# Synchronized practice helps bearded capuchin monkeys learn to extend attention while learning a tradition

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Culture extends biology in that the setting of development shapes the traditions that individuals learn, and over time, traditions evolve as occasional variations are learned by others. In humans, interactions with others impact the development of cognitive processes, such as sustained attention, that shape how individuals learn as well as what they learn. Thus, learning itself is impacted by culture. Here, we explore how social partners might shape the development of psychological processes impacting learning a tradition. We studied bearded capuchin monkeys learning a traditional tool-using skill, cracking nuts using stone hammers. Young monkeys practice components of cracking nuts with stones for years before achieving proficiency. We examined the time course of young monkeys' activity with nuts before, during, and following others' cracking nuts. Results demonstrate that the onset of others' cracking nuts immediately prompts young monkeys to start handling and percussing nuts, and they continue these activities while others are cracking. When others stop cracking nuts, young monkeys sustain the uncommon actions of percussing and striking nuts for shorter periods than the more common actions of handling nuts. We conclude that nut-cracking by adults can promote the development of sustained attention for the critical but less common actions that young monkeys must practice to learn this traditional skill. This work suggests that in nonhuman species, as in humans, socially specified settings of development impact learning processes as well as learning outcomes. Nonhumans, like humans, may be culturally variable learners.

primates | attention | development | learning | tool use

**T**raditions are behaviors shared among members of a group that are reliably learned by new individuals, in part, with social support (1). The concept of tradition highlights behavioral consistency over time and across individuals. Here, we emphasize the origin of traditions in learning. Learned behavior is one manifestation of developmental plasticity, and generation of novel behavior is another. Novel behavioral variants may be learned by others, thus modifying existing traditions or leading to new ones (2). In this way, developmental plasticity enables heritable modification of behavior through learning, with the result that culture may extend biology (3, 4). Traditions appear to be widespread in the animal kingdom (5–7), leading theorists to propose that cultural evolution, rather than being restricted to recent human history, has general evolutionary significance (8, 9). Apes (6, 10) and monkeys provide several examples of traditions. Among monkeys, for example, vervet monkeys learn their mothers' food-processing techniques (11) and white-faced capuchin monkeys learn odd social games, such as poking a finger in another monkey's eye, that become established intermittently in groups (2, 12).

Given the essential role of learning in traditions, cognitive processes associated with learning that show developmental plasticity themselves, should be incorporated into our understanding of how culture can extend biology (13–15). However, cognitive processes associated with learning are not yet well integrated into theories of cultural evolution and niche construction (16). Here, we illustrate how growing up in a group with a prevailing tradition of using tools in foraging could affect cognitive development in young monkeys in ways that support their learning this traditional skill. This work opens a bridge between the learning sciences and the field of cultural evolution.

## Social Experience Influences the Development of Attention

In humans, social experiences are implicated in the development of attention, memory, and individual learning styles (16–18). Cultural influences on long-term memory development include, for example, the development of particular ways of chunking and rehearsing information to be remembered, such as the construction of "memory palaces" used by the ancient Greeks and the cultures that succeeded them (19) and the use of written lists and notes in the present day. Culture also impacts the development of working memory, which incorporates structures and processes used for the temporary storage and organization of information about events recently heard or seen or about activities recently performed (20, 21). Working memory is dependent on sustained attention, and therefore sensitive to attentional disruption. It is intimately related to motor processes, and limited in span to perhaps three to four "chunks" of information at one time. In humans, working memory typically lasts from a few seconds to more than 1 min depending on emotional salience; whether the information to be remembered is about events, actions, or space; and other factors (20).

It is thought that humans share with other primates general attentional and working memory capacity, although humans develop skills, many of which are cultural, to control attention, and thus to extend working memory (20, 22). Consider the deep attention humans develop through meditative practice and in the course of reading and writing, all of which are explicitly cultural skills. Cultural variation in learned attention and skilled actions in humans suggests we should seek similar variations in nonhuman primates and other taxa that, like humans, live in socially constructed

environments. To the extent that the development of sustained attention and working memory is biased by the actions of social partners, the process and outcome of social learning are likely to vary across groups and across species. Other features of socially constructed niches, such as the creation of artifacts, can also promote sustained attention by providing opportunities and reminders to practice particular actions, and thus add another source of cultural or taxonomic variation in socially biased learning (23). Small shifts in attentional processes and perceptual biases can shift the trajectory of learning with far-reaching consequences, as has been proposed for humans learning language (24).

