May-July 2011 (Dry season), Jan-Feb 2012 (Rainy season), May-July 2012 (Dry season), Jan-Mar 2013 (Rainy season) and June-July 2013 (Dry season).

Subjects

At the beginning of the study, there were 11 juveniles and babies in the group, aged from 3 months to 4.5 years. Five more infants were born during the study. Data on the oldest juvenile (Tomate) were collected only in the first two collection periods. At the beginning of the study, none of the subjects could crack open a whole nut of the more resistant species (*Orbygnia* and *Attalea*). The two oldest juveniles, and to some extent two others, mastered this skill through the duration of the study. Apart from our subjects, the group included 3 adult males and 5 adult females. All but one female habitually crack nuts. Body mass of the subjects in this study taken during the three dry season collection periods are presented in Table 2.1. We define infants as individuals through 12 months of age; juveniles between age one and four, and subadult in ages five and six.

Data collection

All observers used hand-held devices with Pocket Observer© software by Noldus Information Technology. An observer followed one of the subjects to obtain a continuous record of the focal subject's location and activities. All observations lasted 20min, or until the focal subject went out of view and could not be followed; but not less than 5min.

Our ethogram included three categories:

1. Location – on a tree, on the ground, or within arm's reach of an identified anvil
2. Behavioral state – resting, locomoting, engaging in social behavior (groom, play etc.), engaging in manipulation of objects of any kind, or watching nearby adults
3. Specific actions – including eating (nuts or other objects), direct percussion of an object on a surface (nuts or other objects, on tree, ground or anvil), manipulating nuts or other objects in a non-percussive way, combinatorial percussion (striking a nut with a stone and striking a nut with another nut), and more (see Table 2.2). Because eating and direct percussion often occurred in prolonged bouts, we recorded the activity every 3 seconds as long as the bout persisted. When recording combinatorial percussion, each strike was recorded separately.

At each data point, a quarter to half of the observations were collected in our field laboratory - an open area, about 12m in diameter, that the monkeys visit 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, Pickering et al. 2010; Fragaszy, Greenberg et al. 2010; Massaro, Liu et al. 2012; Fragaszy, Liu et al. 2013). Many nut shells and debris from years of nut-cracking can be found on and around the anvils, and all around the lab area.

Reliability

Focal observations: Reliability was calculated using GSEQ: Generalized Sequential Querier ©, URL: http://www2.gsu.edu/~psyrab/gseq/index.html. Time unit kappa was at or above 0.7, which is considered highly reliable (Bakeman, Deckner et al. 2005)

Data analysis

For each subject in each collection period, we collected between 19 and 53 observations, which lasted, together, between 5.3 hours to 27.1 hours (table 2.3). Al observations for the same subject were collated for each season. Ten subjects appeared in all five collection periods, and therefore have 5 values in our analysis.

The observations were exported from The Observer© to GSEQ© software. We obtained rate per 10 min for various activities, under different conditions (near or away from an anvil, with or without group activity). In some cases, we combined several codes to create new variables:

- Direct percussion of nuts on anvil, tree and anvil was combined to create “direct percussion of nuts”
- All direct percussion with nuts, combinatorial percussion and other non-percussive manipulation with nuts was combined to create “nut manipulation”

- Bouts of nut manipulation and direct percussion was nuts were calculated as encompassing events of this kind that were 5sec or less from each other, and the time between those events. That enables us to calculate the duration of nut manipulation and of percussive manipulation of nuts.

SAS© software was used to test general mixed linear models.

We used count variables which did not distribute normally (tested with Shapiro-Wilk); therefore the Poisson distribution was used. We used total time of observation as an offset to test rates, and total duration of nut manipulation as offsets to test proportions. Our independent variables were age, mass and sex.

Results

Time spent in different locations

The percentage of time juveniles spent on the ground increased with age (estimate=1.09, p=0.02). The increase in time spent on the ground is sharpest between the first and the second year of life. There is a significant difference between the percentage of time infants in the first year of life spent on the ground vs. juveniles age one to four (17% percent for infants, 35% for juveniles; p <.0001; Fig. 2.1, panel A). There was no significant difference between juveniles and subadults (age 5 and 6).

-------Insert fig. 2.1 here-------

Order and age of appearance for different actions

All subjects were seen manipulating nuts (whole or shells) and other objects at the very first time period in which we observed them – the youngest being 3 months old at the beginning of the data collection period. Those were single object actions – mainly picking the objects up, sniffing them, or putting them in their mouth.

Direct percussion was seen in the first 6 months of life in five out of seven subjects, but rarely (between 1 to 7 occasions per monkey, during 120-300 minutes of observation per subject). Interestingly, all direct percussive actions at this age were done with nuts or parts of nuts. More than 70% of percussion events (18 out of 26) occurred on an anvil. At 18 months, all subjects were seen percussing nuts and other objects regularly (rates 0.02 to 3.77 per 10 minutes at the second year of life).

Combinatory actions – combining a nut with another object – were not seen in the first year of life. Subjects began to show this behavior around 15 months. Of the five individuals we observed between 1 and 2 years of life, three were seen striking a nut with a stone; one of these was seen doing it more than 20 times (Coco, 114 actions were recorded, at 7 different occasions, over almost 400 minutes of observations). Of the others, one was observed performing this action 11 times over 4 occasions, and the other 20 times over 5 occasions.

A different combinatorial action – hitting a nut with another nut – appeared at around the same age. Four out of the five subjects that were followed between 12 and 24 months were seen to engage in this behavior. One (Coco, that same monkey that struck a nut with a stone most often) did this 65 times on 10 different occasions; the other monkeys, 2 to 9 times on 1 to 3 different occasions. Most subjects did not start hitting nuts with other objects regularly until they were around 3-3.5 years old.

Ontogeny of specific actions

The rate of all manipulations of any object increased with age (estimate = 1.1, p= 0.02) from a median of 10.7 per 10 min for 1 year olds to 16.5 per 10 min in 5 year olds. However there were differences in this regard between different objects. In two of our five collection periods we recorded separately the manipulation of embedded food – nuts, fruits and invertebrates that require processing before consuming - and non-embedded food. The rate of manipulation of embedded food increased with age (estimate = 1.17, p=0.01), from a median of 0.7 per 10 min for 1 year olds to 1.4 per 10 min in 5 year olds. The rate of manipulation of nuts and nut shells, a subset of embedded foods (from all five collection periods) correlated positively with age at about the same magnitude as other embedded foods (estimate= 1.21, p=0.03, Fig 2.2). Conversely, the rate of manipulation of non-embedded food did not correlate with age (p = 0.59) and there was no significant difference between any two age groups in manipulation of non-embedded foods (Fig 2.2), with a median rate of 6 per 10 minutes across all age groups. As a result of this pattern, the percentage of the manipulations involving nuts increased. This increase is driven by the younger cohort (age 3-29 months at the last observation period; N=8, four observed in more than one collection period). In this group, we saw a significant increase with age in the percentage of nut manipulation out of all manipulation (estimate=2.1, p=0.01). The rate of manipulation of nuts in the first year of life (med = 0.5 per 10 min) differed significantly from the rate seen in juveniles age one to four (median = 4.09); p=0.032), but the rate seen in juveniles was not significantly different from that seen in subadults (age five and six; median = 3.23).

-----Insert fig. 2.2 here------

Direct percussion of nuts

Rate of direct percussion of nuts on a surface did not correlate with age overall. However, when looking only at the younger cohort (8 subjects, age 3-29 months), the rate of direct percussion of nuts correlated positively with age (estimate=2.08, p=0.04), from a median of 0.02 per 10 minutes in the first year to 0.7 in the second year. In the older cohort, the rate was **negatively** correlated with age (estimate=0.607, p=0.007, Fig. 2.3, panel A), from a median peak of 1.5 per 10 minutes in the fourth year to 0.5 in the over 5 years old. Direct percussion of objects other than nuts did not correlate with age (Fig 2.3, panel B).

Combinatorial actions

Hitting an object with another object starts in the second year of life, and is usually seen with nuts – either hitting a nut with a stone which is the only way to crack it open – or hitting a nut with another nut, which would not result in cracking. The rate of striking a nut with a stone rises with age from median = 0.3 and 0.4 in the second and third years to median = 1.7 in the over five year olds, but with high variability across individuals, the data do not reveal a significant correlation with age (Fig 2.3, panel C). Striking a nut with another nut, which as mentioned is an inefficient behavior, is seen from the second year of life. It is rare in all ages, and the least common of all actions involving a nut (median = 0.01 per 10 minutes); Fig 2.3, panel D).

-----Insert fig. 2.3 here-----

The proportions of different actions performed with nuts also change with age. In the younger cohort (age 3-29 months; N=8), the proportion of time spent in direct percussion of nuts correlated positively with age (estimate=2.54, p=0.0004), from a mean of 6% (median of 0) in the first year to a mean of 19.5% (median of 18.2%) in the second year. In the older cohort, the trend was opposite (the proportion of time spent percussing goes down with age, from a peak of 27.5% in the third year to only 6.6% in the over five year old) but the trend is not quite significant (estimate=1.2, p=0.06) (Fig 2.4, panel A). The proportion of time spent in hitting a nut with another object did not correlate significantly with age (Fig. 2.4, panel B).

Proportions within combinatory actions

All observed combinatorial actions were performed either with a stone striking a nut or with a nut striking another nut. As our subjects got older, the proportion of striking a nut with a stone – the efficient way – out of all combinatory actions increased (estimate=1.07, p=0.03), from a median of only 52% in the second year to 98.3 in the sixth, and the proportion of striking with a nut decreased (estimate=0.675, p=0.003, Fig 2.4, panel B) from 40.9% in the second year to 1.6% in the sixth.

----Insert fig. 2.4 here-------

Rate of manipulation before and after weaning

There was a significant increase in rate of manipulation of embedded food (including nuts) between pre-weaning and post-weaning (p=0.02), from a median of 0.78 per 10 minute to 1.27 per 10 minutes, but no significant difference between the year post weaning and the subsequent years. However, for non-embedded food, there was no significant difference across age groups (Fig 2.5).

-------Insert fig. 2.5 here--------

Influence of body mass

We have data on body mass for the three dry seasons, for all subjects except one (see Table 2.1). Age and mass were, unsurprisingly, highly correlated in our subjects ($R^2=0.907$, $p<0.0001$). Thus the influences of age and of body mass are deeply confounded, and we cannot use both variables in the same model. We compared the two models - one with age and one with mass - only from the dry seasons. For most of the variables, the results were very similar, but there were a few cases in which a model based on mass offered the better fit, and no variable showed a clear better fit for age. In the dry seasons, rate of manipulation of nuts increased with mass (estimate=1.8, p=0.04), but not significantly with age. In the younger cohort, the percentage of nut manipulation out of all manipulation increased both with age and with mass, but the increase was more strongly predicted by mass than age (p=0.0496 for age, 0.0091 for mass). Proportion of time devoted to direct percussion decreased with mass in the older cohort (estimate=2.66, p=0.02), while the correlation with age in the dry seasons was not significant.

Differences by sex

Most comparisons do not show any difference between males and females, when age is taken into account. One variable did show a difference: in the younger cohort, the males percuss with nuts more than the females (median: 0.5 per 10 minutes for males vs. 0.13 for females, p=0.02.

The effect is probably not a result of difference in weight, since it is seen also after factoring in the weight (p=0.0305, weights from the dry seasons).

Discussion

In this report we describe the developmental trajectory of tool use in a wild group of bearded capuchins (*Sapajus libidinosus*) and test a set of predictions linking the development of tool use with weaning, body mass, chronological age and sex. Infants and juveniles were followed during 5 collection period, over 3 years. Locations and activities, with special focus on any activity related to nut cracking, were recorded.

We examined five predictions:

1. The frequency of all foraging-related manipulations increases rapidly around the time that the infants are weaned
2. Interactions with nuts and stones increase in both frequency and variety with age. Eventually the variety of actions decreases.
3. Actions used specifically for nut cracking – putting a nut on an anvil and hitting it using another object - appear around the time of weaning.
4. Combinatory actions, and especially actions involving hammer stones, increase in frequency with body mass
5. The frequency of nut cracking and related actions differs between males and females, mediated by differences in body mass.

Prediction one: relation between rate of foraging and weaning

Difference between manipulation of hard-to-access food items and other food items

The trajectory of manipulating easy-to-access foods is different from that of hard-to-access foods, including nuts. Both start within the first six months of life, but manipulation of easy-to-access food items increases rapidly and quickly reaches a plateau, so that the rate of manipulation in the first year of life is not different significantly from that of subsequent years. Conversely, the rate of manipulation of nuts and other food items which require processing increases more slowly, with the big increase occurring in the second year of life. From this follows, that as capuchins get older, they dedicate more of their manipulation efforts to extractive foraging, including nuts.

Major transitions in manipulative behavior

The biggest change in rate of manipulation of different actions was found between the first and second year. Capuchins begin to eat solid foods that they procure for themselves near the end of the first year, and are weaned around the age of 1.5 years, as determined by the mother conceiving another offspring, but they continue to nurse at a low frequency for several months longer. During the extended process of weaning, the juveniles rely more and more on the food they find and process themselves. The rate of manipulating embedded food increases sharply between the pre-weaning period and the year after weaning, but did not change significantly between the year just after weaning and subsequent years. Non-embedded food did not show this pattern – rate of manipulation were not significantly different before and after weaning.

Therefore, our first prediction – that the frequency of foraging-related manipulations increases rapidly around the time of weaning – is only partly supported. It is true only in regard to embedded, hard to process food items. The difference in the frequency of foraging on easily obtained food vs. food items which require special processing fits with previous studies on the ontogeny of foraging in non-human primates. Most foraging behaviors of post-weaning juveniles are very similar in pattern to those of adults. As discussed earlier, in white-faced capuchins, juveniles one year and older showed foraging patterns not significantly different from those of adults, especially in relation to plant material (MacKinnon 2006). In squirrel monkeys (*Saimiri oerstedi*), by 4.5 months, most foraging patterns are indistinguishable from those of adults. As weaning in this species start around 16 weeks, these data are also from shortly after weaning (Boinski and Fragaszy 1989). Similar patterns are seen in baboons (Rhine and Westlund 1978) and mountain gorillas (Watts 1988).

Our prediction is supported only when the foraging requires detection of visually hidden items, precise motor control and/or strength. In our study, these items include, apart from cracking nuts using stones, foraging for termites hiding in branches, opening several types of fruits to feed on their seeds, digging for tubers, and rarely, hunting for vertebrates. Capuchins at other sites display the same pattern while foraging for different items. For example, when foraging for larvae hiding in bamboo stalks, tufted capuchins (*Sapajus apella*) need first to detect the larvae. The frequency of tapping the stalks and sniffing them correlated positively with age and there was a significant different in frequency between infants and young juveniles to adults. However the extractive action itself – ripping apart the stalks – appeared in the first year, and did not correlate with age (Gunst, Boinski et al. 2010). In the same population, when foraging on maripa fruits, which require strength to harvest, infants in the first year of life spent significantly less time attempting to harvest them (though they compensated by gnawing on un-plucked fruits or picking up partially-processed fruits left by others) (Gunst, Leca et al. 2010). In long-tailed macaques (*Macaca fascicularis*), infant and juveniles one and two years old forage more on soft, small fruits and avoid those with hard rinds, while the adults preferably fed on bigger, harder fruits (Van Schaik and Van Noordwijk 1986). Weaning in this species is estimated to be around 9.5 months (Ernest 2003), so the data are again from shortly *after* weaning. Hard-to-process food items that require tools for processing show the same pattern. Termite fishing and nut-cracking in chimpanzees take years to master (Inoue-Nakamura and Matsuzawa 1997; Lonsdorf 2005), and wild orangutans start to use tools in foraging around age four (van Schaik, Fox et al. 2003).The relation with weaning time is more complicated with the great apes, since the weaning process is more prolonged for them than it is for monkeys. Chimpanzees are only completely weaned around 4.5-5 years (Thompson 2013), and orangutans around 7 years (van Noordwijk and van Schaik 2005), but both start manipulating and eating other food items long before that.

In summary, in several primate species, feeding on hard-to-process food items shows a different ontogenetic trajectory than feeding on more easily obtained foods.

Second and third predictions: trajectory of nut-related activity

Infant capuchins in our study site started manipulating nuts within the first 6 months of life. Most of them started pounding objects (especially nuts) on a surface at around the same time, though they did not do it regularly and frequently until their second year. Combinatorial, two-object actions (specifically, hitting a nut that is lying on a surface using another object) appear at around 15 months, and become frequent in the third year. This finding supports our third prediction – that actions specific to nut cracking appear around the age of weaning (1.5 years) and increase in frequency in the subsequent years.

The rate for all types of manipulation of nuts increases with age, especially between the first and second year. It is interesting to note that the time subjects spend on the ground also increases with age, and also shows the biggest increase between the first and second year. Since nut-cracking takes place on the ground (specifically on anvils), spending time there enables the juveniles to encounter nuts, nut shells, stones and anvils, and to act with them, which should aid in learning their properties and their potential.

The rate of direct percussion of nuts on a surface has a more complicated relationship with age. We separated the younger cohort, eight subjects that were few months old when first observed and three of them (who were infants in the first collection period) were just over two years old in the last collection period, from the older cohort, who were around two years old or older when we started observing them. We found that in the younger cohort, the rate of percussing nuts increased with age, but in the older cohort, the opposite trajectory was seen. The rate of direct percussion of nuts reached its highest point in subjects age three to four, and then decreased again. A similar result is seen when looking at the percentage time the subjects dedicate to direct percussion out of the time they spend manipulating nuts.

To understand the trajectory of this behavior, we need to look at the function it fills. Percussion is a natural action for capuchin, and is seen readily with many objects in many different situations, and from a very young age (Adams-Curtis and Fragaszy 1994). In the context of nut-cracking, direct nut-to-surface percussion cannot open the hard-shelled nuts the capuchins in our field site feed on. However, this action *is* useful when trying to pry out kernels from half-opened nuts. Young capuchins that are not yet skillful enough to use combinatory actions and/or strong enough to handle large stones spend a lot of their time hitting nuts and nut shells directly on a surface – mainly on the anvils. They do it both because it is part of their natural repertoire, and because it is in some cases rewarding: juveniles often pick up open shells that were left from previous cracking episodes, and some of those shells still contain tiny pieces of kernels, which can be dislodged using vigorous percussion. Around the age when combinatory actions – the efficient way to crack open nuts – become more frequent, the rate of direct percussion goes down. However, as it does serve a function, it never goes away completely, and is seen also in the adults' repertoire. Combinatory actions, although rare, appeared regularly from the fourth year – just as the rate of direct percussion is decreasing. When we looked at the different types of combinatory actions – hitting a nut with a stone or hitting a nut with another nut – we found that at the second year of life, the juveniles perform both those actions at about the same rate (though both are seen only rarely at this age). From this point on, the percentage of hitting with a nut decreases with age, and the percentage of hitting with a stone increases. Hitting a nut with another nut is an example of a completely inefficient action – there is nothing to be gained by it, but it is easier than using the large, heavy stones. As juveniles get older they drop this behavior and focus on a more efficient, though more effortful, strategy. By age six, hitting a nut with another nut has almost disappeared.

This supports our second prediction, that infants would start interacting with nuts and stones very early in life, and that the repertoire of actions would increase in age and then decrease, due to increased focus on the efficient behaviors. We see this trajectory both with direct percussion and with hitting a nut with another nut.

These results are similar to those described by Resende et al. (2008, 2014) in a semi-free, tool-using population of capuchins in Tiete Ecological Park, Brazil. The repertoire of the juveniles increased from single-object actions (including direct percussion) that appeared already in first six months, to hitting one object with another, around age two (Resende, Ottoni et al.

2008). Juveniles successfully cracked their first nut during the third year, but did not yet reach the adults' efficiency level. Juveniles age three and older used more inefficient strikes (in which the nut falls from the anvil or flies away) than did adults, and the efficiency of strikes improved with age. The most efficient monkeys – who used just one or two strikes to open a nut – were the ones who used the optimal sequence, and did not use any other, inefficient actions. The use of this optimal sequence correlated positively with age (Resende, Nagy-Reis et al. 2014).

The development of tool use in young capuchins follows the same trajectory as development of complicated, extractive foraging tasks in other primates. Interaction with the food items starts very early, years before efficient processing is achieved. The repertoire of extractive actions increases rapidly with age, and then decreases, when inefficient actions are dropped and replaced by more efficient ones. As we have seen, white-faced capuchins which forage on the hard-shelled Luehea fruits try a variety of actions in their first and second seasons, including "juggling, twirling, shaking, scratching, bouncing on the fruit, and flailing it" [(Perry 2009), pg. 710]. During the next three seasons, the juveniles gradually eliminate those inefficient variants, and usually settle on one of the efficient methods used by adults: pounding or scrubbing. Studying chimpanzees in Tanzania which feed on Saba fruits, Corp and Byrne found that all procedures that were included in the adult repertoire increased with age, while those that were not declined with age (Corp and Byrne 2002). Processing of the fruits by adults consisted of detaching them from the vine, opening them, removing unwanted shell and then extracting and eating the pulp. Infants showed interest in the fruits from a very young age – at 8 months they were already seen mouthing and chewing on fruits they could not yet open. At that age they only ate pulp from already-opened fruits held by their mothers or retrieved from the forest floor. Only in the third year did they start getting a large proportion of the pulp they eat from fruits they opened themselves. At this stage, they were still using procedures not seen in the adults, such as biting the shell off and discarding it rather than tearing open the fruit. By the end of the fifth year, juveniles were processing the fruit in the same way of adults, although they often did it with the fruit still attached to the vine, while adults would detach it.

A similar picture is seen in chimpanzees' tool use. In Gombe, a successful termite fishing session was achieved by some juvenile only by age 5.5 years, but infants started manipulating termite-fishing tools (sticks and stems of grass that were used by their mothers and discarded) at around age 1.5 years. During those years they investigated the mound and the tools in ways that did not contribute directly to obtaining termites. These actions included sweeping the vegetation of the mound, poking it with their finger, and later pressing tools to the mound or swiping at it (Lonsdorf 2005). Goodall (1968) described inefficient behaviors of infants who were using sticks that were too short, too thin or too thick, and also using them in inefficient ways. On some occasions the tools were used completely out of context, probably as a way to investigate the characteristics of the tool – as when an infant puts a tool through the hairs on his own leg (van Lawick-Goodall 1976). In Bossou, infant chimpanzees started manipulating nuts and stones in the first year of life, and actions that are essential for nut cracking – putting a nut on a stone, and hitting it with another stone – started appearing at age 2.5-3.5 years. Other, unessential actions that were seen before that age – raking the nuts, rolling a nut around and more – declined quickly with age and were not seen after 3.5 years.

Thus, in both capuchins and chimpanzees, tool use emerges gradually after years of practice. The food items consumed using those tools are manifestly not essential to the juveniles' diet, since they do not have reliable access to them for several years.

Prediction four: influence of body mass

As can be expected from a sample of infants and juveniles, age and mass were highly correlated in our study – which made it very hard to parse out the influence of body mass from that of maturation.

There were a few variables that showed significant correlation with mass, but not with age – rate of manipulation of nuts (in the dry seasons) increased with mass but not with age, and time spent on direct percussion out of all nut manipulation, decreased with mass in the older cohort (the 8 older subjects that were two years old or older in their first collection period), but not with age. Overall, when there was a difference between the two variables, body mass was the better predictor. These findings fit with our fourth prediction, which was that body mass affects the frequency with which different actions are performed. However, we expected to see it mainly in regard to actions with stones, which was not the case – partly because those actions were not very common in our dataset. Among the adults in our study site, body mass correlates positively with nut-cracking efficiency (as measured by number of strikes needed to crack a nut) (Fragaszy, Pickering et al. 2010). This does not seem to be the case during development, though because of the confounding effect of age we cannot draw strong conclusions on this issue.

In many foraging behaviors, mass is probably a limiting factor for efficient foraging, e.g., processing maripa fruits by capuchins (Gunst, Leca et al. 2010) and Saba fruits by chimpanzees (Neumann 1971). Since many studies do not have body mass data for their subjects, and because of the close relation between age and mass in infants and juveniles, it is very hard to pin down the exact role that mass plays in skill development.

Prediction five: influence of sex

Among adults in our field site, males account for more nut cracking episodes than do females, and males are more efficient – which can be explained by their higher body mass (Fragaszy, Pickering et al. 2010). We did not see that pattern in juveniles, partly because our sample is too small to determine sex differences at any particular age. The only variable in which we saw an effect of sex when age is taken into account was the rate of direct percussion of nuts, and that only in the younger cohort. At that age group, males percuss more than females. This is probably not related to differences in mass between the sexes, which are very small at that age. And indeed, our analysis showed that effect remains even when we take mass into account.

Our fifth prediction, drawn from observation of adults in this population, was that the frequency of nut cracking and related actions would differ between males and females after weaning, and that these differences would be mediated by differences in body mass. Our results do not support this prediction. The difference we did find is apparently not influenced by mass, and might represent a difference in disposition between the sexes. It interesting to note that similar differences in disposition are known to exist in humans: in both infants (Campbell and Eaton 1999) and children (Eaton and Enns 1986), males consistently show higher levels of activity than do females.

These findings contrast with those from chimpanzees, where a female bias is seen in several populations, in regard to nut-cracking (Boesch and Boesch 1981), termite fishing (McGrew 1979) and even the newly-discovered tool-assisted hunting of bushbabies (Pruetz and Bertolani 2007). We are aware of only one study that examined sex differences in the *development* of tool use: Lonsdorf reported that females start termite fishing, on average, more than a year before their male counterparts (Lonsdorf 2005). Those differences, both during development and as adults, are not a result of mass differences, since the tasks do not require much force (and if it did, we would expect the larger, stronger males to practice it more frequently). To get the complete picture of sex differences in the development of tool use and of foraging skills in general, we need more developmental studies that will take this variable into account.

Theoretical background

This long period of manipulations, and the increase followed by decrease in actions variability, fit with the predictions of Dynamic System Theory. This theory views complex behavior as emergent phenomena, a product of many decentralized and local interactions. It does not focus solely on internal processes, but sees organisms as complex systems, composed of many elements, embedded in, and open to, a complex environment (Smith and Thelen 2003). According to this perspective, the ability to use tools does not arise from an internal maturation, but is a long process that involves repeated exposure to, and manipulation of, the tools and other related objects. Through this repeated exploration and play young animals (and children) learn the properties of objects, how they relate to other objects, and what actions can be performed on them. Therefore, the many manipulations of nuts by the juveniles, even if they do not seem to achieve anything immediately, are essential for skill development. It is this long practice that supports their efficient nut cracking in the future (Lockman 2000; Kahrs and Lockman 2014).

From our data, we cannot rule out the possibility that the limiting factor is size –when individuals reach a certain size they pick up nut cracking with little need for practice. We believe this to be less plausible, however, since when captive capuchins were given nuts and stones, adults did not readily pick up cracking – only few of them learned it and they needed practice to become efficient. In fact, in those captive studies, status had an influence on nut cracking, but size did not (Visalberghi 1987; Fragaszy and Visalberghi 1989).

Summary

This study addresses nut-cracking as a foraging task, gradually developed, and related to physical growth and weaning. Unlike many previous studies, we examined manipulation of objects in addition to consumption, and so could follow the interactions of our subjects with nuts, whether rewarded or not. Our comprehensive recording of activities and the wide range of ages of our subjects enables us to get a more complete picture of skill development. Specifically, it enables us to examine the period before the juveniles start cracking nuts, and the manipulations of nuts that take place in those years.

Our findings support our predictions only in part. The frequency of foraging on hard-to-process items increased around the age of weaning, as predicted, but the foraging on more accessible food items did not. Our predictions regarding the trajectory of manipulation of nuts were supported by the data. We found that subjects start manipulating nuts when they were few month old, long before they could crack them open. The rate of manipulation increases rapidly around the time that they are weaned, in the second year of life. Manipulation starts with single-object manipulation and object-to-surface actions, and combinatory actions – hitting an object with another object – appeared later, shortly after weaning. We could also see the development of a more efficient strategy with age, and with it a decrease in less-efficient actions.

Our final predictions address the relation of sex and age to the development of nut cracking. We found some support for the prediction that body mass correlates positively with nut manipulation, but sex differences were seen in only one variable – direct percussion – and only in the younger cohort. Overall, our small sample and the high correlation between age and mass in our dataset prevent us from drawing any strong conclusions on these issues.

One of our main findings is the long period of practice and manipulation of nuts, during which juveniles do not get any food reward for their efforts. There are presumably other factors that keep the juveniles interested in nuts and support their practice throughout this period. The example of adults who are cracking nuts nearby, and the availability of nuts and tools and their vicinity, can serve as those factors (for further discussion:(Fragaszy, Biro et al. 2013)). We will examine this subject in subsequent papers.

Figures

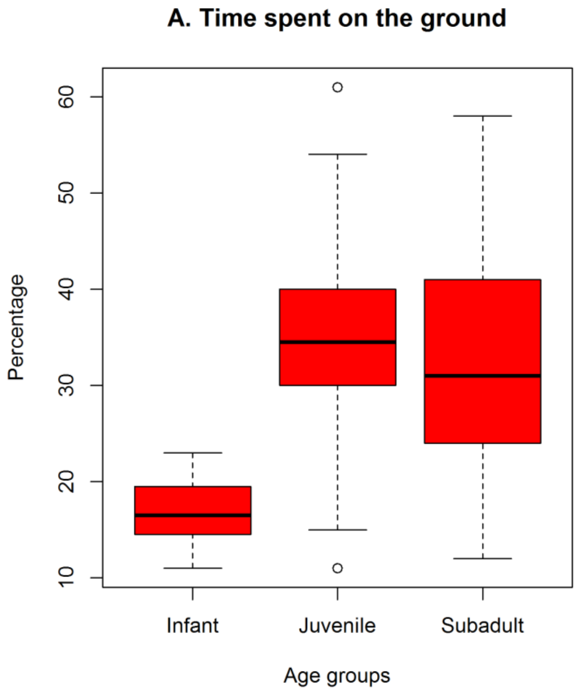

Fig. 2.1: Percentage of time spent on the ground. Infants: age 0-1 years, juveniles – age 1-4 years, subadult – age 4-6 years.

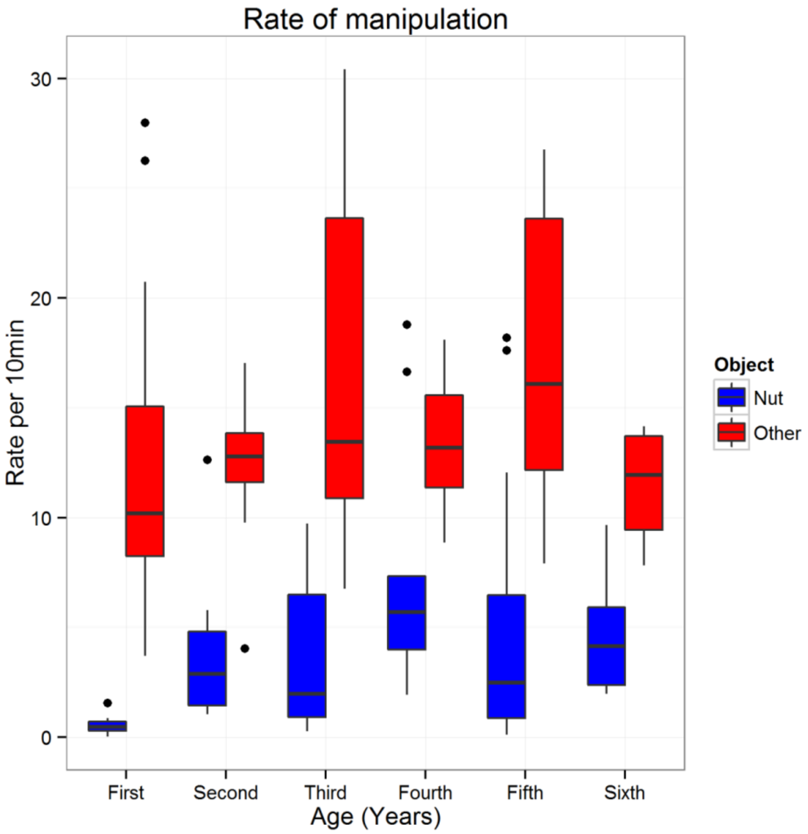

Fig 2.2: Rate of manipulation for nuts and other objects, by year

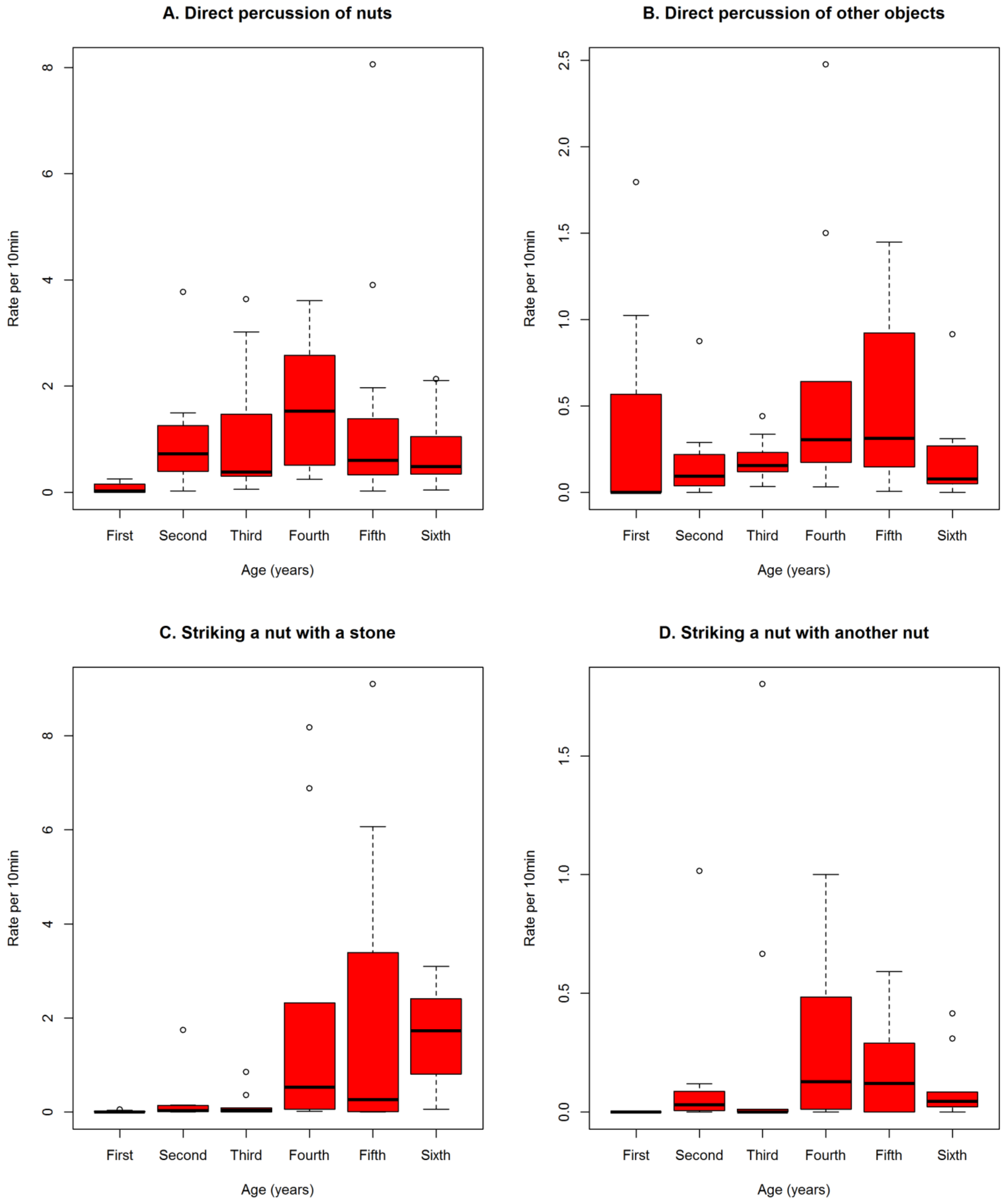

Fig 2.3: Rate of direct, object-to-surface percussion of nuts (A) and other objects (B), and combinatory actions with a stone on a nut (C) and a nut on another nut (D).

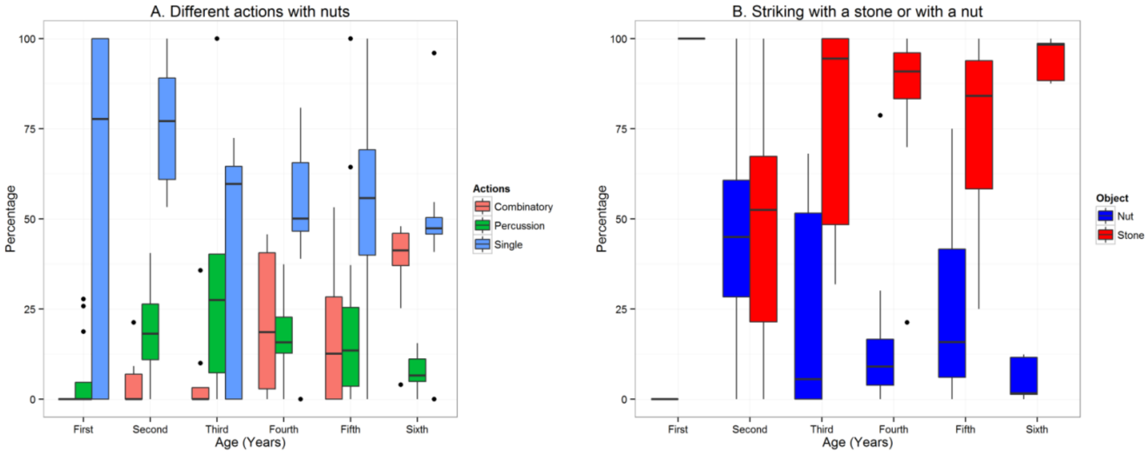

Fig. 2.4: A. Time devoted to different types of actions out of the time devoted to manipulation of nuts. B. time devoted to striking a nut with a stone and with another nut, out of the time devoted to all combinatory actions with nuts.

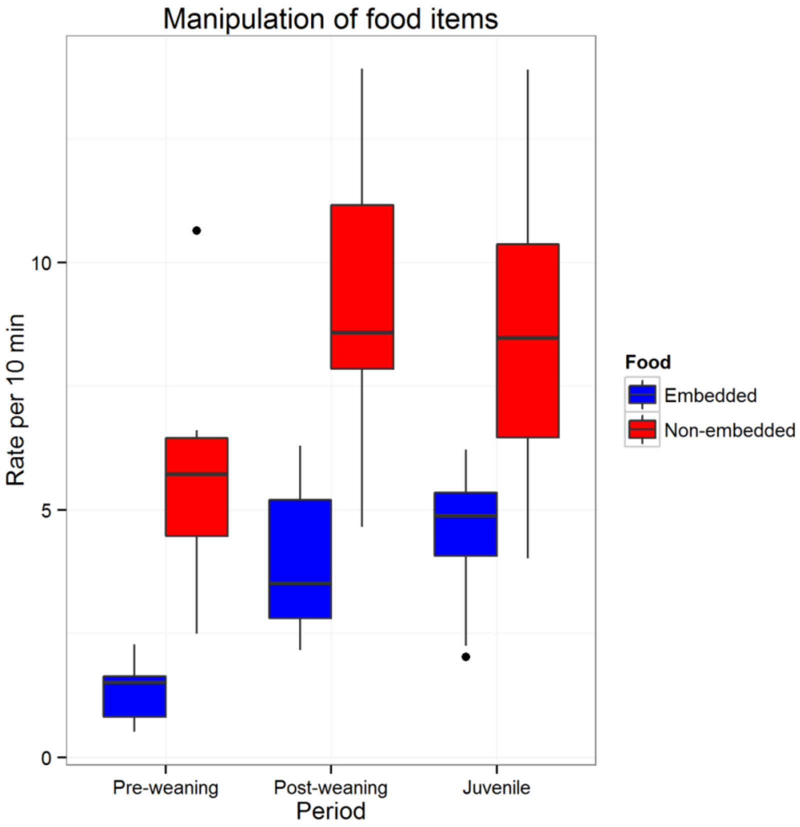

Fig 2.5: Rates of manipulation for embedded food (including nuts) and non-embedded food, before and after weaning. Pre-weaning: 0-18 months. Post-weaning: 18-30 months. Juveniles: over 30 months.

Tables

Table 2.1. Demographic data on the subjects

Name	**Estimated date of birth (estimated)**	**Gender**	**Mother**	**Mass 2011 (Kg)**	**Mass 2012 (Kg)**	**Mass 2013 (Kg)**

Donzela	January 13, 2013	F	Doree	_	_	0.4
Patricia	January 11, 2013	F	Piassava	_	_	0.53
Titia	January 3, 2013	F	Teninha	_	_	0.66
Divina	November 7, 2012	F	Dita	_	_	_
Cachassa	March 15, 2012	M	Chuchu	_	0.42	1.11
Presente	February 15, 2011	M	Piassava	0.24	0.99	1.47
Thais	February 1, 2011	F	Teninha	0.42	1.09	1.34
Chani	December 15, 2010	F	Chuchu	0.46	1	1.16
Coco	July 14, 2009	M	Chuchu	1.14	1.44	1.66
Passoca	January 1, 2009	F	Piassava	1.18	1.32	1.62
Pamonha	January 1, 2009	F	Piassava	1.23	1.37	1.57
Doree	November 9,	F	Dita	1.37	1.56	1.78

	2007					
Pati	November 2, 2007	M	Piassava	1.68	2.08	2.5
Cangaceiro	September 20, 2007	M	Chiquinha	1.83	2.08	2.36
Catu	February 5, 2007	M	Chuchu	1.81	2.07	2.46
Tomate	December 1, 2006	M	Teninha	1.8	1.99	2.34

Table 2.2. Ethogram

<table>
<tr><td colspan="3">Manipulating events: instantaneous activities, recorded the second they are performed, or in some cases, every few seconds as long as they are happening</td></tr>
<tr><th>Event</th><th>Modifier</th><th>Description</th></tr>
<tr><td>Hitting a nut</td><td>Anvil/tree/ground</td><td>Subject holds a nut and strikes the nut directly onto the surface – ones or more than once in a sequence. As long as the behavior continuous, it is recorded every 3 seconds</td></tr>
</table>

Hitting another object	Anvil/tree/ground	Subject holds an object and strikes it directly onto the surface – ones or more than once in a sequence. As long as the behavior continuous, it is recorded every 3 seconds
Light tap		Fingertip tap (usually on rigid surface)
Striking - hitting		Striking a nut with a stone. Recorded every time the stone hits the nut
Striking with nut		Striking one nut with another nut. Recorded every time the nut hits the other nut
Positioning		Subject put the nut down and leaves it before striking it
Scrounging	Adult present/ adult left	Subject take a nut, or part of a nut, that another monkey was cracking, while s/he was there or within 5 seconds after s/he left
Nut cracked		Nut shell is broken (Observer sees or hears)

Manipulation	Nut Nut shell Stone Sand (including digging for tubers) Tuber Non-embedded plant material (e.g., grass, flowers, fruits) Embedded plant material (e.g., seeds within a shell) Non-embedded invertebrates (e.g., flying insects, spiders) Embedded invertebrates (e.g., termites inside branches) Vertebrates	Picking up, rubbing between the hands on the body, rolling on surface, manipulating in hand in another way (including hand/mouth actions), NOT including eating, or hitting it directly. If done continuously, recorded every 3 seconds
Eat	Drinking	Biting into a food item or putting it in

	Nut Nut shell Tuber Non-embedded plant material (e.g., grass, flowers, fruits) Embedded plant material (e.g., seeds within a shell) Non-embedded invertebrates (e.g., flying insects, spiders) Embedded invertebrates (e.g., termites inside branches) Vertebrates	the mouth. If done continuously, recorded every 3 seconds
<u>Location states. Mutually exclusive, recorded from the second they start until subject moves to another location</u>		
Location		**Description**
Ground		Including rocks and outcrops (unless

		used as anvils)
Near/on anvil		Arm's reach from an anvil (see definition of anvil below)
Tree		Including fallen logs (unless used as anvils)

Table 2.3: duration of observations

Year	Total time in seconds (mean)	Number of subjects
First	30714	8
Second	53773	5
Third	42878	6
Fourth	47175	6
Fifth	41910	7
Sixth	51461	4

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CHAPTER 3

WHEN AND WHERE TO PRACTICE: SOCIAL INFLUENCE ON THE DEVELOPMENT OF NUT CRACKING IN BEARDED CAPUCHINS (*SAPAJUS LIBIDINOSUS*)[1]

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1. Eshchar, Y., D. M. Fragaszy, et al. (In process).
   "When and where to practice: social influence
   on the development of nut cracking in bearded capuchins
   (*Sapajus libidinosus*)"
   To be submitted to Animal Cognition

Abstract

The habitual use of tools by wild capuchin monkeys presents a unique opportunity to study the maintenance and transmission of tradition. Young capuchins spend several years interacting with nuts before they can crack them efficiently. We set out to examine the social influences that motivates this long period of practice. We followed 16 infants and juveniles in five collection periods during 26 months, recording their behavior and the behavior of other individuals around them. We show that the juveniles match the behavior of the adults in both time and space. The rate of manipulation of nuts by the juveniles was higher when others in the group cracked and ate nuts, and also when the juveniles themselves were near the anvils, where nut-cracking takes place. We suggest a model for the social influence on nut-cracking skill development that is based on two related processes: social facilitation from observing groupmates engaged in nut-cracking, and the opportunity for practice provided by the anvils, hammer stones and nut shells on and around the anvils. Nut-cracking activity by others can support learning by drawing the juveniles to the anvils, where extended practice can take place, and by providing the materials for practice at these places. This study presents a novel method for studying social influence on development of foraging skills in a natural setting.

Keywords: tool use, social learning, social facilitation, skill acquisition, artifacts

Introduction

Social learning was defined by Heyes as “Learning that is facilitated by observation of, or interaction with, a conspecific, or its products’’ ((Heyes 1994), pg. 207). Learning from others is common throughout the animal kingdom, and is found in fish, birds, mammals and insects (Galef 1996; Galef and Laland 2005; Leadbeater and Chittka 2007). When a behavior that is acquired, at least partly, through social influence persists over time, and is transmitted from generation to generation, it can be called a tradition (Fragaszy and Perry 2003; Whiten 2009).

Social learning can be achieved through different processes (for example, imitation, emulation, social or response facilitation and local enhancement). Imitation is broadly defined as "copying the form of an action" ((Whiten, McGuigan et al. 2009), pg. 2418), and in some cases, more narrowly, as copying the exact actions of an agent. Emulation, on the other hand, is defined as copying the end-state of an action – in this process, the learner observes the changes to the inanimate world that are the result of the behavior of another individual, and designs its own actions to achieve the same changes (Tomasello 1996). Response facilitation (sometimes called social facilitation) takes place when the presence of a demonstrator performing an action, or a set of actions, increases the probability of an animal observing the other to engage in the same activity (Heyes 1994; Visalberghi and Addessi 2000). Local or stimulus enhancement is defined as a situation in which exposure to an individual's activity, or to the products of this activity, draws the observer's attention towards the location of the activity and/or a specific object in this location involved in the activity (Heyes 1994; Hoppitt and Laland 2008). The observer then interacts with the object or explores the location, but does not necessarily perform the same activity as the "demonstrator". Local enhancement can be conceived as coordination of activity in space, and social facilitation as coordination of activity in time (Coussi-Korbel and Fragaszy 1995).

Studies have shown that animals, while undoubtedly learning from their groupmates, rely on different mechanisms than those humans apply for the same end. Unlike humans, animals almost never engage in active teaching (although rare cases have been suggested, see (Boesch 1991; Thornton and Raihani 2008)). In addition, while humans imitate readily from a very young age, and do it without a need for external motivation (Meltzoff 1996), this is not the case for non-human animals. It is not yet clear to what extant true imitation - observing a demonstrator and faithfully copying its movements – exists in animals, and whether it can explain the spread of novel behaviors in a population. Several studies have shown that various animals are capable of at least some form of imitation (Akins and Zentall 1996; Moore 1996; Zentall, Sutton et al. 1996). However, when asking whether imitation plays a major role in the way non-human animals learn from each other, the answer seems to be a qualified “no”: there is very little evidence for imitative learning in the wild (e.g., (Tomasello 1994; Boyd and Richerson 2005; Rendell, Fogarty et al. 2011), although see (Voelkl and Huber 2000)).

Instead, animals learn from each other mainly through emulation, local enhancement, and social facilitation (Tomasello 1994; Hoppitt and Laland 2008). Captive studies in various species, from graylag geese (Fritz, Bisenberger et al. 2000) to chimpanzees (Nagell, Olguin et al. 1993), show that animals can learn to solve a foraging task through local enhancement, without repeating the exact actions they are seeing.

It is important to note that social and asocial learning are not mutually exclusive. In learning a complex behavior, social and asocial processes play complementary roles. This was termed “socially biased learning”: individual learning is informed and influenced by social input (Galef 1995; Fragaszy and Visalberghi 2004). Matthews et al. built a learning model incorporating social and asocial learning processes to describe the behavior of captive capuchins presented with a two-option task. The monkeys had to open one of two doors on a plastic tune to gain access to a food reward. The researchers showed that a model incorporating learning through local enhancement followed by the asocial process of reinforcement learning, and concluded that those processes can produce and maintain traditions (Franz and Matthews 2010; Matthews, Paukner et al. 2010). Similar results were obtained from a study on wild meerkats presented with a novel foraging task. Hoppitt et al. identified nine learning processes, six asocial and three social, that influenced the learning of the task – including observation and local enhancement (Hoppitt, Samson et al. 2012).

Importance of artifacts

Social influence can be exerted not only through direct observation, but also from interactions with the artifacts left by a certain behavior. This is the often-neglected part of the Heyes' definition of social learning, its last three words: "or its products". Enduring artifacts associated with technical activities – such as open shells, broken branches, holes dug in the ground and more – can help individuals master the same tasks (Fragaszy, Biro et al. 2013). Artifacts provide opportunities for learning and practice, and can also be associated with the actions performed by the adults, and thus reinforce the lessons learned through observations.

The importance of artifacts was demonstrated in several studies, the most well-known of which might be Aisner and Terkel's study on the foraging behavior of the black rat (Aisner and Terkel 1992). In this species, pups learn the correct way strip pine cones and eat their seeds while foraging with the mother. Careful experimentation on wild-caught rats showed that the cones themselves play a major role in this process. When the researchers gave naïve rat pups half-stripped cones, about 70% of them learned to strip them the rest of the way, and 90% of those pups ended up learning to strip intact cones. In contrast, pups that were presented only with intact cones never learned to strip them. The authors suggest that wild rat pups learn to strip cones in a similar way: they steal partially open cones from their mothers; learn first how to continue to strip them, and then how to strip an intact cone.

Thus, behavior can be transmitted socially and traditions can be maintained over time with processes that lead to the coordination in space and time of activity by the learner with the activity of others (local enhancement and social facilitation), processes that can at times take place even without direct observation.

Tool use

One category of foraging that receives a lot of attention in the animal behavior literature is tool use. One of the more widely used definitions of tool use is Alcock’s definition from 1972 - “the manipulation of an inanimate object, not internally manufactured, with the effect of improving the animal's efficiency in altering the position or form of some separate object” [(Alcock 1972), pg. 464]. In non-human primates, the most thoroughly studied habitual tool-use behaviors are nut-cracking in chimpanzees (Sakura and Matsuzawa 1991; Boesch, Marchesi et al. 1994; Matsuzawa 1994), termite-fishing and ant-dipping in chimpanzees (Goodall 1964; Humle and Matsuzawa 2002; Sanz, Call et al. 2009), extracting seed from fruits by orangutans (Van Schaik and Knott 2001), nut cracking in capuchin monkeys (Fragaszy, Izar et al. 2004; Ottoni and Izar 2008), and pounding and scraping oysters and snails with stones in long tailed macaques (Gumert and Malaivijitnond 2012). All those behaviors were claimed to be traditions – to be transmitted from generation to generation, at least in part, by asocial learning.

Unfortunately, showing that social transmission occurs is not an easy task, especially in natural settings. One of the more widely used methods to study tradition in wild populations is called the ethnographic method, or the method of exclusion. It is based on comparing the pattern of variation in the behavioral repertoire of two or more group. Social transmission is inferred to be responsible for those variations, if genetic and ecological influences can be excluded (Laland and Hoppitt 2013). This method was used to study tool-use behavior and other behaviors that were seen as potentially traditional. For example, Whiten et al. found 39 patterns of behavior that were habitual or customary in some chimpanzee populations and absent in others, including (but not limited to) tool use (Whiten, Goodall et al. 1999), and Van Schaik and Knott described the distribution of tool use to extract the seeds of the Neesia fruits in orangutans (Van Schaik and Knott 2001).

However, the ethnographic method is logically flawed. It presents only circumstantial evidence for social transmission, and its conclusions are always speculative – social learning is assumed until a convincing genetic or ecological explanation comes up, although what constitutes convincing evidence cannot be stated in advance (Fragaszy and Perry 2003) This flaw is revealed by Humle and Matsuzawa's (2002) study examining ant-dipping in chimpanzees – a behavior that varies in its details across populations, and thus was thought by some to be (Whiten, Goodall et al. 2001). Humle and Matsuzawa found that individuals in a single population used more than one technique, and that the technique used by an individual at a given time was influenced heavily by the type of prey and the circumstances under which the dipping took place (Humle and Matsuzawa 2002). This does not mean that social factors do not contribute to the maintenance of ant-dipping in the population. Rather, it shows that ecological circumstances also play a role in the particular forms of the behavior expressed in a given population.

Another method to show social transmission is to look for correlations between social learning opportunities and skill acquisition or proficiency across individuals. Humle et al. (2009) found that young chimpanzees whose mothers spent more time ant-dipping (and therefore had more opportunities for observation) acquired the behavior earlier and made fewer errors (Humle, Snowdon et al. 2009). Lonsdorf found that the mother's time spent alone or with maternal relatives – which is correlated to the time spent termite-fishing – is positively correlated with the acquisition of critical elements of termite fishing by the offspring (Lonsdorf 2006). This method can be used in species such as chimpanzees and orangutans, in which young individuals spend years in close proximity to their mothers, that are therefore their main resource for social learning. In other, more gregarious species, we cannot assume that learning opportunities across individuals differ substantively as a function of the mother's behavior.

In order to gain the most comprehensive understanding of the maintenance of established traditions in the wild and their transmission methods, one has to examine the ontogeny of those behaviors (Galef 1992; Fragaszy and Perry 2003; Meulman, Seed et al. 2013). Both in capuchins and chimpanzees, studies have looked at the development of tool use in young individuals (e.g., nut-cracking in chimpanzees - (Inoue-Nakamura and Matsuzawa 1997), termite-fishing in chimpanzees - (Lonsdorf 2005), nut-cracking in capuchins - (Resende, Ottoni et al. 2008; Resende, Nagy-Reis et al. 2014). They provide a good description of the steps the young animals go through on their way to becoming proficient tool users. One aspect they all have in common is the long period from the time infants first interact with the tools and the food items to the time when they start using the tools successfully. In termite fishing in Gombe, Tanzania, infants start interacting with the tools at 18 months, but successful extraction of termites was seen in some individuals only at age 5.5 years (Lonsdorf 2005). The chimpanzees in Bossou interact with nuts and stones in their first year of life, but first nut cracking is seen at around age 3.5 years (Inoue-Nakamura and Matsuzawa 1997). Finally, capuchin monkeys in Tiête Ecological Park, Brazil, interact with nuts before they reach 6 months old, and start nut cracking in their third year of life (Resende, Ottoni et al. 2008). It is not clear what keeps the infant and juveniles interested in nuts and stones throughout this period, and drive them to repeated interactions with them. One possibility is that the observations of adults in the group using tools, and the opportunities afforded by discarded tools and cracked shells, play an important role in keeping the youngsters' interest level high.

The ontogeny of nut-cracking behavior by chimpanzees in Bossou, Guinea was studied with special attention to social influence (Matsuzawa, Biro et al. 2001; Biro, Inoue-Nakamura et al. 2003; Biro, Sousa et al. 2006). Young chimpanzees are weaned at around age 3.5, and in the first 4-5 years spend most of their time next to their mother. During this time the mother is highly tolerant towards her offspring, let them sit next to her as she cracks nuts, touch the stones and her hands and even take kernels of cracked nuts. Those kernels are often the first nuts that the infants eat, years before they can crack themselves. In this way, the mother provides the infants and juveniles with "an excellent setting in which learning aided by observation can take place" [(Biro, Sousa et al. 2006), pg. 496]. Matsuzawa, Biro et al. propose that juvenile chimpanzees have to figure out the details of successful nut cracking by themselves, but they do that in an environment that facilitate this learning. Matsuzawa called this form of social transmission, in which juveniles learn from being exposed to the target behavior but without direct instructions, "master-apprentice relationship" (Matsuzawa, Biro et al. 2001).

Tool use in capuchins

This study examines the social influence on activities with nuts and stones in young wild bearded capuchin monkeys (*Sapajus libidinsus*) that live in a group in which most individuals crack nuts using stone hammers, at the Fazenda Boa Vista in Brazil (Fragaszy, Izar et al. 2004). The monkeys in this population habitually crack several species of palm nuts using hard stones as hammers and large sandstones or logs as anvils. Since 2004, tool use was reported in other populations of the same species and in related species of tufted capuchins (genus Sapajus) (Ottoni and Izar 2008; Canale, Guidorizzi et al. 2009; Ferreira, Jerusalinsky et al. 2009; Garber, Gomes et al. 2012).

Developmental trajectory in capuchin monkeys

Capuchins are manipulative by nature. Studies in captivity show that tufted capuchins (*Sapajus* spp.) start getting off their mothers' back at around 6 weeks of age, and about the same time start to explore and manipulate objects around them (Byrne and Suomi 1995). Percussion – hitting objects on a surface – is a common behavior in capuchins of all ages (Izawa 1979; Galetti and Pedroni 1994; Yamakoshi 2004), and is already performed within the first 2-3 months of life (Adams-Curtis and Fragaszy 1994). The rate of all manipulative actions increases rapidly through the first year of life, as does the proportion of more dexterous actions (Fragaszy and Adams-Curtis 1997). Capuchins are weaned at around 18 months (Fragaszy, Izar et al. In process). We have recently shown that infants manipulate objects at much the same rate as do adults, with the exception of hard-to-processes items, including nuts, for which the rate of manipulation increases sharply to the adult level around the time of weaning (Eshchar, Fragaszy et al. In process). Capuchins take years to master nut cracking. In previous studies, successful cracking of *Syagrus* palm nuts (small, relatively soft nuts) was first seen in the third year of life (Resende, Ottoni et al. 2008); juveniles take about 2-3 more years to be as efficient as the adults at cracking these nuts with stone hammers (Resende, Nagy-Reis et al. 2014).

Social interactions in capuchin monkeys

Capuchins live in mixed-sex, mixed age cohesive groups with a high level of tolerance, especially towards their young. Tolerance is often defined as allowing other animals to stay in the vicinity while feeding (van Schaik 1989). Other measures – such as frequency of agonistic encounters and reconciliations – can also be taken as a measure of tolerance (De Waal and Luttrell 1989). Capuchin monkeys often show a high degree of tolerance, even sharing food with each other (de Waal, Luttrell et al. 1993). At Fazenda Boa Vista, adult females exhibit a clear and stable linear dominance, and agonistic behavior between females occurs most often while feeding on clumped food (between 0 to 5 events per bout of feeding). However, most of the time, high-ranking females allow lower-ranking females to remain near them, even when feeding on clumped resources (Verderane, Visalberghi et al. 2013). Previous studies have shown that infant and younger juvenile capuchins are also highly tolerated (Coussi-Korbel and Fragaszy 1995). For example, infants trying to take a preferred food from adults were tolerated over 90% of the time, and even when they were refused the interaction was not aggressive (Fragaszy, Feuerstein et al. 1997). In a recent paper, studying a semi-free, nut-cracking population of capuchin monkeys, it was found that infants and juveniles often fed on kernels from open nuts in the presence of the tool-user. Infants took food on 89% of the nut-cracking events they watched, and juveniles on 58% of them (Coelho, Falótico et al. 2015).

Tolerance towards immatures decreases with age and younger juveniles are more comfortable being next to adults during feeding compared to older juveniles. Janson found that, compared to younger juveniles, juvenile wild tufted capuchins around 4 years of age are less tolerated by the adults and are targets of aggression much more often (Janson 1990). In a study that looked at captive capuchins (*Sapajus* spp.) learning a foraging task, juveniles could interact with the same apparatus in a group setting (when the adults could also approach the apparatus) or in a place that was approachable only by juveniles. The group site was used more often by juveniles younger than 20 months, while older juveniles preferred the “juvenile only” location, thus shifting from coordination in time and space (as the younger juveniles did), to coordination in time but not in space (Fragaszy, Vitale et al. 1994).

Studies have shown that tufted capuchin monkeys pay close attention to the activities of other individuals in the group during foraging, including nut cracking (Ottoni, de Resende et al. 2005). Capuchins in captivity were shown to be influenced by others’ activities, and interact with objects that other monkeys interacted with, even in the absence of a reward (local enhancement) (Bonnie and de Waal 2007). In another study, capuchins were more likely to eat when seeing their groupmates eating (social facilitation) (Visalberghi and Addessi 2000). Since monkeys, like apes, exhibit both social facilitation and local enhancement, we suggest that juvenile capuchins learn through prolonged individual practice that is facilitated by the behavior of expert nut crackers around them. And, similar to the case with chimpanzees, we suggest that artifacts – anvils, hammer stones and nut debris – play an important role in facilitating this practice. Both anvil sites and hammer stones are used again and again by different members of the group, and anvils often accumulate a large amount of nut debris on and around them (Visalberghi, Fragaszy et al. 2007). Thus, anvil sites present the perfect environment for interacting with nuts and practicing nut cracking.

Current study

In this study we examine the influence of seeing adults cracking nuts, as well as the proximity to hammer stones and nut debris, on the tendency of infants and juveniles to interact with nuts. We followed 16 infant and juvenile monkeys in a wild, habituated group of bearded capuchins and recorded concurrently their behavior and the presence and behavior of others in the group. This method enables us to examine quantitatively the influences of other monkeys' activity on our subjects, and how the influences change with age.

Following the studies of Matthews et al. (2010) and Hoppitt et al. (2012) described above, we suggest that our subjects learn by a combination of social influence and asocial learning. The models in those studies (Matthews, Paukner et al. 2010; Hoppitt, Samson et al. 2012) involve two-option tasks (opening a container in two different ways, on different sides), and thus their details could not be directly applied to our situation. However, the more general concepts are applicable. Hoppitt et al. found that the rate of interaction with the baited container was positively associated with the number of previous observations of conspecifics gaining access to it, and was higher in the period immediately after a conspecific interacted with the container - which was attributed to local enhancement. Importantly, seeing others gaining access to the container also correlated negatively with the rate at which the subject abandoned the task –they were less likely to "give up" if they saw conspecifics receiving reward. Since there was only one container, the subjects could not interact with it at the same time as the demonstrator. In our study, nuts and nut shells are abundant around the anvils on which the adults crack them, and our subjects can interact with them while other group members are cracking. Therefore, we suggest that in our population the rate of interaction with nuts would be higher not only after, but also while the infants and juveniles see the adults cracking and eating nuts.

Both models emphasize the important role of asocial learning mechanisms. For example, in Hoppitt et al. (2012), successful interactions with the container correlated positively with future rates of interactions.

The same combination of processes is likely to take place in our population: we suggest that the sight and sound of adult group members cracking and eating nuts draws the attention of juveniles and infants, and increases their interest in nuts as well as in the anvils and hammer stones. The possibility of getting crumbs and leftovers, combined with the tolerance of the adults towards infants and young juveniles, draws them to the anvils where the nut-cracking takes place. While near an anvil, they have abundant opportunities to engage with nut shells and with the tools, and the motivation to do so – having just seen others acting with them, leading to social facilitation, and the reward that can be gained from acting with these objects, providing vicarious reinforcement (Bandura 1977). We suggest that these social influences synergistically help sustain the juveniles' practice of nut cracking in the years before they can successfully crack.

Therefore, our specific predictions are:

1. Infants and juveniles manipulate nuts and nut debris at a higher rate when they can see and/or hear other individuals crack and eat nuts around them.

2. Infants and juveniles manipulate nuts and nut debris at a higher rate when they are next to an anvil.

3. Infants and juveniles spend more time near anvils when other individuals crack and eat nuts around them.

4. Social influence is strongest when juveniles are between the ages of 1 year old and 4 years old. At this age the juveniles already interact with nuts regularly, and are still highly tolerated and allowed to stay near the adults.

This study addresses the question of social transmission in a unique way, by examining social influences, exerted both by observations and interactions with artifacts, on the motivation of juveniles to practice nut-cracking. To our knowledge, this is the first quantitative study of social influence of this kind. The model suggested here is applicable not only to non-human primates, and not only to tool-use tasks. Foraging tasks that require a long period of learning and practice can be seen throughout the animal kingdom. Examining this phenomenon in a way that takes into account both social and asocial processes can shed new light on the development of foraging skills across many taxa.

Methods

Study site

Our site is located 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 masl) punctuated by sandstone ridges, pinnacles, and mesas rising steeply to 20–100 m above it. The climate in the region is seasonally dry. At our site, annual rainfall in 2006 – 2008 averaged 1290 mm per year. From May to September rainfall averaged 25 mm and from October to April 1266 mm.

Anvils

An anvil is defined as a flat, or nearly flat, horizontal 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 (hard stone weighing 150 g or more) 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.

Study duration

Data were collected in five discrete collection periods; each consisted of six to nine weeks of observations. Three of those collection periods took place during the dry season, and two during the rainy season. The time points were: May-July 2011 (Dry season), Jan-Feb 2012 (Rainy season), May-July 2012 (Dry season), Jan-Mar 2013 (Rainy season) and June-July 2013 (Dry season).

Subjects

At the beginning of the study, there were 11 juveniles and babies in the group, aged from 3 months to 4.5 years. Five more infants were born during the study (see table 3.1). Data on the oldest juvenile (Tomate) were collected only in the first two collection periods. At the beginning of the study, none of the subjects could crack open a whole nut of the more resistant species (*Orbygnia* and *Attalea*). The two oldest juveniles, and to some extent two others, mastered this skill through the duration of the study. Apart from our subjects, the group included 3 adult males and 5 adult females. All but one female habitually cracked nuts.

Data collection

All observers used hand-held devices with Pocket Observer© software by Noldus Information Technology. All observations lasted 20 min, or until the focal subject went out of view and could not be followed; but not less than 5 min.

Observations were collected using two-people teams. One observer followed one of the subjects to obtain a continuous record of the focal subject's location and activities.

This ethogram included two categories:

1. Location – on a tree, on the ground, or within arm's reach of an identified anvil
2. Specific actions – including eating (nuts or other objects), direct percussion of an object on a surface (nuts or other objects, on tree, ground or anvil), manipulating nuts or other objects in a non-percussive way, combinatorial percussion (striking a nut with a stone and striking a nut with another nut), and more (see Table 3.2).

Concurrently, the other member of the team recorded, as an instantaneous observation every minute, the identity, location and activity of other monkeys in the vicinity of the focal monkey.

At each collection period, a quarter to one half of the observations were collected in our field laboratory - an open area, about 12 m in diameter, that the monkeys visit 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, Pickering et al. 2010; Fragaszy, Greenberg et al. 2010; Massaro, Liu et al. 2012; Fragaszy, Liu et al. 2013). Many nut shells and debris from years of nut-cracking can be found on and around the anvils, and all around the lab area.

Reliability

Observers first learned to identify all members of the group with the help of long-term field assistants. Subsequently, observers were trained on the ethogram. Reliability for focal observations was calculated using GSEQ: Generalized Sequential Querier ©, URL: http://www2.gsu.edu/~psyrab/gseq/index.html. Time unit kappa, which provides a measure of alignment of two observations, was at or above 0.7, which is considered highly reliable (Bakeman, Deckner 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 for every minute. 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 groupmates into three categories – whether the focal monkey had no groupmates within 5 m, one to three groupmates, or more than three. We also looked at whether or not at least one of them was cracking or eating nuts. Because of this pooling, the limitation of this method – the inability in some cases to code exhaustively all monkeys in the area – does not affect the results here.

Data analysis

For each subject in each collection period, we collected between 19 and 53 observations, which lasted, together, between 5.3 hours to 27.1 hours (table 3.3). 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. We obtained rate per 10 min for various activities, under different conditions (near or away from an anvil, with or without group activity). In some cases, we combined several codes to create new variables:

- All actions with nuts were combined and termed “nut manipulation”
- “Nut-cracking activity nearby” is defined as time when one or more individual is cracking or eating nuts within 10 m of the focal subject, or nut-cracking can be heard.

SAS© software was used to test general mixed linear models (GLM) and ratio t-tests were used to evaluate the differences in activity under different conditions. Our independent variables are: Number of monkeys within 5 m from the focal monkey (three categories), presence of nut-cracking activity in the group (yes/no), and proximity of the focal monkey to an anvil (near/away).

Our dependent variables are counts – frequency of different activities and number of seconds spent in different locations. Working with counts rather than rates enables us to take into account the fact that the durations of the different conditions were not the same. We used total time of observation as an offset to test rate.

The count variables did not distribute normally (per Shapiro-Wilk test); therefore the Poisson distribution was used. Unless otherwise stated, the statistics are taken 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 two categories of the independent variable.

Result

Time spent with other group members

Infant and juveniles spent on average around 30% of their time by themselves, with no other monkey within 5 m of them. They spent 40% of their time with one to three other monkeys within 5 m, and 30% with more than three monkeys in that range. When there was nut cracking in the group – when group members cracked and eat nuts within a radius of 10 m from the subject, or nut cracking could be heard – this picture changed, and our subjects tended to have more group members around them. In those times, our subjects spent only 24% of the time with no other monkeys within 5 m, 34% with one to three monkeys around them, and 43% with more than three monkeys within 5 m (Fig 3.1). Statistical analysis shows that subjects were significantly more likely to be near three or more group members when there was nut-cracking activity in the group than they are to be alone (p=0.0003, estimate=1.3).

---------Insert fig. 3.1 here

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

The rate of manipulation of nuts by our subjects was significantly higher when others in the group were cracking or eating nuts in their vicinity (within 10 m) (median: 6.8 vs. 3.8 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 in the vicinity (median: 10.8 vs. 6.3 per 10 min, p=0.0001, estimate = 1.43, Fig 3.2). Very similar results are seen when looking only at the collection period in the dry season, when nut cracking was more common (for nut manipulation: p<0.0035, estimate= 3.28, for manipulation of other objects: p=0.0104, estimate = 1.3), and in the wet season, when nut cracking was seen less often (for nut manipulation: p=0.0015, estimate = 5.06, for manipulation of other objects: p=0.0069, estimate = 1.2).

The monkeys were sometime provisioned with nuts in a specific place in their home range, called the field lab area. This provisioning was done only during the dry seasons. We tested the influence of nut-cracking activity in the group specifically in the place – and time – in which provisioning took place. The influence of others in the group cracking or eating nuts in their vicinity on the rate of manipulation by our subjects holds under those conditions as well (p=0.0406, estimate=2.33). Overall the effect is robust across seasons and circumstances (locations).

------------Insert fig. 3.2 here------------

Influence of vicinity to an anvil on manipulation of nuts and other objects

When on an anvil or within arms' reach from one, the subjects manipulated nuts at a higher rate (median: 2 vs. 19.7 per 10 min, p<0.0001, estimates: 9.9). Those differences were significant in both the dry and wet seasons (p<0.0001 in both cases, estimates: 8.3 for dry seasons, 10.01 for wet seasons). The rate of manipulation of other objects was higher when subjects were *not* near an anvil (median: 11.5 vs. 4.5 per 10 min, p<0.0001, estimate = 2.19, Fig 3.3). The same was true if looking only at the dry seasons, but in the wet seasons there was no significant difference in manipulation rates of other objects near and away from anvils.

The influence of vicinity to anvils holds when we look at the lab area during dry seasons, where the monkeys were sometimes provisioned (p<0.0001, estimates: 8.4)

---------Insert fig. 3.3 here-----------

Relation between group activity and vicinity to anvils

Nut-related activity in the group has an effect on manipulation of nuts by the subjects 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 was significant whether or not the subjects were near an anvil, and vice versa. The rate of nut manipulation was lower when the subjects were away from anvils and there was no nut-related activity in the group (median: 1.4 per 10 min), slightly higher when the subjects were away from anvils but others were cracking and eating nuts around them (median: 3.75 per 10 min), higher still when the subjects were near an anvil, but there was no group activity (median: 16.3 per 10 min), and highest when the subjects where near an anvil and others were engaging in nut-related activity nearby (median: 28.8 per 10 min, fig 3.4 and table 3.4). 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.

-------Insert table 3.4 here-------------

The opposite picture is seen with manipulation of objects other than nuts (fig, 3.4, table 3.5). The effect of nut-related activity in the group was significant even when taking into account vicinity to anvils, and vice versa (p<0.0001 in both cases).

------Insert table 3.5 here-------

-----Insert fig. 3.4 here-----------

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 hitting the nut with a stone. This action first appeared in some subjects as early as age 15 months, but was only seen frequently at the fourth year of life (Eshchar, Fragaszy et al. In process). This action showed the same pattern as overall manipulation with nuts. Striking a nut with a stone was seen almost exclusively near an anvil (median: 0.04 vs. 1.05 per 10 min, $p<0.0001$, estimates: 38.6, fig 3.5), and the rate was significantly higher when there was nut-cracking activity nearby (median: 0.05 vs. 0.09 per 10 min, $p=0.0006$, estimates: 2.2). it should be noted that the stones the juveniles used – especially the younger juveniles – were not necessarily the hammer stones used by adults. Often they were smaller stones found in the area.

---------Insert fig. 3.5 here----------

Time spent near the anvils

Subjects spent more of their time near an anvil while others in the group cracked and ate nuts around them (median: 10.2% vs. 3.6%, ratio t-test $p=0.0073$, fig 3.6). The effect was significant in the two wet seasons ($p=0.0052$), but not in the three dry seasons ($p=0.0839$). When looking only at the observations taken *in the lab area* during dry seasons, we again see that the subjects spent significantly more of their time near an anvil when there was nut-cracking activity nearby (p<0.0001).

---------Insert fig 3.6 here-----------

Scrounging

Infants and juveniles, especially those younger than four years old, are highly tolerated and often stay quite close to the adults while they are cracking and eating nuts. This is true not only in regard to their mothers, but also adults of both sexes. On occasion, juveniles scrounged (gained access to nut crumbs that were left from a nut cracking session), or even licked the anvil after an adult cracked a nut there. Less frequently, they were seen taking cracked nuts from the hands of others, in what is sometimes called “tolerated taking” (Fragaszy, Feuerstein et al. 1997)

Scrounging can be done with any food item, but in our site it was much more likely to occur near an anvil (mean: 0.27 vs. 0.03 per 10 min, p<0.0001, estimate = 6.89), and when there is nut-cracking activity nearby (mean: 0.22 vs. 0.08 per 10 min, p<0.0001, estimate = 6.95, see table 3.5). 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.

Infants begin scrounging at a few months old, and the rate of scrounging peaks at age one to two years. All subjects between one and two years old were seen scrounging at least twice, and one as many as 29 times. The rate of scrounging decreases with age (estimate = 0.64, p=0.008), and scrounging becomes extremely rare in subadults age five and older (only one subject age 5.7 years, was seen scrounging, on just two occasions).

-------Insert table 3.5 here--------

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

Proximity to anvils influenced the rate of manipulation of nuts significantly in all age groups, $p<0.0001$ for all comparisons. The influence of nut-cracking activity nearby was different in the different age groups (see fig. 3.7). In the first year of life, the rate of manipulation of nuts was not significantly influenced by nut-related activity nearby. However, at that time subjects already spent more time near anvils during nut-related activity in the group (median: 3.3% vs. 1.7%, $p=0.0120$)

In the second year of life, the rate of manipulation was higher during nut-related activity in the group (median: 7.3 vs. 2.7 per 10 min, $p=0.0229$, estimate=3.4). They also spent more time near anvils during nut-related activity in the group (median: 6.9% vs. 3.4%, 0.0086).

In the third year of life, the rate of manipulation was higher during nut-related activity in the group (median: 5.8 vs. 2 per 10 min, $p=0.0192$, estimate=4.6). Subjects also spent more time near anvils during nut-related activity in the group (median: 30% vs. 9%, $p=0.0007$).

In the fourth year of life, the rate of manipulation was higher during nut-related activity in the group (median: 5.8 vs. 2 per 10 min, $p=0.0178$, estimate=4.4). They also spent more time near anvils during nut-related activity in the group (median: 15.5% vs. 5.6%, 0.0001).

In the fifth year of life, the rate of manipulation was higher during nut-related activity in the group (median: 5.2 vs. 2.4 per 10 min, $p=0.0304$, estimate = 5.2). They also spent more time near anvils during nut-related activity in the group (median: 6.5% vs. 3.3%, 0.0153).

In the sixth year of life, the rate of manipulation of nuts was not influenced by nut-related activity nearby. However, subjects did spent more time near anvils during nut-related activity in the group (median: 16.6% vs. 5.9%, p=0.0064).

-------Insert fig. 3.7 here--------

The rate of manipulating nuts increased with age. The effect of observing others cracking and eating nuts on the rate of manipulation changes with age, but not in a uniform way – some subjects showed a larger effect as they grow older, and some a smaller effect (fig. 3.8).

------Insert fig 3.8 here --------

Discussion

We present here quantitative evidence for social facilitation and local enhancement in capuchin monkeys. Infants and juveniles interact with nuts and hammer stones at higher rates when others crack and eat nuts around them. They are also more likely, under those conditions, to spend time near an anvil - a location rich with nut-cracking artifacts. We suggest that social influence is exerted both through observation of the nut cracking itself – which motivates the juveniles to interact with nuts – and through the creation of artifacts, that provide opportunities for those interactions. Thus, the juveniles are likely to match the adults' behavior with nuts and stones both in time (manipulating and striking nuts when they see other cracking) and in space (manipulating nuts near and on the anvils used for nut-cracking).

First prediction: infants and juveniles 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 meters from the focal subjects (infants and juveniles), or when the sound of nut-cracking could be heard. The rate of manipulation of nuts by our subjects under those circumstances was about 4 times higher compared with times where 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 rate of those actions was more than twice as high when there was nut-cracking activity in the group.

One possible interpretation of these data is that the monkeys engage with nuts and stones wherever those are available. When coming to an area rich in nuts, many of them will crack, or interact with the nuts in some other way. According to this explanation, we see higher rates of manipulation of nuts and stones in our subjects during times of nut-cracking activity because both behaviors occur mainly in the same places and times.

We do not think this explanation is sufficient to explain our findings, for two reasons. First, the monkeys spend some of their time in an area designated “the outdoor laboratory”, where there are many anvils and hammer stones and the monkeys are sometimes provisioned with nuts. Nut cracking is very common in this area, and the ground near the anvils is covered in nut shells and debris. When the group is in this area, opportunities to interact with nut shells are always available. When looking only at data collected while the monkeys were in the outdoor laboratory area, we still see the influence of nut-cracking activity nearby. Second, even when the subjects are already near an anvil, the rate at which they manipulate nuts and stones is higher when others are cracking nuts nearby. There are usually plenty of nut shells near the anvils for the subjects to interact with, regardless of whether or not nut-cracking activity is taking place at the same time. Therefore, we see coordination in both space *and* time, that cannot stem simply from environmental cues that are nut cracking.

Another explanation is that nut-cracking activity near our subjects provokes an increase in activity by our subjects (essentially, an effect of non-specific arousal). If that were true, we would see a higher rate of manipulation of all objects. Our data show, however, that the rate of manipulation of objects other than nuts and stones *decreases* when there is nut-cracking activity nearby. The influence of other group members' nut-related activity on our subjects is specific to interactions with nuts and stones.

This leads us to the conclusion that the higher rate of manipulation of nuts and stones by infants and juveniles is evidence of social facilitation and local enhancement. The presence around them of group members engaged in cracking and eating nuts motivates them to interact with the same items in the same places.

As discussed above, there is plenty of evidence for the power of social facilitation in transmitting information. Clayton lists 24 studies, from the 1930s to the 1970s, which found social facilitation in feeding behavior in fish, birds and mammals (Clayton 1978). Many studies since then have come to the conclusion that seeing a groupmate engaging in a specific activity often leads to higher likelihood of the observer to engage in the same behavior. Hoppitt et al showed specifically how 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 (Hoppitt, Samson et al. 2012). The situation in Hoppitt et al's study was similar to that in our study (a field experiment;

groups of wild animals), but different 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 *after* observing others engaging in the task.

We can also look at the nut-cracking situation as a special case of a two-action task. In two-action studies, the subjects encounter a task that can be solved in two ways. They see a proficient individual demonstrating one of the options, and then may approach the task themselves. Many studies, on various animals, showed that subjects preferably attend to the option demonstrated to them (for example, (Hoppitt, Samson et al. 2012) mentioned above, (Matthews, Paukner et al. 2010) in capuchin monkeys). In our study, the subjects could choose between interacting with nuts and stones and interacting with other food items and objects. Our results show that, similar to the results in the two-action studies, our subjects tended to match their behavior to the behavior of their group mates.

Second prediction: Infants and juveniles manipulate 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: our subjects did most of their nut-related activity within arm-reach of an anvil site (the rate of manipulating nuts was almost 10 times higher near an anvil). Striking a nut with a stone was done almost exclusively near an anvil – the rate for this action was almost 40 times higher near an anvil than elsewhere. This finding is not surprising, since there are usually many nut shells and debris in and around the anvils, which give the juvenile and infants plenty of opportunities to interact with them, and at least one stone (the hammer stone). It should be noted though that nuts and nut-shells are also found away from the anvils, and nut manipulation did occur at locations other than the anvils, albeit at a lower rate. And though other objects are found near the anvils as well (leaves, pieces of wood, etc.), we see that our subjects preferably interacted with nuts and stones in those locations, and the rate of manipulation of other objects is lower near the anvils compared to other places.

We suggest that the ability to interact with the artifacts made by nut-cracking, in the place where nut-cracking has taken place and in vicinity to the tools (hammer stones) needed for it, might be very important for this period of practice. Other studies have shown the effect of interacting with artifacts created by specific activities on the learning of same activities. For example, rats were shown to learn how to strip pine cone from interacting with partly stripped cones (Aisner and Terkel 1992), young meerkats learn where to dig for prey by examining the holes made by older groupmates (Thornton and Hodge 2009), and young capuchin monkeys learn to find larvae in bamboo stalk by interacting with stalks already broken by adults (Gunst, Boinski et al. 2008). Similarly, by interacting with nuts and stones near the anvils our subjects associates the nuts with the anvil and the hammer stone (which is often left on the anvil) and discover the correct way to act with the stone and nuts. The fact that using stones to hit nuts was done almost always near an anvil supports this hypothesis.

Third prediction: Infants and juveniles spend more time near anvils when other individuals crack and eat nuts.

This prediction was also supported by our data; our subjects spent almost 3 times more of their time near an anvil when there was nut-cracking activity around them. Our study group is quite cohesive, with infants and juveniles spending 70% percent of their time in the vicinity (within 5 meters) of at least one group member, and 30% of their time in the vicinity of three or more group members. During nut-cracking activity in the group, our subjects spent slightly more time in the vicinity of others – 76% with at least one groupmate and 34% with three or more. This is in line with previous studies, that shows that capuchin society is relatively tolerant, even in the context of feeding, and especially towards infants and young juveniles (Coussi-Korbel and Fragaszy 1995; Verderane, Visalberghi et al. 2013).

We suggest that infants and juveniles are drawn to the anvils while nut-cracking is taking place there partly by their attraction to open nuts or their crumbs. As a rule, adults were very tolerant towards those attempts. They did not stop 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 is seen in all young juveniles, and its rate peaks in the one to two years old age group. Scrounging is also more likely to take place near an anvil, when there is nut-cracking activity nearby. Older juveniles and subadults (4 years and older) scrounge much less. When they approach a nut-cracking adult, they were sometimes threatened, but were never attacked.

This again is in line with previous studies. For example, Fragaszy et al showed that infant capuchins successfully scrounged from adults on about 90% of their attempts, and were never answered with aggression (Fragaszy, Feuerstein et al. 1997). Captive adult capuchins were also seen either sharing food or tolerating the taking of food between each other (de Waal, Luttrell et al. 1993). In a semi-free, nut-cracking population of capuchins in Brazil, infants scrounged in 89% of the nut-cracking events they watched, and juveniles scrounged on 58% of the events they watched (Coelho, Falótico et al. 2015). The difference between the rates of scrounging of infants and juveniles reported by Coelho et al. (2015) fits the data that we present here.

All this supports the conclusion that infants and juveniles are coming to the anvils during nut-cracking in an attempt to get food. Their approach is reinforced by intermittent success at scrounging. While there, as discussed above, they have ample opportunity to engage in nut-related activity and to learn to associate nuts, anvils and hammers.

Fourth prediction: Social influence is strongest when juveniles are between the ages of one and four years old.

The data partly support this prediction. First, subjects from all age groups manipulated nuts (and when they start hitting nuts with stones, stones as well) at a significantly higher rate while near an anvil. It seems that the influence of being near an anvil – presumably through providing opportunities for nut-related activity – is strong at all ages.

Similarly, in all age groups, subjects spent more time near the anvil when there is nut-cracking activity nearby. This is somewhat surprising: scrounging is all but gone by age five, and the older juveniles and subadults are sometimes threatened when they stand too close to an adult during nut-cracking. Therefore, we would expect that at older ages, our subjects would not be drawn to the anvil by nut-cracking activity, or at least that the influence would be much smaller. This is not what we have seen. One way to interpret this could be that subadults are coming to the anvils during nut-cracking for different reasons than do younger juveniles and infants. They do not scrounge for crumbs, but they might still be attracted to others cracking nuts there out of intrinsic interest in this noisy activity. At that age some of them can crack nuts themselves, and if the nut-cracking activity in the group motivates them to engage with nuts, they might go to an anvil to try and crack nuts there.

The influence of nut-cracking activity nearby on the rate of nut manipulation of our subjects is seen in all age groups accept the one year old infants and monkeys older than five years (subadults). The infants are only starting to interact with nuts, and seem to do that very 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.

As predicted, the oldest age group – subadults age five and older – was also not influenced by nut-cracking behavior nearby. This might be related not only to the fact that they are less tolerated by the adults, but also to the fact that at that age most subadults can already crack nuts quite efficiently (Resende, Nagy-Reis et al. 2014; Eshchar, Fragaszy et al. In process). They are drawn to the anvils at times of nut-cracking in the group, as we have seen, but they do not spend their time there interacting with nuts, shells or stones. They do not spend much time practicing and trying different actions, as the younger juveniles do.

Overall, the data support our prediction that social influence will be most apparent at the "young juvenile" stage, when the juveniles are already feeding themselves, show interest in interacting with nuts and stones, and are still tolerated by the adults. The fact that the influence of nut-cracking activity nearby on rate of nut manipulation is still seen at age four to five years, and the influence on location – being next to an anvil – is evident even in the subadults, might suggest that tolerance is still extended to subadults. Alternatively, those places and activities might remain attractive even though adults tolerate subadults less than they do juveniles. Intermittent reinforcement produces behavior resistant to extinction (Bandura 1977); perhaps we see in the persistence of local enhancement in the subadults the consequences of intermittent reinforcement of scrounging in the past.

Model of social influence

From the data, 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 groupmates cracking and eating nuts encourage infants and juveniles to interact with nuts and stones themselves. This influence is exerted in two ways:

    a. Through social facilitation, as seen in previous studies (e.g., (Nagell, Olguin et al. 1993; Matthews, Paukner et al. 2010; Hoppitt, Samson et al. 2012)). Seeing groupmates engage in a particular behavior, and seeing them getting a reward from it (which serves as vicarious reinforcement,(Bandura 1977)) , motivates the observers to engage in the same activity.

    b. Through drawing infants and juveniles towards 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 opportunities to interact with those artifacts. 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, Boinski 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 understand they need to act using the anvil and hammer stone. This mechanism increases the breadth of social influence beyond the limited time in which others are cracking nuts.

Social influence is clearly not the only factor in skill acquisition. We suggest that the processes described above provide the opportunity for the juveniles to manipulate nuts and stones in different ways, especially on the anvil sites, and motivate them to continue with this manipulation even in the absence of tangible reward. Through this type of practice they master nut-cracking.

The same model can be applied to the development of other extractive foraging tasks, especially those that take time to master. For example, young tufted capuchins were shown to take years to become efficient in processing Maripa fruits (Gunst, Leca et al. 2010), and white-faced capuchins show a similar pattern in processing Luehea fruits (Perry 2009). The development of several extractive foraging tasks were studied in chimpanzees – for example, 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, Gray 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 it is social influence that provides the motivation for this long practice. The importance of artifacts was also noted in some studies (e.g.,(Carvalho, Biro et al. 2009).

This study presents a novel method for evaluating quantitatively social influence on the development of skill in a natural setting. We suggest that similar examination of other extractive foraging behaviors in other species will reveal a learning process not unlike the one described here, with a role for social facilitation and for the practice-opportunity provided by artifacts. We hope that future studies will build on this model, to elucidate the often-elusive role of social input in skill development, thereby strengthening our understanding of tradition in nonhuman taxa.

Figures:

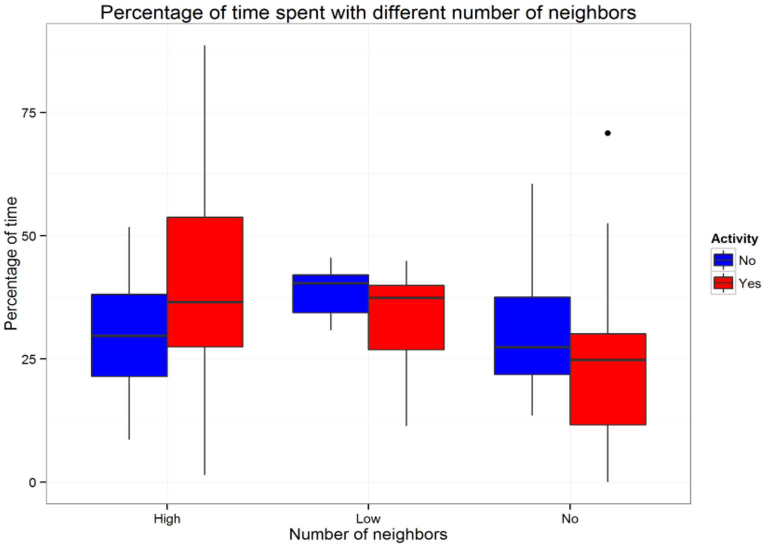
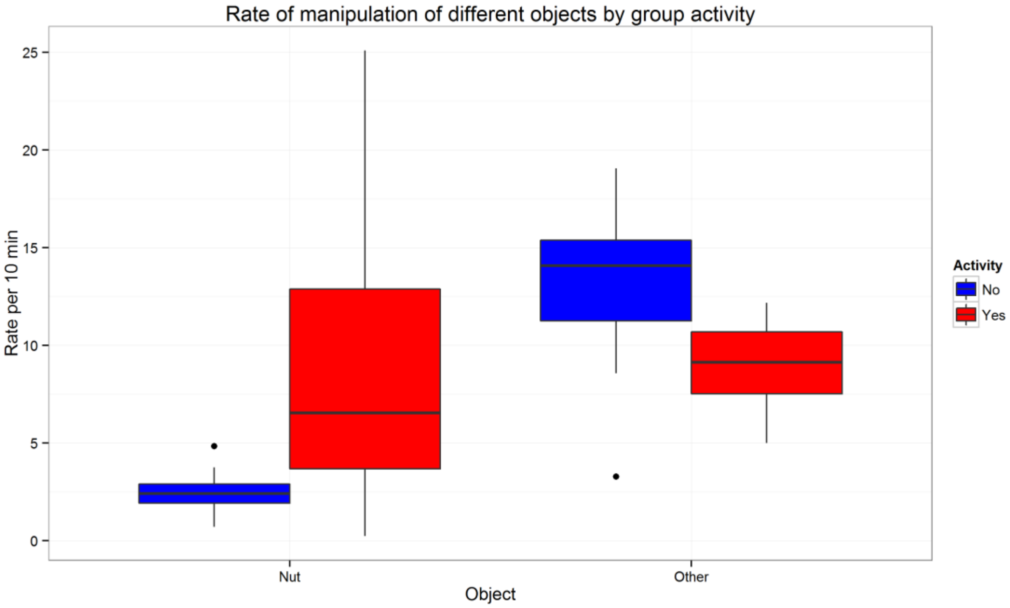


Fig 3.1: Percentage of time spent with no other groupmates within 5 m, with one to three groupmates within 5 meters (Low) and with more than three groupmates within 5 m (High), at times of nut-cracking activity within 10 m of the focal subject (activity=yes) and no nut-cracking activity (activity=no).



<u>Fig 3.2:</u> Rate per 10 minutes 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).

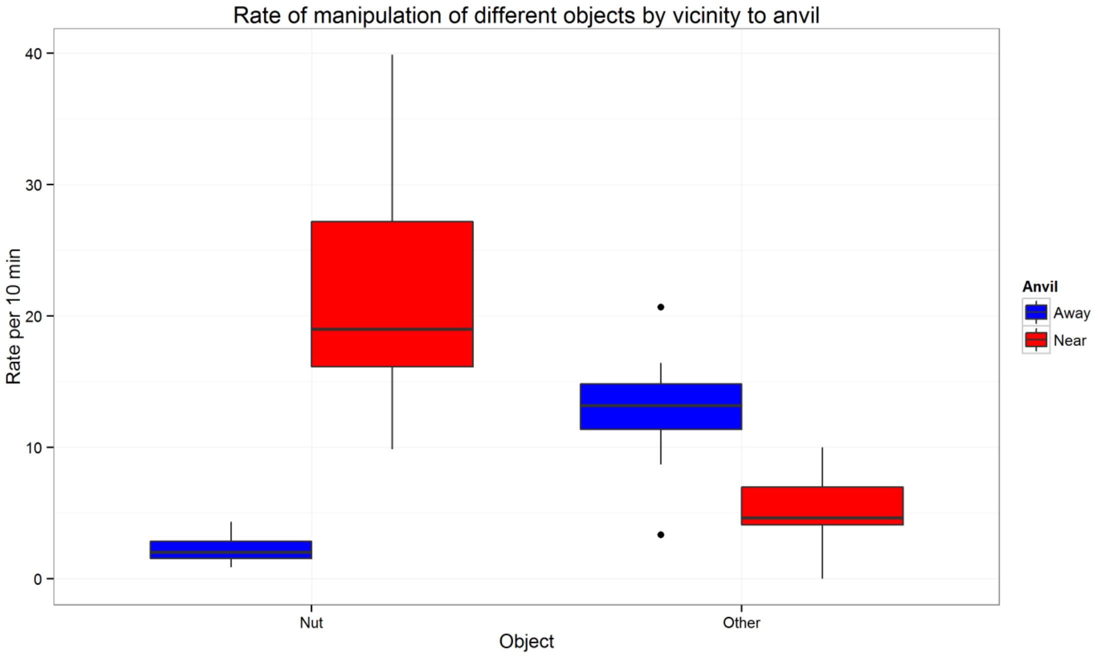
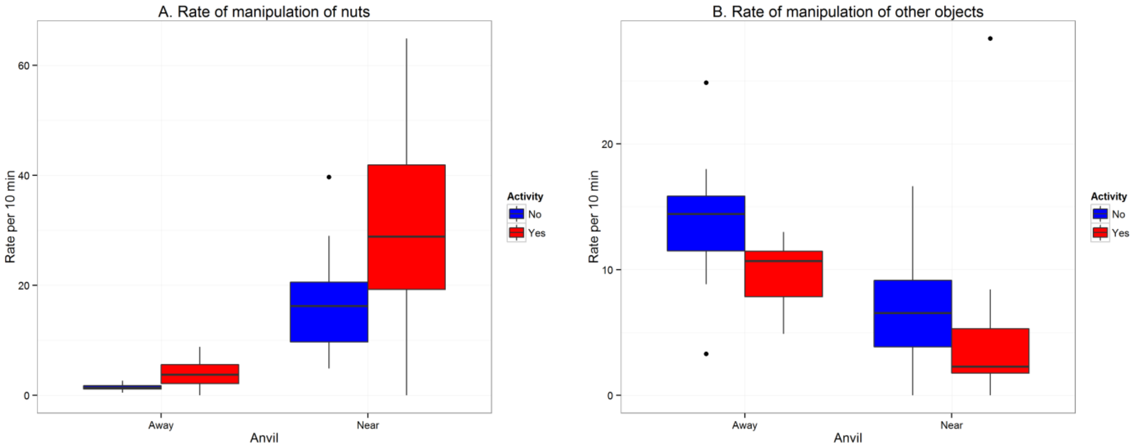


Fig 3.3: Rate per 10 min of manipulation of nuts and of other objects, when the subject is on or within arm's length of an anvil, and at other times.



<u>Fig 3.4:</u> Rate per 10 minutes 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.

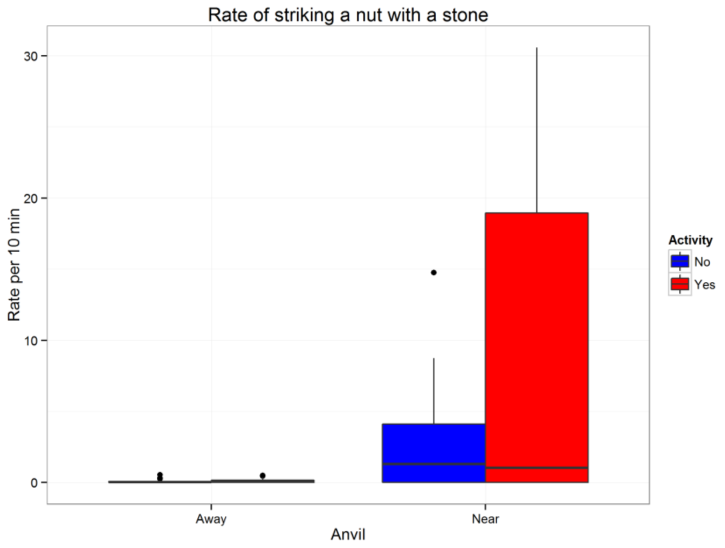


Fig 3.5: Rate per 10 minutes of striking nuts with a stone, at times of nut-cracking activity within 10 m of the focal subject (activity=yes) and no nut-cracking activity (activity=no), and when the subject is on or within arm's length of an anvil, and at other times.

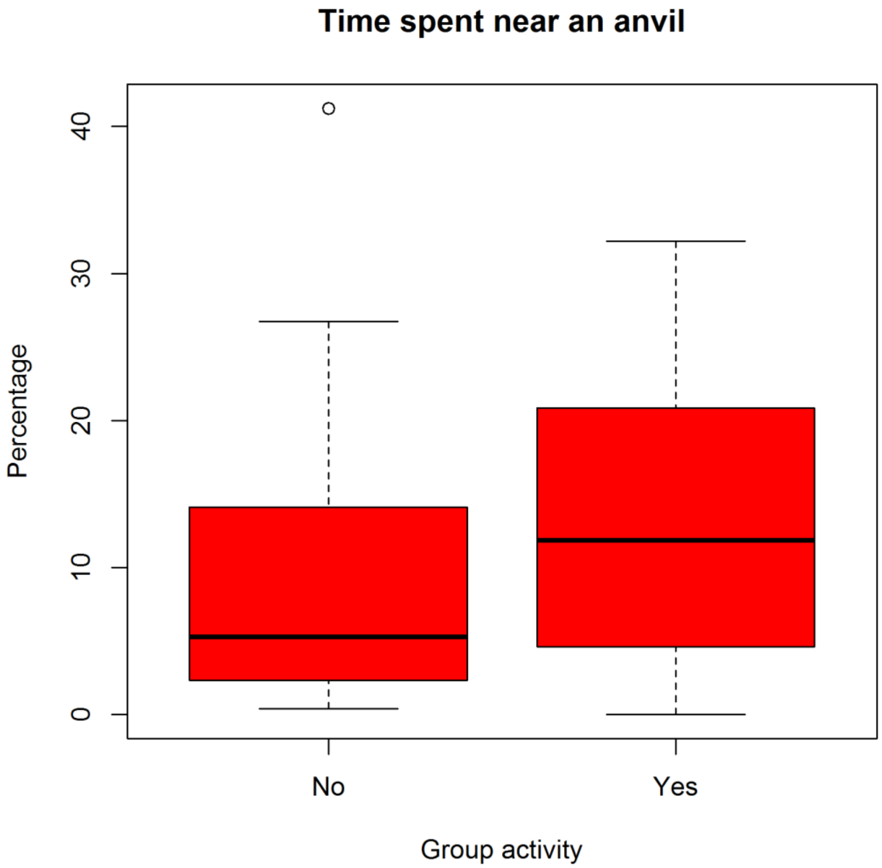


Fig 3.6: Percentage of time spent on or within an arm's length from an anvil, at times of nut-cracking activity within 10 m of the focal subject (activity=yes) and no nut-cracking activity (activity=no).

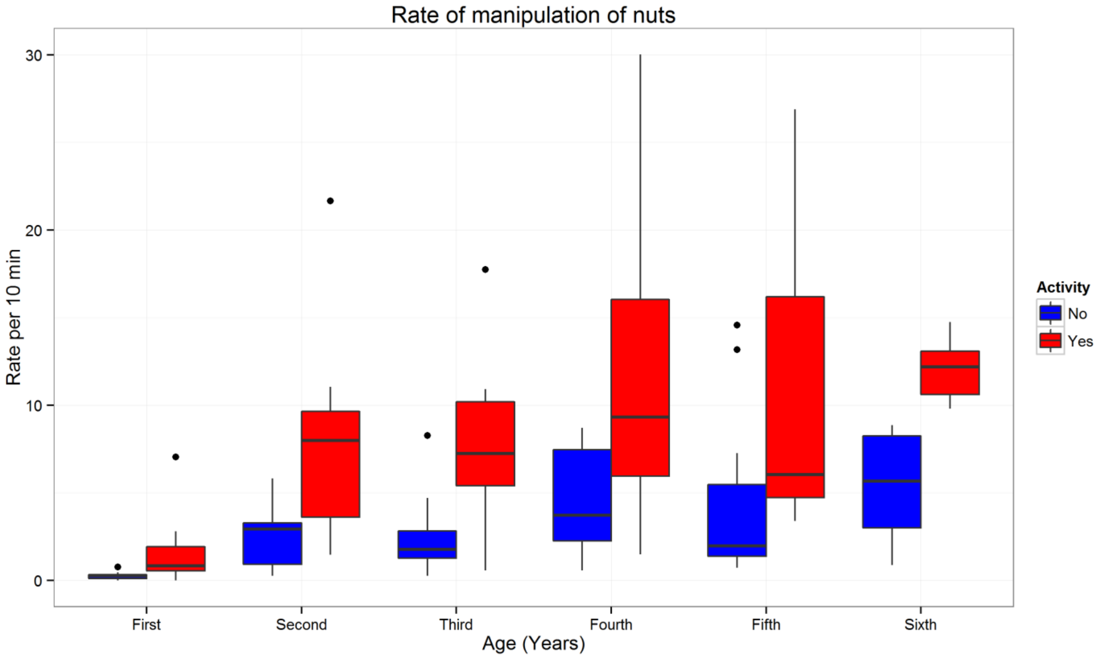


Fig 3.7: Rate per 10 minutes of manipulation of nuts and of other objects, at times of nut-cracking activity within 10 m of the focal subject (activity=yes) and no nut-cracking activity (activity=no), by age.

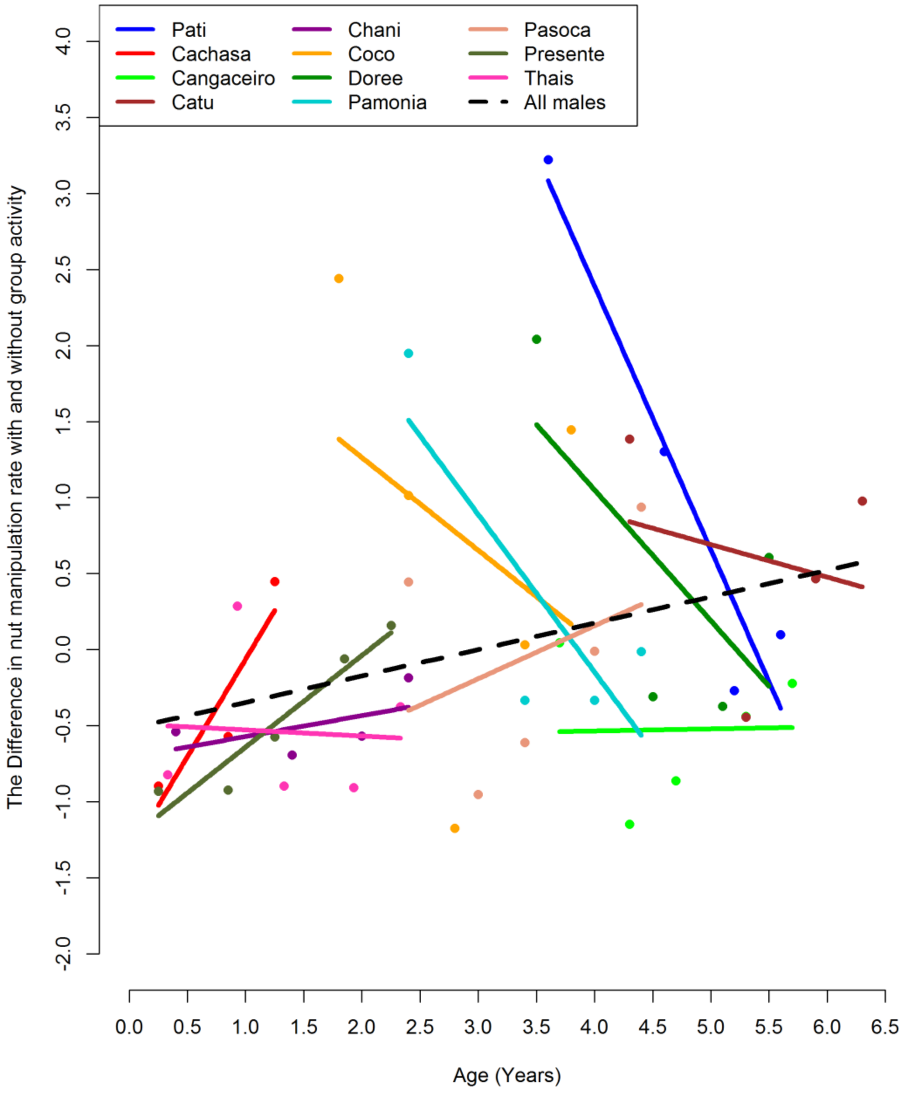


Fig. 3.8: Normalized effect of nut-cracking activity in the group on rate of nut manipulation, for each individual, as a function of age. The effect was calculated by deducting the rates during times without nut-cracking activity in the group from the rates during times *with* activity. The values were normalized by deducting the mean and dividing by the standard deviation.

Tables

Table 3.1. Demographic data on the subjects

Name	**Estimated date of birth (estimated)**	**Gender**	**Mother**	**Mass 2011 (Kg)**	**Mass 2012 (Kg)**	**Mass 2013 (Kg)**
Donzela	January 13, 2013	F	Doree	_	_	0.4
Patricia	January 11, 2013	F	Piassava	_	_	0.53
Titia	January 3, 2013	F	Teninha	_	_	0.66
Divina	November 7, 2012	F	Dita	_	_	_
Cachassa	March 15, 2012	M	Chuchu	_	0.42	1.11
Presente	February 15, 2011	M	Piassava	0.24	0.99	1.47
Thais	February 1,	F	Teninha	0.42	1.09	1.34

	2011					
Chani	December 15, 2010	F	Chuchu	0.46	1	1.16
Coco	July 14, 2009	M	Chuchu	1.14	1.44	1.66
Passoca	January 1, 2009	F	Piassava	1.18	1.32	1.62
Pamonha	January 1, 2009	F	Piassava	1.23	1.37	1.57
Doree	November 9, 2007	F	Dita	1.37	1.56	1.78
Pati	November 2, 2007	M	Piassava	1.68	2.08	2.5
Cangaceiro	September 20, 2007	M	Chiquinha	1.83	2.08	2.36
Catu	February 5, 2007	M	Chuchu	1.81	2.07	2.46
Tomate	December 1, 2006	M	Teninha	1.8	1.99	2.34

Table 3.2. Ethogram

Manipulating events: instantaneous activities, recorded the second they are performed, or in some cases, every few seconds as long as they are happening		
Event	**Modifier**	**Description**
Hitting a nut	Anvil/tree/ground	Subject holds a nut and strikes the nut directly onto the surface – ones or more than once in a sequence. As long as the behavior continuous, it is recorded every 3 seconds
Hitting another object	Anvil/tree/ground	Subject holds an object and strikes it directly onto the surface – ones or more than once in a sequence. As long as the behavior continuous, it is recorded every 3 seconds
Light tap		Fingertip tap (usually on rigid surface)
Striking - hitting		Striking a nut with a stone. Recorded every time the stone hits the nut
Striking with nut		Striking one nut with another nut. Recorded every time the nut hits the other nut

Positioning		Subject put the nut down and leaves it before striking it
Scrounging	Adult present/ adult left	Subject take a nut, or part of a nut, that another monkey was cracking, while s/he was there or within 5 seconds after s/he left
Nut cracked		Nut shell is broken (Observer sees or hears)
Manipulation	Nut Nut shell Stone Sand (including digging for tubers) Tuber Non-embedded plant material (e.g., grass, flowers, fruits) Embedded plant material (e.g., seeds within a shell) Non-embedded	Picking up, rubbing between the hands on the body, rolling on surface, manipulating in hand in another way (including hand/mouth actions), NOT including eating, or hitting it directly. If done continuously, recorded every 3 seconds

	invertebrates (e.g., flying insects, spiders) Embedded invertebrates (e.g., termites inside branches) Vertebrates	
Eat	Drinking Nut Nut shell Tuber Non-embedded plant material (e.g., grass, flowers, fruits) Embedded plant material (e.g., seeds within a shell) Non-embedded invertebrates (e.g., flying insects, spiders) Embedded invertebrates	Biting into a food item or putting it in the mouth. If done continuously, recorded every 3 seconds

	(e.g., termites inside branches) Vertebrates	
Location states. Mutually exclusive, recorded from the second they start until subject moves to another location		
Location		**Description**
Ground		Including rocks and outcrops (unless used as anvils)
Near/on anvil		Arm's reach from an anvil (see definition of anvil below)
Tree		Including fallen logs (unless used as anvils)

Table 3.3: duration of observations

Year	Total time in seconds (mean)	Number of subjects
First	30714	8
Second	53773	5
Third	42878	6
Fourth	47175	6
Fifth	41910	7
Sixth	51461	4

Table 3.4: mean and median of rate of nut manipulation under different conditions

Activity	Anvil	Mean	Median
No	Away	1.49	1.39
No	Near	17.15	16.26
Yes	Away	3.96	3.75
Yes	Near	29.4	28.84

Table 3.5: mean, median of rate of manipulation of other objects under different conditions

Activity	Anvil	Mean	Median
No	Away	13.98	14.41
No	Near	6.82	6.55
Yes	Away	9.71	10.68
Yes	Near	4.54	2.28

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CHAPTER 4

TEMPORAL PROPERTIES OF SOCIAL INFLUENCE ON NUT CRACKING IN WILD BEARDED CAPUCHIN MONKEYS (*SAPAJUS LIBIDINOSUS*): CONSIDERING A NEW DIMENSION OF SOCIAL LEARNING[1]

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[1] Eshchar, Y., D. M. Fragaszy, et al. (In process). "Temporal properties of social influence on nut cracking in wild bearded capuchin monkeys (Sapajus libidinosus): considering a new dimension of social learning" To be submitted to Animal Biology

Abstract

Social facilitation and local enhancement have been shown time and again to play a very important role in transmission and maintenance of tradition in non-human animals. However, very little attention was given to the dynamics of this influence. When the temporal aspect of social facilitation is being studied at all, it is usually in the form of checking its presence after a predetermined interval, rather than an examination of its decline. We have shown in a previous paper that young bearded capuchins (*Sapajus libidinosus*) in a wild, nut-cracking population interact with nuts and stones at higher rates when others in the group crack nuts around them (Eshchar et al., in process). Here we examine the dynamic of this effect. We show that the rate of manipulation of nuts by infants and juveniles declines exponentially in the minutes following the end of nut-cracking activity around them. Percussive actions with nuts also declined exponentially, but showed a shorter half-time compared to other activities with nuts. The time infants and juveniles spent near an anvil was also higher during nut-cracking activity in the group, and showed the same pattern of exponential decline. The dynamics of social facilitation changed with the age of the juveniles, with the older juveniles showing a longer half-time. This is the first such study of a natural behavior in a wild population.

Key words: tool use, development, *Sapajus*, social learning, social facilitation,

Introduction

The ability of animals to learn from each other, and the idea of tradition transmitted from generation to generation in animal societies, have long captured the imagination of researchers from various fields. In the last few decades this interest has blossomed to what Galef and Giraldeau called “an explosion of research”, specifically in the area of social influence on foraging behavior (Galef and Giraldeau 2001).

This interest was partly driven by the discovery of tool use traditions non-human primates, first in chimpanzees (Goodall 1964; Boesch and Boesch 1981; Sakura and Matsuzawa 1991), and later in orangutans (Van Schaik and Knott 2001), capuchin monkeys (Fragaszy, Izar et al. 2004) and recently, long-tailed macaques (Gumert and Malaivijitnond 2012). Together with the first detailed description of social transmission in wild population (e.g., (Kawai 1965)), those discoveries led to heated discussions about the extent to which the term “culture” can be applied to non-human animals, and the relation between animals’ traditions and the evolution of culture in our own species (e.g., (Galef 1992; Boesch 2003; Byrne, Barnard et al. 2004; Laland and Janik 2006; Whiten 2010) among many, many others).

While the debate about animal culture is still raging, the presence of traditions in non-human animals is much more established. “Tradition” is defined as any behavior that is acquired, at least partly, through social influence, and persists over time (Fragaszy and Perry 2003). Many studies were published about potential natural traditions both in non-human primates (Perry, Panger et al. 2003; Biro, Carvalho et al. 2010; Perry 2011) and other animals (Terkel 1996; Sargeant and Mann 2009).

Studying traditions

Establishing the role of social learning in the transmission of these behaviors is not easy. Different studies apply different approaches to the problem. In the ethnographic method, researchers compare the pattern of variation in the behavioral repertoire of two or more group, and can infer social transmission to be the cause of those variations, if genetic and ecological influences can be excluded (Laland and Hoppitt 2013). This method was used intensively in non-human primates' studies, including tool-use and other foraging traditions in chimpanzees (Whiten, Goodall et al. 1999) and orangutans (Van Schaik and Knott 2001). Other studies looked at the correlation between behavioral variations used by mothers and those used by their offspring (Perry 2009; Sargeant and Mann 2009; Holzhaider, Hunt et al. 2010). Both methods attempt to answer the question of the presence or absence of social influence on learning, but do not touch on the question of *how* this influence is exerted. Most studies that examined the processes of social learning are done on captive subjects (e.g., (Dindo, Thierry et al. 2008; Tennie, Call et al. 2010)), where all interactions with specific tasks, locations of all group members, observations of any activity etc. can be recorded. Those studies are invaluable for understanding the learning processes that different species are capable of, and which ones they are likely to use under different conditions. From those studies we know that although non-human primates can imitate under specific conditions, they do not do it readily, and rely more on emulation (copying the end-state of an action, as opposed to copying the form of the action) and on processes such as local enhancement and social facilitation (Visalberghi and Fragaszy 1990; Tomasello 1996). A model based on captive studies shows that social facilitation alone can, in fact, support the creation and maintenance of traditions in a population (Franz and Matthews 2010; Matthews, Paukner et al. 2010).

Those studies, however, can only tell us how animal **can** learn, not how they **do** learn species-typical behaviors, under natural conditions. To answer that question, we need to turn to observational, developmental studies on wild populations. Several such studies were published (for a review - (Meulman, Seed et al. 2013). Biro et al. followed the ontogeny of nut cracking and leaf folding in chimpanzees, and detailed the possible social influences on the development of those behaviors (Biro, Inoue-Nakamura et al. 2003; Biro, Sousa et al. 2006). Lonsdorf studied termite-fishing in chimpanzees, and how the time a mother dedicates to fishing correlates with skill development of her offspring (Lonsdorf 2005). Coelho et al. studied nut-cracking capuchin monkeys, and showed that the juveniles preferentially observe nut-cracking sessions performed by dominant adults and proficient nut-crackers (Coelho, Falótico et al. 2015).

Those and other studies, including previous publications of the study we present here (Eshchar, Fragaszy et al. In process; Eshchar, Fragaszy et al. In process), point towards individual learning and practice over a long period – often years – facilitated and motivated by social input.

Modeling social learning

Recent years have seen a rapid increase in studies using mathematical formulations to model various aspects of social learning. Most models deal with social learning at the population level. Those include models of the evolution of social learning (Boyd and Richerson 1985; Kendal, Giraldeau et al. 2009), social learning as part of a general social foraging theory (Giraldeau, Caraco et al. 1994) and more. Here we will focus on agent-based models, which rely on individual-level rules.

Those models can be purely mathematical, like the model of Van der Post and Hogeweg, that modeled individuals in a diverse, patchy environment that have to learn what to eat. This model showed that simple grouping behavior (following others while foraging) exerts sufficient social influence on learners for supporting the inheritance of diet traditions (van der Post and Hogeweg 2008). Others build on previous experiments in order to test hypotheses, like the model of Franz and Matthews, which used an experiment with capuchin monkeys to show that a combination of reinforcement learning and local enhancement can create and maintain stable traditions (Franz and Matthews 2010). Other studies use mathematical formulations to identify the specific processes used in a social learning experiment, as did Hoppitt et al, who identified nine different processes – both social and asocial – used by wild meerkats in learning a novel foraging task (Hoppitt, Samson et al. 2012). The approach of Hoppitt et al. can enable researchers to study social learning under more natural conditions, while still being able to quantify specific processes, and describe their dynamics.

Dynamic of social facilitation

Social facilitation is the process by which seeing a demonstrator performing an action, or a set of actions, increases the probability of the observer to engage in the same activity (Heyes 1994). Its importance in learning was demonstrated in various species, from primates (Nagell, Olguin et al. 1993; Dindo, Whiten et al. 2009) to birds (Fritz, Bisenberger et al. 2000) and many in between (Clayton 1978). The effect is usually measured as the activity before observation compared to during or immediately after this observation. Most studies do not address the question of timing – how long after the observation the effect lasts. When this question is addressed, studies usually only check if the effect persists after some fixed interval (e.g., (McQuoid and Galef 1992)). As far as we know, the only paper that attempted to estimate the decay of this effect is Hoppitt et al (2012). In this study, wild meerkats were presented with baited boxes, and the all interactions with the box, as well as the observations of conspecifics interacting with – and solving – the task, were recorded. The researchers found that individuals were more likely to interact with the box immediately after observing a conspecific interacting with it, and they also estimated the duration of this effect. When fitting an exponential model, the half-life of the effect – the time it takes it to halve in magnitude – was 20 seconds.

Since the literature on decay of social influence is, as mentioned, extremely scarce, we can turn to the literature on learning by reinforcement. When an animal receives an incentive – such as a food reward - its arousal state increases. This increase has the effect of increasing the activity of the animal. If the incentive was coupled previously with a specific response, the animal will be more likely to perform this behavior following the incentive. This arousal decays exponentially, so that at time t after delivery of the incentive,

$$A_t = A_0 * e^{-\beta t}$$

Where A_0 is the level of arousal at the time of delivery, and β is the rate by which the level declines with time (Killeen 1979; Killeen 1998).

This is the same equation Hoppitt et al. used to model the transient effect of observing a conspecific interacting with the box. In their model, A_0 denotes the strength of social facilitation effect, and β denotes the rate by which the effect dies away. Therefore, the incentive in this case is not a reward, but an observation of others engaging in a specific behavior – which was shown time and again to indeed be a strong motivator. We use the same equation in this study.

Tool use in capuchins

Wild bearded capuchin monkeys, *Sapajus libidinosus,* of both sexes, use stone tools to crack palm nuts to obtain the kernel, and they do so on specific anvils composed of stone or wood (Fragaszy, Izar et al. 2004). In the last decade, this behavior was intensively studied, in several locations, with wild and semi-free populations. Studies that examined the ontogeny of this behavior describe a long period of interacting with nuts and stones, starting at age six months or earlier. Cracking started around a year after that at the earliest, but juveniles do not crack successfully and habitually until years later (Resende, Ottoni et al. 2008; Resende, Nagy-Reis et al. 2014; Eshchar, Fragaszy et al. In process).

We have shown previously that when group members are cracking and eating nuts, infants and juveniles spend more time next to the anvils, interact more with nuts, and also engage more in percussion of nuts and in striking a nut with a stone, compared to times when no one in the group was cracking nuts. Interactions with objects that are not nuts showed the opposite pattern (Eshchar, Fragaszy et al. In process). We suggest that observing conspecifics cracking nuts motivates the young capuchins to engage in the same activity themselves. Part of this influence is exerted through drawing the juveniles towards the anvils, where nut-cracking is taking place. The juveniles are probably drawn by the prospective of scrounging some nuts from the adults. This type of scrounging is common and almost always tolerated by the adults (Coelho, Falótico et al. 2015; Eshchar, Fragaszy et al. In process). When near the anvils, the juveniles have ample opportunities to interact with nut and nut shells, which were left behind from previous cracking sessions. And they use those opportunities – the rate of manipulation of nuts is much higher near those anvils. Thus, the nut-cracking behavior of adults in the group affects the nut-related behavior of the juveniles in several ways: creating artifacts that the juveniles can interact with and learn from, drawing them to the place where a lot of those artifacts are, and, by being the target of observation while their cracking and eating nuts, motivate the juveniles to practice this behavior themselves.

Tolerance in capuchin monkeys

Capuchin monkeys are a gregarious species, and are known to tolerate others nearby while eating, and even to share food with each other (de Waal, Luttrell et al. 1993). Special tolerance is extended towards infants and juveniles. Around age four the adults' attitude start to change, and they are less willing to let older juveniles observe them closely while eating or take food from them (Coussi-Korbel and Fragaszy 1995; Fragaszy, Feuerstein et al. 1997; Eshchar, Fragaszy et al. In process). We previously showed that in our field site, the social facilitation exerted by observing others cracking or eating nuts, which resulted in increased rates of nut-related activity in infants and juveniles as a whole, has no effect on subadults age five to six years. This group did not show a significant difference in rates of nut manipulation when others cracked nuts around them compared to other times (Eshchar, Fragaszy et al. In process).

Current study

In this study we examine the temporal aspect of social facilitation. The data are taken from 16 infant and juvenile monkeys in a wild, habituated group of bearded capuchins. We have followed our subjects in five collection periods over 26 months, and recorded concurrently their behavior and the presence and behavior of others in the group. As mentioned above, we have suggested that social facilitation plays an important role in the ontogeny of nut-cracking. The rate of manipulation of nuts – and specific actions with nuts – by infants and juveniles is significantly higher when others crack and eat nuts around them (Eshchar, Fragaszy et al. In process).

Here we set out to describe the dynamics of this effect, and specifically of its extinction. It is hard to believe that the motivation to interact with nuts completely disappears when the adults stop cracking nuts. Following Hoppitt et al. (2012) and the reinforcement literature described above, we predict that the effect will decay exponentially, following the equation:

$$A_t = A_0 * e^{-\beta t}$$

Where t is the time since nut-cracking activity in the group stopped. A_0 is the strength of the effect on the rate of nut manipulation, or a specific action with a nut. We look at this rate in the 7 minutes after the nut-cracking activity stopped, in order to build this model.

It is hard to predict the half-life of this effect. In the Hoppitt et al study, the half-life was very short – about 20 seconds. We predicted that in our study the half-life would be longer. In many cases – and in contrast to the Hoppitt study – our subjects were already interacting with nuts when the nut-cracking activity stopped. And since we know that young capuchins often interact with the same objects for several minutes, we predicted that they will continue this interaction for, on average, 2-3 minutes.

As mentioned above, we have also seen that during nut-cracking activity in the group, infant and juveniles spend more time near the anvils (Eshchar, Fragaszy et al. In process). We would predict that when the nut-cracking stops, they will gradually leave those anvils, and we will see a similar exponential decline in the time spent in vicinity of anvils.

In our previous paper we showed that not all age groups responded to nut-cracking around them in the same way. The younger age group – 0-1 year old infants - and the oldest age group – 5-6 years old subadults – did not show a difference in nut manipulation when others cracked and ate nuts around them, unlike all other age groups (Eshchar, Fragaszy et al. In process). In the case of the infants, this was attributed to the fact that their overall rate of nut manipulation was quite low, and their activity was mainly driven by opportunity – they interacted with nuts when and where those happened to come their way.

The case of the subadults is more interesting. At age five most subjects can crack at least some of the nuts, but to do that, they need a hammer stone and an anvil. Therefore, they are already in a state of competition with the adults for those resources. The nut-cracking activity of the adults around them might motivate them to engage with nuts like it does for other age groups, but unlike the younger juvenile, they are not restricted simply to manipulate nut shells, but want to try to crack nuts themselves. Often they have to wait until the adults leave the anvil in order to do that. Therefore, we predict that striking a nut with a stone – the efficient action of cracking – will not show the same exponential decay as other actions with nuts after nut-cracking activity in the group stopped. At least in the older juveniles group, we might even see a small rise in the rate of striking, when the juveniles can take over the anvils and hammer stones left by the adults when they stopped cracking.

For the same reason, we will also predict different dynamics in the subadult group for decline in time spent near the anvils after the nut-cracking activity in the group stops. The subadults will take advantage of the recently-evacuated anvils to crack nuts themselves, and therefore will stay there longer than other age groups will.

In sum, our predictions are:

1. When nut-cracking activity in the group stops, the effect of the rate of nut manipulation of infants and juveniles will decline exponentially. The half-life of this social effect will be 2-3 minutes.

2. The social effect on time spent near an anvil will decline in a similar way, with a similar half-life.

3. The subadult group, age four to six, will show a distinct pattern: in this group, the rate of nut manipulation, and especially of striking a nut with a stone, will not decline and might even rise slightly after the nut-cracking activity stops.

4. In the subadult group, the dynamics of the social effect on time spent near the anvils will be different compared to the other age groups. They will spend more time near the anvil after nut-cracking in the group stops, so that the half-life of this effect will be larger than in the other age groups.

Methods

Study site

Our site is located 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 masl) punctuated by sandstone ridges, pinnacles, and mesas rising steeply to 20–100 m above it. The climate in the region is seasonally dry. At our site, annual rainfall in 2006 – 2008 averaged 1290 mm per year. From May to September rainfall averaged 25 mm and from October to April 1266 mm.

Anvils

An anvil is defined as a flat, or nearly flat, horizontal 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 (hard stone weighing 150 g or more) 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.

Study duration

Data were collected in 5 discrete collection periods; each consisted of 6-9 weeks of observations. Three of those collection periods took place during the dry season, and two during the rainy season. The time points were: May-July 2011 (Dry season), Jan-Feb 2012 (Rainy season), May-July 2012 (Dry season), Jan-Mar 2013 (Rainy season) and June-July 2013 (Dry season).

Subjects

At the beginning of the study, there were 11 juveniles and babies in the group, aged from 3 months to 4.5 years. Five more infants were born during the study (see table 4.1). Data on the oldest juvenile (Tomate) were collected only in the first two collection periods. At the beginning of the study, none of the subjects could crack open a whole nut of the more resistant species (*Orbygnia* and *Attalea*). The two oldest juveniles, and to some extent two others, mastered this skill through the duration of the study. Apart from our subjects, the group included 3 adult males and 5 adult females. All but one female habitually crack nuts.

Data collection

All observers used hand-held devices with Pocket Observer© software by Noldus Information Technology. All observations lasted 20min, or until the focal subject went out of view and could not be followed; but not less than 5min.

Observations were collected using two-people teams. One observer followed one of the subjects to obtain a continuous record of the focal subject’s location and activities.

This ethogram included two categories:

1. Location – on a tree, on the ground, or within arm's reach of an identified anvil
2. Specific actions – including eating (nuts or other objects), direct percussion of an object on a surface (nuts or other objects, on tree, ground or anvil), manipulating nuts or other objects in a non-percussive way, combinatorial percussion (striking a nut with a stone and striking a nut with another nut), and more (see Table 4.2).

Concurrently, the other member of the team recorded, as an instantaneous observation every minute, the identity, location and activity of other monkeys in the vicinity of the focal monkey.

At each collection perdiod, a quarter to half of the observations were collected in our field laboratory - an open area, about 12m in diameter, that the monkeys visit 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, Pickering et al. 2010; Fragaszy, Greenberg et al. 2010; Massaro, Liu et al. 2012; Fragaszy, Liu et al. 2013). Many nut shells and debris from years of nut-cracking can be found on and around the anvils, and all around the lab area.

Reliability

Observers first learned to identify all members of the group with the help of long-term field assistants. Subsequently, observers were trained on the ethogram. Reliability for focal observations was calculated using GSEQ: Generalized Sequential Querier ©, URL: http://www2.gsu.edu/~psyrab/gseq/index.html. Time unit kappa, which provides a measure of alignment of tow observations, was at or above 0.7, which is considered highly reliable

(Bakeman, Deckner 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, 10 individuals at the most could be coded. In some cases, the observers did not have the time to code all monkeys within 10m for every minute. 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 looked whether or not at least one of them was cracking or eating nuts. Because of this pooling, the limitation of this method – the inability in some cases to code any monkey in the area – does not affect the results here.

Data analysis

For each subject in each collection period, we collected between 19 and 53 observations, which lasted, together, between 5.3 hours to 27.1 hours (table 4.3). 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. We obtained rate per 10 min for various activities, under different conditions (near or away from an anvil, with or without group activity). In some cases, we combined several codes to create new variables:

- All actions with nuts were combined and termed “nut manipulation”

- "Nut-cracking activity nearby" is defined as time when one or more individual is cracking or eating nuts within 10 meters of the focal subject, or nut-cracking can be heard.

SAS© software was used to test general mixed linear models (GLM), to evaluate the differences in activity under different conditions, and exponential models to evaluate the decline of the effects. Our independent variable is the presence of nut-cracking activity in the group (yes/no).

Our dependent variables are counts – frequency of different activity and no. of seconds spent in different locations. Working with counts rather than rates enables us to take into account the fact that the durations of the different conditions were not the same. We used total time of observation as an offset to test rate

The count variables did not distribute normally (per Shapiro-Wilk test); therefore for the GLM models, the Poisson distribution was used. The statistics are taken 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 two categories of the independent variable.

Results

We looked at the rate of manipulation of nuts and of other objects, during nut-cracking activity in the group, in seven minutes after the nut-cracking activity stopped, and in other times (more than seven minutes after nut-cracking activity, or in observations in which there was not such activity).

Nut manipulation

The rate of nut manipulation is highest during nut-cracking activity (median=8.29 acts per 10min), and lowest at times more than seven minutes after activity stopped (median=0.94 per 10min). The difference between them is highly significant (estimate = 1.98, p<0.0001, fig 4.1). From the time during nut-cracking activity in the group to seven minutes after this activity stops, the rate of manipulation of nuts declines exponentially (in $A_t = A_0 * e^{-\beta t}$, estimates: A=9.96, p<0.0001, β=0.325, p=0.0013). The half-life of the effect is 2.1 minutes. The rate of manipulation during nut-cracking activity is significantly higher than in the first minute after the activity stopped (p<0.0001), and all subsequent minutes. The rate of nut manipulation at the first to fifth minutes after the activity stopped is significantly higher than the rate at times more than seven minutes after activity stopped (p<0.0001 for 1-4 minutes after activity stopped, p=0.0146 for the fifth minute). There was no significant difference between the rate of nut manipulation at the sixth and seventh minutes after nut-cracking activity stopped and at times more than seven minutes after. Therefore, by minute sixth after activity stopped the rate of nut manipulation is back to baseline.

--------Insert fig. 4.1 here--------

Other manipulation

The rate of manipulation of other objects follows a different trajectory. The rate is lowest during nut-cracking activity in the group (median=12.8 per 10min), and highest at times more than seven minutes after activity stopped (median=16.7 per 10min). The difference between them is highly significant (estimate = 1.29, p<0.0001, fig 4.2). From the time during nut-cracking activity in the group to seven minutes after this activity stops, the rate of manipulation of other objects *increases* exponentially (in $A_t = A_{0*}e^{-\beta t}$, estimates: A=14.2, $p<0.0001$, $\beta=-0.03$, p=0.015).

There is no significant difference between the rate of manipulation in the first minute after nut-cracking activity stopped – and in the subsequent six minutes – and between the rate at times more than seven minutes after activity stopped. Therefore, the rate of manipulation of objects other than nuts goes back to baseline within one minute after nut-cracking in the group stops.

-------Insert fig. 4.2 here------

Specific actions with nuts

We looked at the rates of two specific actions with nuts, which are related to nut-cracking. One is direct percussion of nuts, and the other is striking a nut with a stone.

Direct percussion of nuts appears very early in life (within the first six months), and peaks at around age four. Nut percussion is often performed by all monkeys – juveniles and adults – as part of the nut-cracking sequence, and as a way to pry the kernels from the shells after cracking. However, it is also performed by infants and juveniles that are not yet able to crack.

The rate of nut percussion is highest during nut-cracking activity (median=1.32 per 10min), and lowest at times more than seven minutes after activity stopped (median=0.23 per 10min). The difference between them is highly significant (estimate = 6.33, $p<0.0001$, fig 4.3).

From the time during nut-cracking activity to seven minutes after it stops, the rate of direct percussion of nuts declines exponentially (in $A_t = A_{0*}e^{-\beta t}$, estimates: A=8.16, p=0.026, $\beta=1.12$, p=0.014). The half-life of the effect is 0.62 minutes.

------Insert fig. 4.3 here---------

Striking a nut with a stone was seen in some subjects as early as 15 months of life, but most subjects only showed this behavior when they were three years or older.

The rate of strikes is again highest during nut-cracking activity (mean=2.01 per 10min. We are using mean in this case because many subjects did not strike at all or did only rarely, and therefore there are many zeros in the dataset). The rate was lowest at times more than seven minutes after activity stopped (mean=0.3 per 10min). The difference between them is highly significant (estimate = 7.18, $p<0.0001$, fig 4.4).

From the time during nut-cracking activity to seven minutes after it stops, the rate of striking declines exponentially (in $A_t = A_0 * e^{-\beta t}$, estimates: A=8.16, p=0.0221, β=1.16, p=0.03). The half-life of the effect is 0.62 minutes.

-------Insert fig. 4.4 here--------

Time spent near an anvil

We could not say exactly when the juveniles that were near the anvil during nut-cracking activity in the group left this location. However, we can look at the percentage of time – out of all observations – in which infants and juveniles spent near an anvil. If this percentage decreases this time, it would mean that our subjects are gradually leaving the anvil.

The percentage of time spent near an anvil is highest during nut-cracking activity (median=13.3%), and lowest at times more than seven minutes after activity stopped (median=2.6%). The difference between them is highly significant (estimate = 6.06, $p<0.0001$, fig 4.5).

From the time during nut-cracking activity to seven minutes after it stops, the percentage of time declines exponentially (in $A_t = A_0 * e^{-\beta t}$, estimates: A=11.94 $p<0.0001$, $\beta=0.25$, $p<0.0001$). The half-life of the effect is 2.8 minutes.

------Insert fig. 4.5 here-------

Social influence in different age groups

We divided our subjects in three groups: pre-weaning infants, age 0 to 1.5 years. Juveniles, age 1.5-4 years, and subadults, age over 4 years.

Manipulation of nuts

In the infant group, the rate of manipulation of nuts did not show an exponential decline after nut-cracking activity in the group stops. The difference between the rate during nut activity was significantly higher than the rate at times more than 7 minutes after this activity stopped (medians: 1.04 vs. 0.16 per 10 minutes, estimate: 9.27, $p<0.0001$). However, the rate during activity was not significantly higher during times of activity than it was in the first minute after activity stopped, nor in any of the subsequent minutes until 7 minutes after activity stopped (fig 4.6, panel A).

In the juveniles group, the rate did decline exponentially (in $A_t = A_0 * e^{-\beta t}$, estimates: A=12.35 $p=0.006$, $\beta=0.281$, $p=0.0036$). The half-life of the effect is 2.5 minutes. The difference between the rate during nut activity was significantly higher than the rate at times more than 7 minutes after this activity stopped (medians: 10.45 vs. 1.78 per 10 minutes, estimate: 9.2 , $p<0.0001$). The rate was also significantly higher during times of activity than it was in the first minute after activity stopped, and in any of the subsequent minutes (fig 4.6, panel B).

In the subadults group, the rate again declined exponentially (in $A_t = A_0 * e^{-\beta t}$, estimates: A=11.4, $p=0.0004$, $\beta=0.19$, $p=0.0172$). The half-life of the effect is 3.7 minutes. The difference between the rate during nut activity was significantly higher than the rate at times more than 7 minutes after this activity stopped (medians: 11.7 vs. 2.95 per 10 minutes, estimate: 5.5 , $p<0.0001$). However, the rate during activity was not significantly higher during times of activity than it was in the first minute after activity stopped, nor in any of the subsequent minutes until 7 minutes after activity stopped (fig 4.6, panel C).

------Insert fig. 4.6 here-------

Striking a nut with a stone

In the infants groups, there are almost no strikes at all (fig 4.7, panel A).

In the juveniles group, in the exponential decline model, the strength of the effect was not significant (estimate of A: 7.8, $p=0.1315$), but the rate of decline was (estimate of β: 1.6, $p=0.0055$). Therefore, the rate did decline after nut-cracking activity in the group stopped, but the overall effect – the difference between the rates at different times – was not significant (fig 4.7, panel B).

In the subadults group we see the opposite picture. The strength of the effect was significant (estimate of A: 4.95, $p=0.027$), but the rate of decline was not (estimate of β: 0.19, $p=0.1078$).

Therefore, the rate *was* different in different times, but it did not decline exponentially. We can see that the rate in the first four minutes after the nut-cracking activity stopped did not show a decline at all (fig 4.7, panel C).

------Insert fig. 4.7 here-------------

Time spent near an anvil

In all age groups, the percentage of time spent near an anvil was highest during nut-cracking activity in the group, and declined exponentially in the seven minutes after this activity sopped (fig 4.8).

In the model $A_t = A_0 * e^{-\beta t}$,

In the infant group - estimates: A=6.6, p=0.0044, β=0.19, p=0.041). The half-life of the effect is 3.7 minutes.

In the juveniles group - estimates: A=16.5, p=0.006, β=0.26, p=0.023). The half-life of the effect is 2.7 minutes.

In the subadults group - estimates: A=12, p=0.0022, β=0.09, p=0.028). The half-life of the effect is 7.5 minutes.

---------Insert fig 4.8 here-----------

Discussion

Though social facilitation is well established in many species, the temporal aspects of this facilitation are largely unexplored. When the question of time is addressed, it is almost always in the form of presence or absence of an effect after a predetermined interval. Looking at *how* the effect declines can give us more information about this important process, (Hoppitt, Samson et al. 2012).

There is, however, an analog process in the learning literature that was studied in such a way. In reinforcement studies, when an animal receives an incentive, the rate by which it performs a specific activity increases – for a while. The effect declines exponentially (Killeen 1979), in the same way that social facilitation does in Hoppitt et al.'s study.

Here we show, for the first time for a natural behavior of a wild population, the dynamics of social facilitation, in this case on nut-related behavior in capuchin monkeys. We found that the rate of manipulation of nuts, and specific actions with nuts, decline exponentially when nut-cracking activity in the group stops. We also found that the older juveniles, or subadults, react differently than other age groups, probably because of the interplay between social facilitation and competition.

First prediction: When nut-cracking activity in the group stops, the rate of nut manipulation by infants and juveniles will decline exponentially. The half-life of this decline will be 2-3 minutes.

This prediction is based on the dynamics of extinction seen in reinforcement learning. When an animal receives an incentive, the rate of specific actions goes up – and this rate then declines exponentially. In Hoppitt et al (2012), the incentive was replaced by an observation of a conspecific solving a task. In that study, meerkats interacted with a baited box and the rate of interaction was highest immediately after observing a conspecific interacting with it, and declined exponentially afterwards. The half-life for facilitation of activity in the meerkats was 20 seconds.

We predicted a similar trajectory but longer half-life in our study. Informally, we have seen quite often young capuchins interacting with the same object for several minutes. Moreover, our subjects were often already engaged in nut-related activity at the time that the nut-cracking activity stopped, and we assumed it would take a few minutes for them to abandon it. The meerkats, on the other hand, initiated activity with the apparatus after the other meerkat had finished and left the box.

Those predictions were mostly supported by the data. When looking at all manipulation of nuts, the results fit the prediction perfectly: the rate of manipulation decreased from a median of 8.29 per 10 min during nut-cracking activity in the group to 0.94 per 10 min in times more than 7 min after this activity stopped, and the decrease in those minutes was exponential, with half-life of the effect of 2.1 minutes. However, while the rate of decline of all manipulations of nuts fit our prediction, the rate of decline of specific nut-cracking actions – direct percussion of nuts and striking a nut with a stone – also declined exponentially, but the decline was much faster – with half-lives of 36-37 seconds. This was surprising to us, since we observed young capuchin engage in those actions for several minutes at a time (sometimes up to 30 minutes).

One interpretation is that a specific social influence affects percussive actions. Those actions are performed regularly by adults while cracking nuts. When the adults stop cracking nuts, the infants and juveniles show a sharp decline in the rate of those actions as well. Thus direct percussion and striking a nut with a stone appear to be more affected by social facilitation than by local enhancement. It is interesting that these two actions are both the most vigorous, involving movements of the greatest speed and amplitude, and produce loud sound. They also directly precede feeding on nuts. Perhaps these components make the actions particularly susceptible to social facilitation. Other actions – picking up, sniffing, biting – are apparently less influenced by direct observation, and more by the opportunity provided by the nut-cracking artifacts.

Previous studies have shown social facilitation for a specific aspect of a task. In Hoppitt et al’s study, the meerkats were presented with two boxes, with two options to get inside. The facilitation was larger for the specific box and option that was observed than for the other box and other option. This was attributed to local enhancement – observing a conspecific interacting with a specific object increases the probability of the observer to interact with the same object. Local enhancement seems to play a role in our study, by increasing the rate of overall interaction with nuts. But the increase in specific actions suggests a different process, of response facilitation – an increase in the rate of the exact *action* performed by the demonstrator. Response facilitation was seen in birds, where seeing a conspecific pecking (a feeding action) increased the rate of pecking by the observer (Tolman 1967) and the rate of preening was increased by the preening behavior of others (Hoppitt, Blackburn et al. 2007). European starlings observing conspecifics perform a foraging task preferred to engage with the same objects the demonstrators used (stimulus enhancement) and also used the same actions (social facilitation) (Campbell, Heyes et al. 1999). Capuchin monkeys were more likely to eat when they saw their groupmates eat (Visalberghi and Addessi 2000), and gorillas were more likely to execute a specific hand gesture after seeing a demonstrator doing the same action (Byrne and Tanner 2006).

Therefore, we suggest that in our study, social facilitation specifically on percussive actions – both direct percussion of nuts and hitting a nut with a stone is strong but short- lived. The local enhancement, that motivated the observers to remain near and investigate places and objects where another was active, enabled subjects to continue to interact with nuts in non-specific ways as long as they were near an anvil.

Second prediction: The time spent near an anvil will decline in a similar way, with a similar half-life as all manipulation of nuts.

This prediction was fully supported by the data. During nut-cracking activity in the group, infants and juveniles spent on average 13.3% of their time near an anvil. This proportion decreased exponentially to 2.6% more than 7 min after this activity stopped. The half-time of the effect was 2.8 minutes. This suggests that juveniles stayed near the anvils a few minutes after the nut-cracking activity stopped, which matches the previous results regarding manipulation of nuts. We suggest that as long as the juveniles stay near the anvils, they take advantage of the many shells and debris on and around them, and continue to interact with them. This is one of the ways in which social influence persists after the activity itself stopped.

The importance of artifacts – objects created or modified by an animal's behavior – to the learning process is often neglected. However, studies that do examine them show that in various species, young animals spend time going through the products of adults' behavior, and presumably learning from them (Gunst, Boinski et al. 2008; Thornton and Hodge 2008;

Fragaszy, Biro et al. 2013). In the case of black rats learning to feed on pine cones, as discussed above, artifacts were shown to be necessary and sufficient for learning (Aisner and Terkel 1992).

Artifacts represent a type of social influence that is much less restricted by time compared to direct observation – individuals can interact with them hours and sometime days and weeks after their creation. In species that use extractive foraging, juveniles often need to develop their skill gradually through a long period (Eshchar, Fragaszy et al. In process). The artifacts created by the same behaviors juveniles have to learn might be very important for this process.

Here, we show how learning through artifacts is enhanced by observation – juveniles see their groupmates cracking nuts on the anvils, go and stay near those anvils, and thus have the opportunity to interact with nuts, nuts shells and hammer stones. And as we see here, they stay near the anvils after nut-cracking activity stops, and continue to interact with the nuts. This is probably the case for other sophisticated foraging skills that juveniles have to learn.

Third prediction: The subadult group, age four to six years, will show a distinct pattern: in this group, the rate of nut manipulation, and especially of striking a nut with a stone, will not decline as sharply after the nut-cracking activity stops.

As mentioned above, we predicted that the subadult group would have a more gradual decline in rate of manipulation, because in this age group social facilitation is not the only factor influencing their behavior - competition also enters the mix. At age four and older, subadults are starting to crack nuts for themselves, and to do so they need anvils and hammer stones. We have shown that subadults are drawn towards the anvils during nut-cracking activity in the group, much like the younger juveniles (Eshchar, Fragaszy et al. In process). However, we suggest that while they are there, they are not content to simply manipulate the nut shells around the anvils, but want to actually crack nuts. When other nut-cracking activity stops, they can get their chance – they can take the hammer stones left by the adults and use the anvils evacuated by those adults.

Therefore, we predicted that subadults will continue to interact with nuts longer than younger juveniles following the observation of other cracking nuts, due to the complex interaction between social facilitation and competition. This is especially true for subadults who are engaged in striking a nut with a stone, which can only be done efficiently with a hammer stone.

This prediction was mostly supported by the data. We divided the subjects into three groups: pre-weaning infants – age 0 to 1.5 years, which is the estimated age of weaning (Fragaszy, Izar et al. In process), juveniles age 1.5-4 years, which is the period in which juveniles interact with nuts and even strike nuts with a stone, but cannot yet crack efficiently, and subadults age four and up, when they start striking nuts with stones more habitually (Eshchar, Fragaszy et al. In process). When looking at all manipulation of nuts, the infant group had a low overall rate and we did not see any social influence on their behavior. The juveniles group did show the same pattern of social effect we saw in the overall population, with an exponential decline in rate after nut-cracking activity in the group stopped. The half-life was 2.5 minutes. The subadult group showed the same pattern, with a longer half-life, of 3.7 minutes. This difference between the groups was even bigger when looking at the rate of striking a nut with a stone, the efficient way to crack nuts. For this variable, the subadult group did not show any significant decline with time after nut-cracking in the group stopped whereas the 1.5- 4 year olds did show an exponential decline.

As discussed above, at age four capuchin monkeys are no longer as tolerated as younger juveniles (Janson 1990). The change in behavior of adults towards juveniles might start even earlier. When juvenile capuchins had the choice of interacting with a foraging task in a place only juveniles could enter or the same task in a place open for all ages, juveniles younger than 20 months preferred the group site, while older juveniles chose the "juvenile only" location (Fragaszy, Vitale et al. 1994).

This lesser tolerance can be associated with less opportunity to learn from others. Several studies have shown that juveniles are more likely to learn new behaviors from others than are adults. In the famous case of potato-washing Japanese macaques, the first to learn this behavior from the inventor were juveniles (Kawai 1965). A similar pattern was seen after introduction of a new type of nut to a nut-cracking population of chimpanzees (Matsuzawa, Biro et al. 2001). We suggest that the pattern of behavior seen here represents the transition from a young juvenile, highly tolerated by the adults and still in the process of learning (thus not presenting a competition to efficient nut-crackers); to an older individual that is less tolerated, competing with the adults on resources, and with less opportunities - but also less need - for learning.

Fourth prediction: The dynamics of the social effect on time spent near the anvils will differ across age groups in a similar way as activity with nuts and stones: Subadults will spend more time near the anvil after nut-cracking in the group stops, so that the half-life of this effect will be longer than in other age groups.

This prediction was fully supported by the data. In all age groups, the percentage of time spent near an anvil declined exponentially with time after the nut-cracking activity in the group stopped, but the dynamics of this decline differed across age groups. In the infants and juveniles groups the half-lives of the effect are 3.7 minutes and 2.7 minutes respectively, and the half-life of the subadult group is 7.5 minutes.

This fits with the previous results, and strengthens the hypothesis that subadults are influenced both by social facilitation and by competition. Observing nut cracking around them motivates them to engage with nuts as well, but they compete with the adults for hammer stones and anvils. After the adults stop cracking, they are more likely than their younger counterparts to stay near the anvils, claim the hammer stones and crack nuts themselves. This leads them to stay near the anvils for a longer time.

Interestingly, the half-time for staying near an anvil is twice as long as the half-time for manipulating nuts in the subadult group (3.7min vs. 7.5min). This might be another example of local enhancement – drawing the subadults towards the anvil – lasting longer than the influence on specific actions.

Conclusion

Even though more and more studies expose the important roles that social facilitation and local enhancement play in social learning and maintenance of tradition in non-human animals, very little attention has been given to their dynamics - how their effect changes through time. Here we present one way by which those questions can be addressed. We show that infant and juvenile capuchins manipulate nuts at a higher rate while seeing others cracking and eating nuts, and this rate declines exponentially when the nut-cracking activity stops. The dynamics are different for different actions, and different age groups. We hope this study will be a stepping stone in the path to a broader understanding of those important processes.

Figures

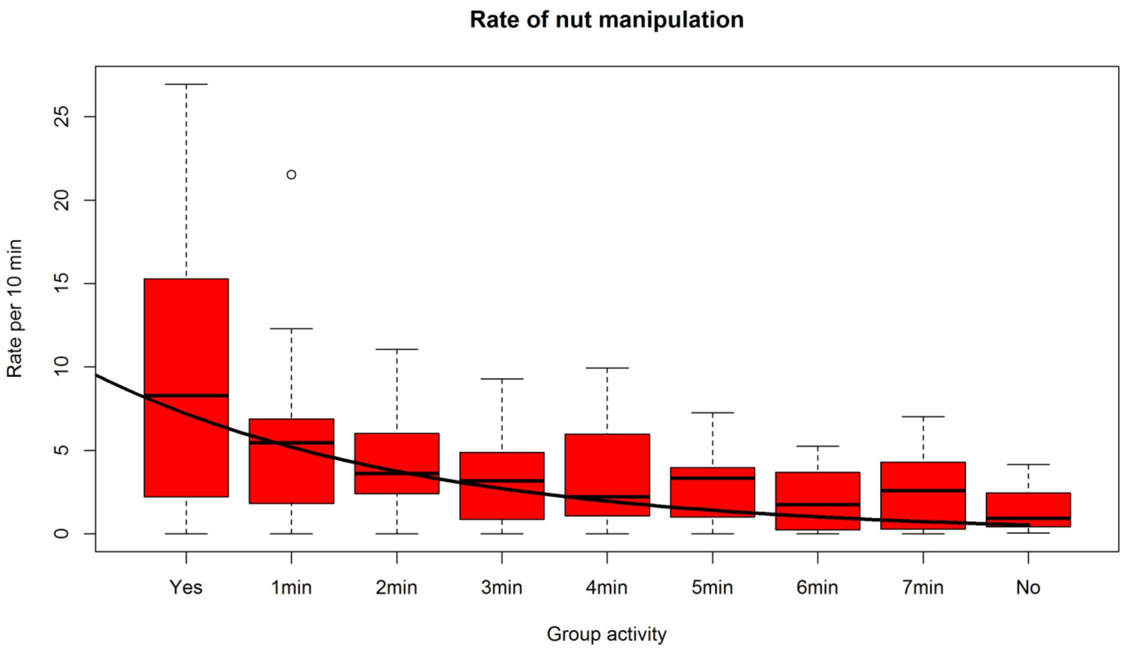

Fig 4.1: Rate of manipulation of nuts during nut-cracking activity in the group (Yes), during the seven minutes after this activity stopped, and in other times (no).

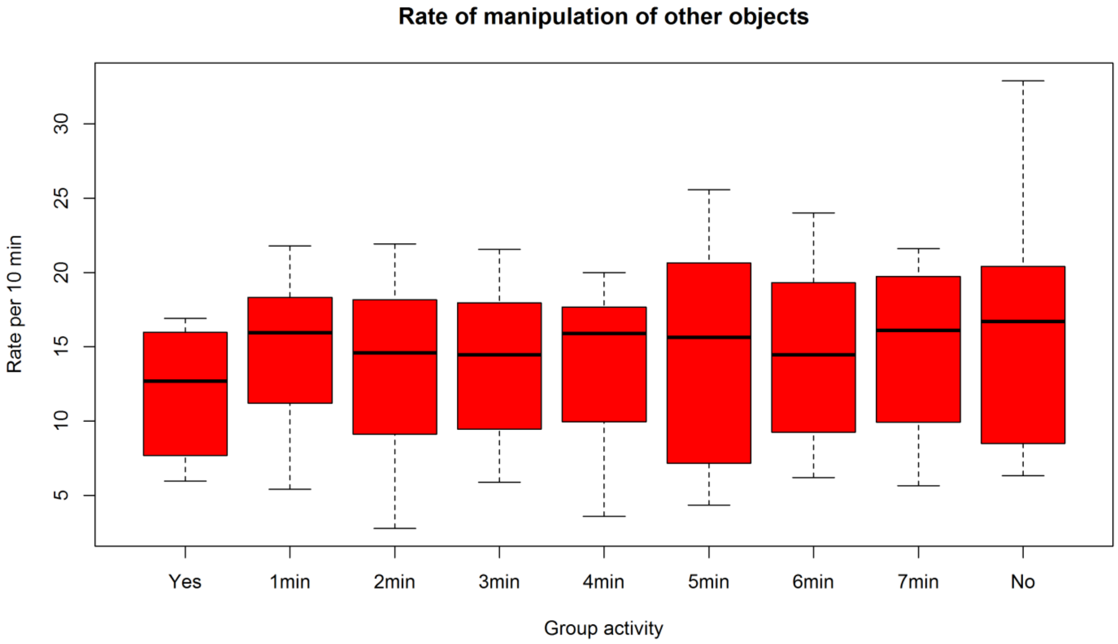

Fig. 4.2: Rate of manipulation of objects other than nuts during nut-cracking activity in the group (Yes), during the seven minutes after this activity stopped, and in other times (no).

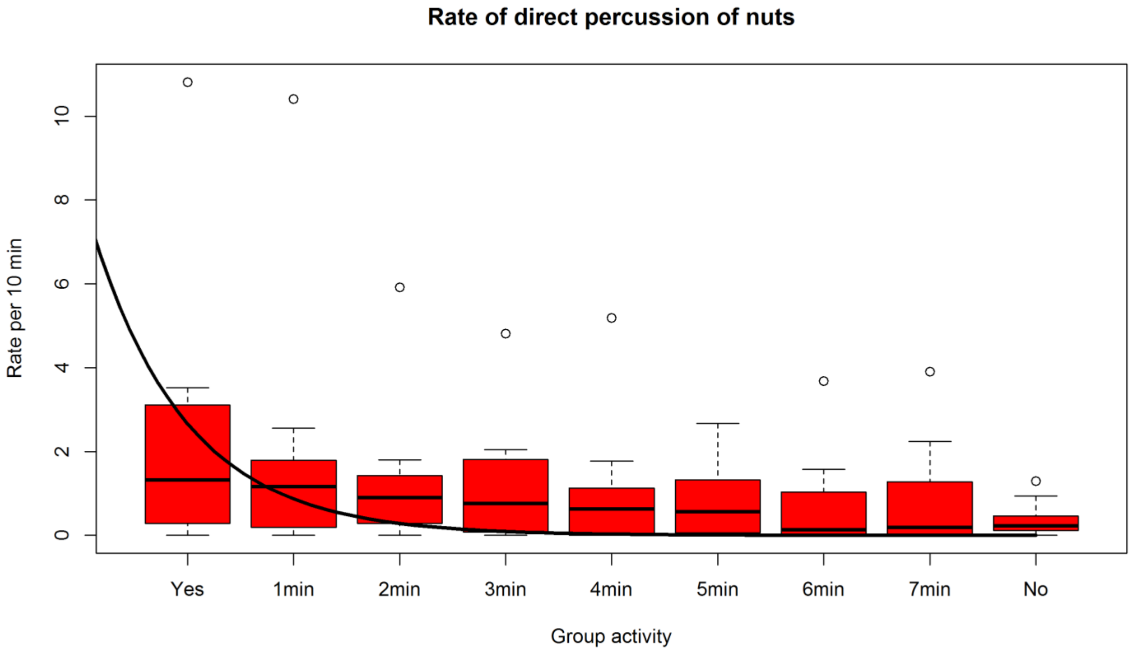

Fig. 4.3: Rate of direct percussion of nuts during nut-cracking activity in the group (Yes), during the seven minutes after this activity stopped, and in other times (no).

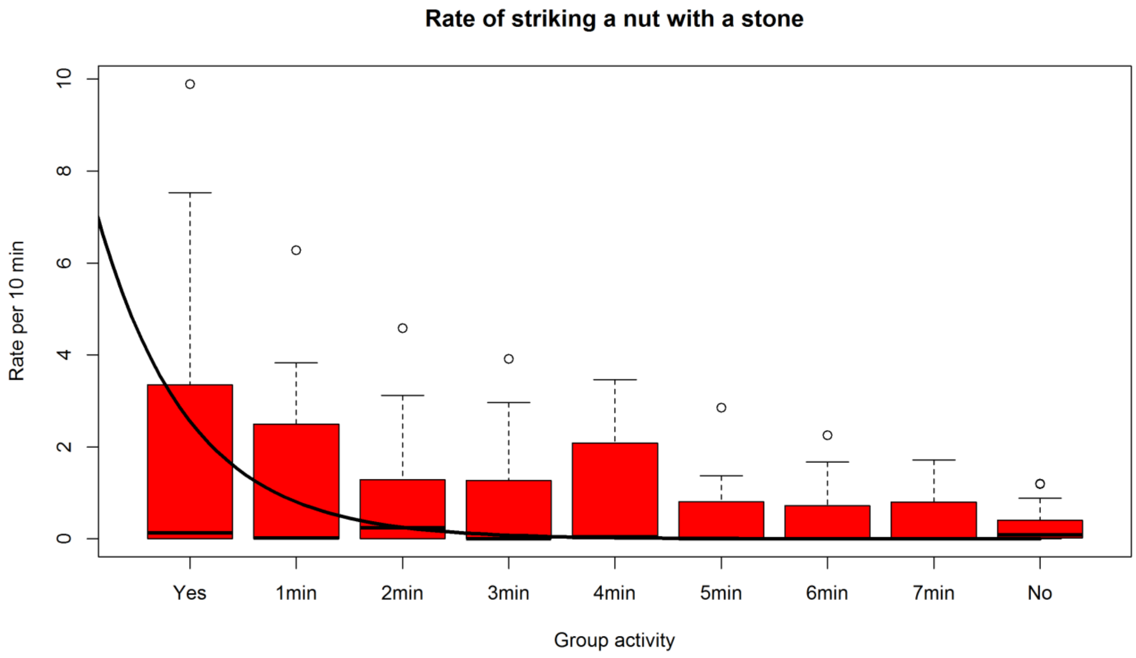

Fig. 4.4: Rate of striking a nut with a stone during nut-cracking activity in the group (Yes), during the seven minutes after this activity stopped, and in other times (no).

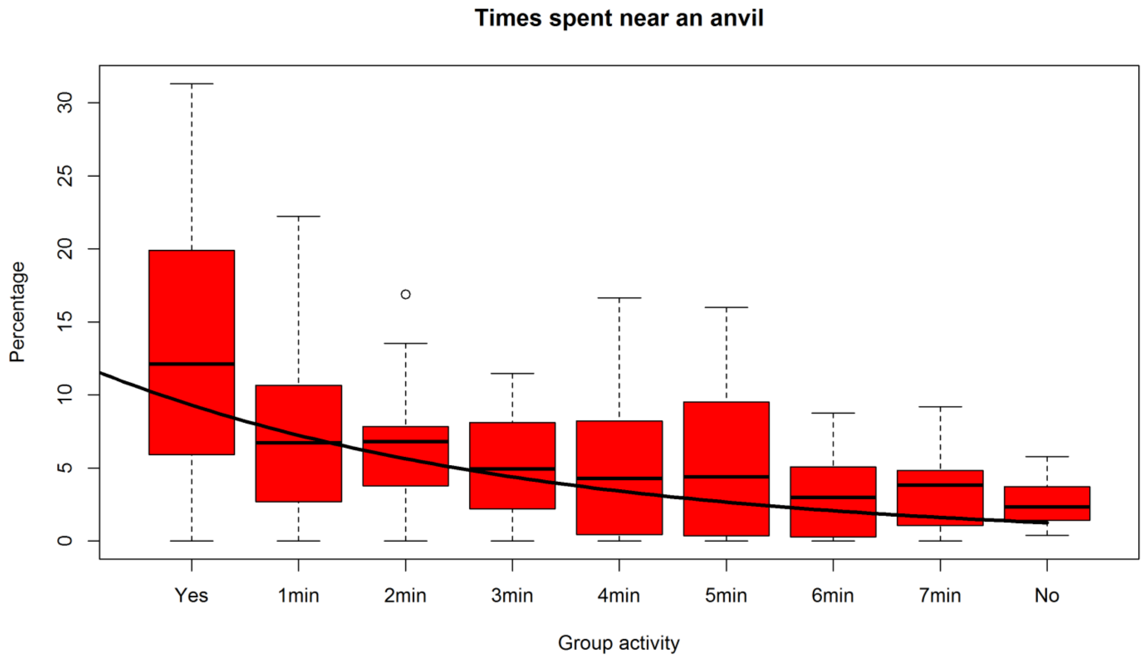

Fig. 4.5: Percentage of time spent within an arm's length of an anvil during nut-cracking activity in the group (Yes), during the seven minutes after this activity stopped, and in other times (no).

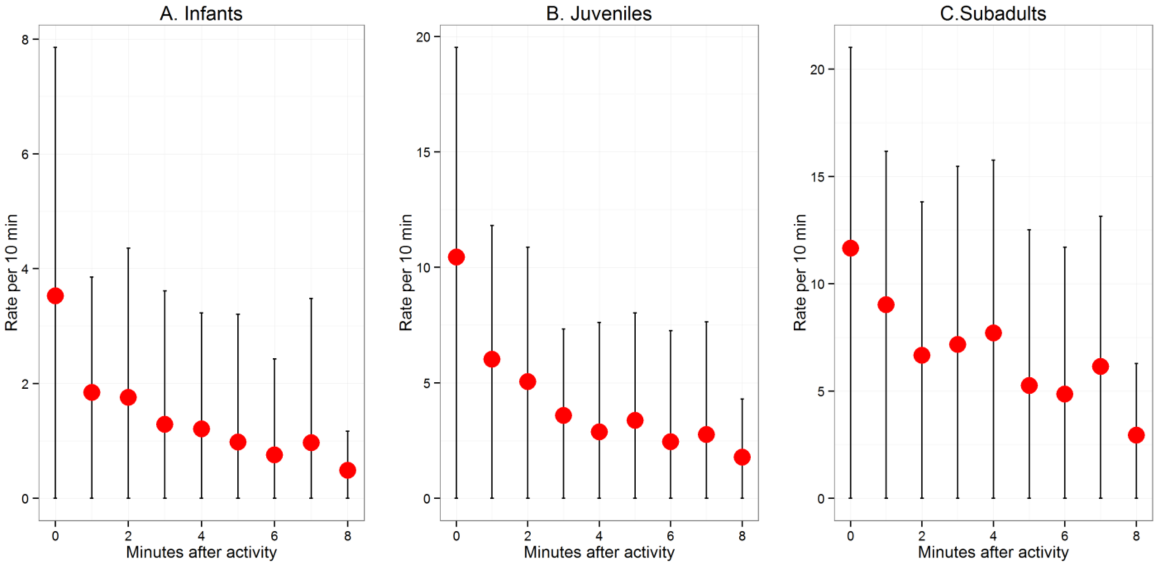

Fig. 4.6: Mean and standard deviation of the rate of manipulation of nuts during nut-cracking activity in the group (0), during the seven minutes after this activity stopped, and in other times (8), in the infant group (A), juvenile group (B) and subadult group (C).

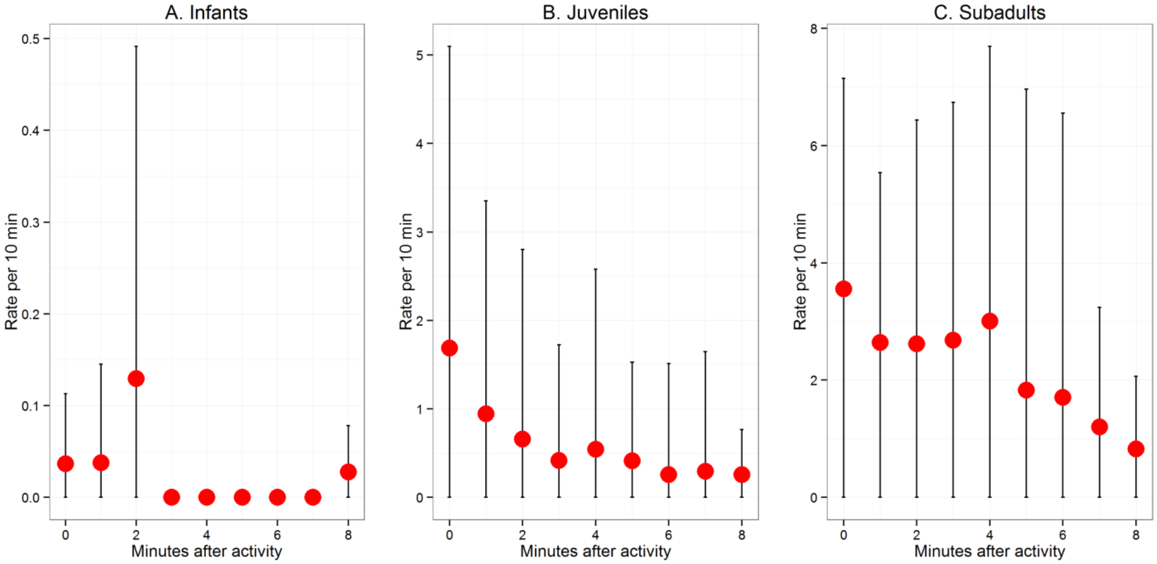

Fig. 4.7: Mean and standard deviation of the rate of striking a nut with a stone during nut-cracking activity in the group (0), during the seven minutes after this activity stopped, and in other times (8), in the infant group (A), juvenile group (B) and subadult group (C).

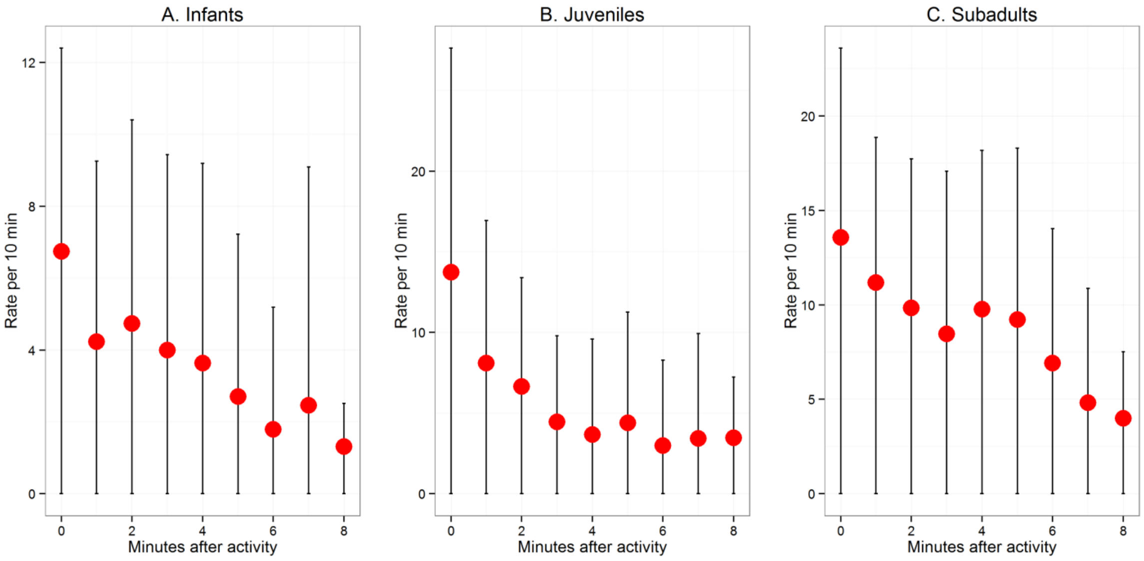

Fig. 4.8: Mean and standard deviation of percentage of time spent near an anvil during nut-cracking activity in the group (0), during the seven minutes after this activity stopped, and in other times (8), in the infant group (A), juvenile group (B) and subadult group (C).

Tables

Table 4.1. Demographic data on the subjects

Name	Estimated date of birth (estimated)	Gender	Mother	Mass 2011 (Kg)	Mass 2012 (Kg)	Mass 2013 (Kg)
Donzela	January 13, 2013	F	Doree	–	–	0.4

Patricia	January 11, 2013	F	Piassava	_	_	0.53
Titia	January 3, 2013	F	Teninha	_	_	0.66
Divina	November 7, 2012	F	Dita	_	_	_
Cachassa	March 15, 2012	M	Chuchu	_	0.42	1.11
Presente	February 15, 2011	M	Piassava	0.24	0.99	1.47
Thais	February 1, 2011	F	Teninha	0.42	1.09	1.34
Chani	December 15, 2010	F	Chuchu	0.46	1	1.16
Coco	July 14, 2009	M	Chuchu	1.14	1.44	1.66
Passoca	January 1, 2009	F	Piassava	1.18	1.32	1.62
Pamonha	January 1, 2009	F	Piassava	1.23	1.37	1.57

Doree	November 9, 2007	F	Dita	1.37	1.56	1.78
Pati	November 2, 2007	M	Piassava	1.68	2.08	2.5
Cangaceiro	September 20, 2007	M	Chiquinha	1.83	2.08	2.36
Catu	February 5, 2007	M	Chuchu	1.81	2.07	2.46
Tomate	December 1, 2006	M	Teninha	1.8	1.99	2.34

Table 4.2. Ethogram

Manipulating events: instantaneous activities, recorded the second they are performed, or in some cases, every few seconds as long as they are happening		
Event	**Modifier**	**Description**
Hitting a nut	Anvil/tree/ground	Subject holds a nut and strikes the nut directly onto the surface – ones or more than once in a sequence. As long as the behavior continuous, it is recorded every 3 seconds

Hitting another object	Anvil/tree/ground	Subject holds an object and strikes it directly onto the surface – ones or more than once in a sequence. As long as the behavior continuous, it is recorded every 3 seconds
Light tap		Fingertip tap (usually on rigid surface)
Striking - hitting		Striking a nut with a stone. Recorded every time the stone hits the nut
Striking with nut		Striking one nut with another nut. Recorded every time the nut hits the other nut
Positioning		Subject put the nut down and leaves it before striking it
Scrounging	Adult present/ adult left	Subject take a nut, or part of a nut, that another monkey was cracking, while s/he was there or within 5 seconds after s/he left
Nut cracked		Nut shell is broken (Observer sees or hears)
Manipulation	Nut Nut shell	Picking up, rubbing between the hands on the body, rolling on surface,

	Stone Sand (including digging for tubers) Tuber Non-embedded plant material (e.g., grass, flowers, fruits) Embedded plant material (e.g., seeds within a shell) Non-embedded invertebrates (e.g., flying insects, spiders) Embedded invertebrates (e.g., termites inside branches) Vertebrates	manipulating in hand in another way (including hand/mouth actions), NOT including eating, or hitting it directly. If done continuously, recorded every 3 seconds
Eat	Drinking Nut Nut shell Tuber	Biting into a food item or putting it in the mouth. If done continuously, recorded every 3 seconds

	Non-embedded plant material (e.g., grass, flowers, fruits) Embedded plant material (e.g., seeds within a shell) Non-embedded invertebrates (e.g., flying insects, spiders) Embedded invertebrates (e.g., termites inside branches) Vertebrates	
Location states. Mutually exclusive, recorded from the second they start until subject moves to another location		
Location		**Description**
Ground		Including rocks and outcrops (unless used as anvils)
Near/on anvil		Arm’s reach from an anvil (see definition of anvil below)
Tree		Including fallen logs (unless used as anvils)

Table 4.3: duration of observations

Year	Total time in seconds (mean)	Number of subjects
First	30714	8
Second	53773	5
Third	42878	6
Fourth	47175	6
Fifth	41910	7
Sixth	51461	4

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CHATER 5

GENERAL CONCLUSIONS

The questions of animal culture and traditions in animal populations have captured the imagination of biologists, psychologists, anthropologists and more for many years. As humans, we are immersed in culture, and our ability to learn from each other is one of our more celebrated characteristics, and the foundation of our civilization. By looking comparing social learning in ourselves vs. our relatives, we can understand something about the roots of our culture.

Despite the high interest this subject invokes, it is very hard to show unequivocally that a behavior seen in a wild population is transmitted from generation to generation via social learning, and is therefore a tradition. Extracting foraging behaviors, including tool use, are often suggested as potential traditions. However, without tracking the origin and spread of a specific behavior, it is hard to show conclusively that it is socially transmitted.

Here we took a developmental approach, and studied the ontogeny of nut-cracking behavior using tools in young capuchin monkeys. By considering the development of all nut related activities, together with the potential social influences on this process, we were able to present strong evidence to support the hypothesis that this behavior is transmitted socially. In addition, we were able to describe the social learning mechanisms that play a role in the transmission of this behavior, and to study their dynamic pattern.

We start by looking at the ontogeny of nut-related behavior – when specific actions appear for the first time, and how the rate by which those actions are performed changes with age. We had the advantage of working with a large group (16 infants and juveniles) over more than two years. We obtained a comprehensive record of all activities of those subjects, nut-related and non nut-related, in multiple locations. Thus, we were able to get a more complete picture of juveniles' behavior and skill development, compared to previous studies that focused only on actions with nuts (Resende, Ottoni et al. 2008; Resende, Nagy-Reis et al. 2014).

We then looked at the social influences exerted on the infants and juveniles throughout this process, both through direct observation and through providing artifacts the young monkeys could interact with and learn from. Social influence on tool-use was studied before in capuchins (Coelho, Falótico et al. 2015) and well as in chimpanzees (Biro, Inoue-Nakamura et al. 2003), but this the first study to present a quantitative approach to this question, and show the different ways by which the activity of adults in the group affect the behavior of infants and juveniles.

Finally, we examined not only the presence of a social effect, but also the dynamics of its decline. The temporal aspect of social influence is almost never considered. As far as we know, there is only one study that examined the decline of social influence after observation is over (Hoppitt, Samson et al. 2012). This study was done in an experimental setting with wild meerkats, and the researchers found an exponential decline in the strength of social influence. Our study is the first to examine the dynamics of social influence on different actions, in the context of a naturally-occurring behavior of a wild population.

Extractive foraging skills that require a long period of learning and practice are by no means unique to capuchins. Other species, similarly, take months or years to master tool use (e.g. (Inoue-Nakamura and Matsuzawa 1997; Lonsdorf 2005; Holzhaider, Gray et al. 2010)) or other extractive foraging behavior (e.g., (Van Schaik and Van Noordwijk 1986; Thornton and Hodge 2009)). We believe that many of the insights gained from the studies presented here can be applied to those – and many other – examples. By providing a deeper understanding of the maintenance of a non-human animal's tradition, they can also illuminate the difference – and similarities - between it and human traditions.

Summary of findings from current studies

In the first paper, we studied the ontogeny of nut-cracking in infant and juvenile wild bearded capuchins. We found that while the rate of manipulation for easy-to-process food items was about as high in pre-weaned infants (before 18 months) as they are in post-weaned juveniles, and rate of manipulation of hard-to-process food – including nuts – increased sharply around the time of weaning. This suggests a distinct trajectory for foraging on hard-to-process food.

Overall manipulation of nuts starts very early in life, within the first six months – and direct percussion is already seen by that time. Combinatorial, two-object actions (specifically, hitting a nut using another object) appear at around 15 months, and become frequent in the third year. The rate of all manipulations of nuts increases with age. The rate of percussing nuts increased with age until around age two, and then the opposite trajectory was seen. In the context of nut-cracking, direct nut-to-surface percussion cannot open the hard-shelled nuts the capuchins in our field site feed on, but *is* useful when trying to pry out kernels from half-opened nuts. Young capuchins that are not yet skillful enough spend a lot of their time hitting nuts and nut shells directly on a surface, both because it is part of their natural repertoire, and because it is in some cases rewarding: if they pick up open shells that still contain tiny pieces of kernels. Around the age when combinatory actions – the efficient way to crack open nuts – become more frequent, the rate of direct percussion goes down. However, as it does serve a function, it never goes away completely, and is seen also in the adults' repertoire.

Hitting a nut with another nut – an inefficient behavior – appeared in the second year of life, and at that age the juveniles performed it at the same rate as the efficient actions of hitting a nut with a stone. From this point on, the percentage of hitting with a nut decreases with age, and the percentage of hitting with a stone increases. Thus, it represents the dropping of inefficient behaviors in favor of more efficient ones as the juveniles master this skill.

One of the main findings of this paper is the long period of practice and manipulation of nuts, during which juveniles do not get any food reward for their efforts. There are presumably other factors that keep the juveniles interested in nuts and support their practice throughout this period. The example of adults who are cracking nuts nearby, and the availability of nuts and tools and their vicinity, can serve as those factors (for further discussion:(Fragaszy, Biro et al. 2013)). We examined those factors in the next paper.

In the second paper, we set out to study the social influence on the behavior of infants and juveniles. We considered two types of influence: directly observing other group members cracking and eating nuts, and interacting with artifacts left by nut cracking (nut debris and hammer stones on/near an anvil). To do so, we examined the rate in which infants and juveniles perform nut-related and non nut-related actions under different conditions: when they are near an anvil or away from it, and when others in the group crack and eat nuts around them compared to times they do not. We found that the rates of manipulation of nuts and of hitting a nut with a stone by our subjects was higher near an anvil (where a lot of nut debris was found) as well as when there was nut-cracking activity nearby. Conversely, the rate of manipulation of objects other than nuts was *lower* near an anvil and during nut-cracking activity nearby. We also found that those two factors were correlated: infants and juveniles spend more of their time near an anvil when others cracked nuts around them.

From those results, we suggested the following model for the social influence on nut-cracking skill development in young capuchin monkeys. The model is composed of two related processes:

2. Seeing groupmates 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: seeing groupmates engage in a particular behavior, and seeing them getting a reward from it (which serves as vicarious reinforcement, (Bandura and McClelland 1977)) , motivates the observers to engage in the same activity.

b. Through drawing infants and juveniles towards the anvils, where nut-cracking is 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 opportunities to interact with those artifacts.

Thus capuchins are motivated to coordinate their behavior with others in both time and space.

3. Interacting with artifacts created by nut-cracking. By interacting with nut shells on and around the anvils, the infants and juveniles can learn to associate nuts with food, and to understand the need to process them using the anvil and hammer stone. This mechanism

increases the breadth of social influence beyond the limited time in which others are cracking nuts.

This social influence was not felt in the same way by all age groups. We found that the influence of being near an anvil on the rate of manipulation of nuts is strong at all ages. The influence of observing nut cracking activity on rate of manipulation was seen in most age groups, but not in the one year old infants and monkeys older than five years (subadults). The infants are only starting to interact with nuts, and seem to do that very opportunistically – whenever a nut or nut shell happens to be next to them. As for subadults, this lack of influence might be related not only to the fact that they are less tolerated by the adults, but also to the fact that at that age most subadults can already crack nuts quite efficiently (Resende, Nagy-Reis et al. 2014). They *are* drawn to the anvils at times of nut-cracking in the group, but they do not spend their time there interacting with nuts, shells or stones. They do not spend much time practicing and trying different actions, as the younger juveniles do.

Social influence is clearly not the only factor in skill acquisition. We suggest that the processes described above provide the opportunity for the juveniles to manipulate nuts and stones in different ways, especially on the anvil sites, and motivate them to continue with this manipulation even in the absence of tangible reward. Thus it sustains the long period of practice required for mastering nut-cracking, as seen in the first paper. In the next paper, we studied this social influence in more detail.

In the third paper, we set out to study the dynamics of social facilitation – how the effect changes *after* the activity that started it end. Though social facilitation is well established in many species, the temporal aspects of this facilitation are largely unexplored. When the question of time is addressed, it is almost always in the form of presence or absence of an effect after a predetermined interval. We went further, to study *how* the effect declines.

We found that the rate of manipulation of nuts decreased in the 7 min after nut-cracking activity in the group stopped, and the decrease in those minutes was exponential, with half-life of the effect of 2.1 minutes. The rate of decline of specific nut-cracking actions – direct percussion of nuts and striking a nut with a stone – also declined exponentially, but the decline was much faster, with half-lives of 36-37 seconds.

One interpretation is that a specific social influence affects percussive actions, which are the actions performed regularly by adults while cracking nuts. These two actions are both the most vigorous, involving movements of the greatest speed and amplitude, and produce loud sound. They also directly precede feeding on nuts. Perhaps these components make the actions particularly susceptible to a strong, but short-lived, social facilitation. Other actions – picking up, sniffing, biting – are apparently less influenced by direct observation, and more by the opportunity provided by the nut-cracking artifacts. Those actions continue as long as the subjects stayed near an anvil.

Indeed, we found that the percentage of time spent near an anvil decreased exponentially during the 7 min after nut-cracking activity in the group stopped. The half-time of the effect was 2.8 minutes, very similar to the half-time for the rate of all manipulation with nuts

Here again, we found that not all age groups were influenced in the same way. The subadult group (age four to six years) showed the same pattern of exponential decrease in rate of manipulations of nuts as did the younger juveniles, but its half-life was different. While juveniles age 1.5-4 years showed a half-life of 2.5 min, the subadult had a half-life of 3.7 min. This difference between the groups was even bigger when looking at the rate of striking a nut with a stone, the efficient way to crack nuts. For this variable, the subadult group did not show any significant decline with time after nut-cracking in the group stopped whereas the 1.5- 4 year olds did show an exponential decline. Similarly, while in all age groups the percentage of time spent near an anvil declined exponentially with time after the nut-cracking activity stopped, the decline was slower in the subadult group. In the infants and juveniles groups the half-lives of the effect are 3.7 minutes and 2.7 minutes respectively, and the half-life of the subadult group is 7.5 minutes.

This can be explained by the fact that at age four and older, social facilitation is not the only factor influencing their behavior - competition also enters the mix. At this age subadults are starting to crack nuts for themselves, and to do so they need anvils and hammer stones. When they approach an anvil, they are not content to simply manipulate the nut shells around it, but want to actually crack nuts. When other nut-cracking activity stops, they can get their chance – they can take the hammer stones left by the adults and use the anvils evacuated by those adults.

Therefore, we suggest that the pattern of behavior seen here represent the transition from a young juvenile, highly tolerated by the adults and still in the process of learning (thus not presenting a competition to efficient nut-crackers); to an older individual that is less tolerated, competing with the adults on resources, and have less opportunities - but also less need - for learning.

Future directions

The papers presented here provide deeper understanding of the development of tool use in bearded capuchins and the social factors that influence this development. However, our dataset broadens this understanding, as it allows us to look both at the larger picture and the smaller details: the overall social ties in a tool-using group, and the social influence of specific individual.

Social network analysis: we would like to study the social ties in the group as a whole. Do monkeys prefer to spend their time in the vicinity of specific groupmates? Do they form groups based on age, sex? Do those ties change with age? Using our dataset, and the new statistical methods of social network analysis, we can answer all those questions and more. We would like to use those methods to examine tool-use related questions as well, such as – does the group dynamic change when many in the group engages in nut-cracking? How does it look compared to other type of foraging? When infants or juveniles interact with a nut, who is likely to be around them? Is it someone different than those who would be around them under different conditions?

This line of investigation would shed light on the social dynamics of wild capuchins and how they change with time, as well as contribute to better understanding of the social behavior in the context of tool-use.

Individual influences on nut cracking: after we established the influence of others cracking and eating nuts on our subjects' behavior, we would like to examine the influence of *specific* individuals. Are juveniles more influenced by the activity of their mothers? Or that of the alpha male? Does that change with the age of the juvenile? Do some individuals have an inhibitory effect on the juveniles?

We plan to use the data from the social network analysis to inform this study: we would check whether individuals that are seen frequently in the vicinity of a specific juvenile have a larger influence on this juvenile.

This study would go beyond the influence of "the group" to consider the details of social facilitation; who exerts it, and how it is felt by different juveniles. Capuchin monkeys, being a gregarious species, are an excellent choice for such a study – and we have the dataset to conduct it.

Significance

We presented here a model for skill acquisition and how it is influenced by social input. We show that a long period of practice without reward is supported by several social learning mechanisms - especially social facilitation and opportunity providing – that are inter-related and feed on each other. Thus, this study provides strong evidence for nut-cracking in capuchins being a tradition, transmitted with the help of social learning.

This model is not limited to tool use or to non-human primates, and can be applied and tested for many different foraging behaviors in various species. We suggest that this combination of social process and long individual practice may be the way in which many foraging traditions are acquired, across species. From this model, we can also hypothesize the conditions under which this type of social transmission can take place – the type of foraging behavior (e.g., a behavior that leaves behind more artifacts can be transmitted more easily), and the social context (e.g., the level of tolerance needed for social transmission). The future studies listed above can shed more light on the social aspect of skill acquisition, and thus help us understand even more the social condition needed to maintain a foraging tradition.

In addition to a model, we present here a novel method for examining – and thinking of – skill acquisition in a social context. By looking at the same time at the behavior of juveniles and infants and the presence and activity of every groupmate around them, we were able to achieve a more complete picture than ever before of how others' activity influences the individual. Furthermore, for the first time in a study of naturally-occurring behavior, we examined the dynamics of social facilitation, and showed that it declines exponentially with time. We suggest that similar dynamics might be seen in other cases of social facilitation as well. We hope that more studies will take into account the important time aspect of social influence.

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