## Developing Sustained Attention for Manual Actions with Objects

Sustained attention and working memory develop throughout childhood in humans, in concert with neural development and social experience (25, 26). Young children extend the duration of sustained attention to an object while an older person shows attention to that object, suggesting how social interactions can support the development of sustained attention in the particular context of handling objects (27). The visual salience to humans of others' hand movements is evident by the second year of life, when toddlers shift their visual attention toward another person handling an object from predominantly toward the face to predominantly toward the hands (28).

There are sound reasons to propose that nonhuman primates are also biased to attend to manual actions. Some species of nonhuman primates in captivity have been shown to attend to humans' manual actions with objects (29–31); they are at least as likely to attend to manual activity of familiar conspecifics, if not more so. Manual activity is salient to all primates: Using the hands with visual guidance to collect food and bring it to the mouth is a primitive characteristic of primates, and all primates use their hands to explore objects and surfaces, as well as to contact others during social interactions, such as grooming and play (32). This fundamental feature of primate behavior is associated with a host of neuroanatomical, perceptuomotor, and cognitive attributes, including strong visual and proprioceptive salience to movements of their own hands and of the hands of others (31).

Through the observer's bias to attend to others' manual actions with objects, others' actions can support the development of attentional control by young monkeys during particular manual activities. In this way, social partners can support young nonhuman primates that otherwise normally experience brief sustained attention to others and to their own activities, learning manual skills that require longer sustained attention. Certainly using tools qualifies as challenging enough to benefit from support of this kind. Acknowledging the cognitive dimension of the constructed niche in nonhuman taxa will strengthen cultural evolutionary theory. Social influence on the development of sustained attention is an appropriate early target for research in this direction. Even if the perceptual biases in primates favoring attention to actions of others are small, they could nevertheless powerfully affect learning trajectories, particularly when magnified by shifts in attention and memory (24).

We hypothesize that nonhuman primates and humans share strong susceptibility to tuning (i.e., extending, strengthening) attention and memory about manual actions and about objects via interest in others' manual activity. However, nonhuman primates face a challenge in sustaining attention to actions with their hands that humans typically do not, or do not face to the same extent, which could be particularly important when learning a skill involving handling objects. Nonhuman primates' attention to their own activity is typically disrupted every few seconds to scan the surroundings briefly (surveying the surroundings in this way is termed "vigilance" in the animal behavior literature) (33, 34). Vigilance, which functions to inform the perceiver about predators, conspecifics, and other relevant dynamic features in the environment, interferes with sustained attention to one's own or another's activity.

## Evaluating Attention to Others' Actions

Duration of gaze is a common measure of sustained attention to others' actions in experimental settings, but this measure is not useful when the activity of interest is auditory or when the experimenter cannot see where the subject is looking. Temporally or spatially synchronized activity between two individuals, commonly measured in studies with nonhuman animals under the general heading of "social influence," is an alternative measure of sustained attention in such cases. We can also measure the decline of synchronized activity once the "demonstrator" stops performing the activity. We propose that the onset of synchronized activity is an indirect measure of the onset of sustained attention and the decline of synchronized activity (i.e., a return to baseline rates of performing a particular behavior) is an indirect measure of the disruption of attention and the subsequent loss of the contents of working memory (in other words, forgetting).

Theories of social learning predict that an individual is aided in learning by attending to the actions or products of actions of another, but are silent about how quickly attention is drawn to the other's actions or products, how long the influence lasts, or how the influence declines over time (35). Not surprisingly, contemporary studies of social learning have not addressed temporal properties of social influence. To our knowledge, Hoppitt et al. (36) provide the only published report to quantify the temporal decline of social influence on behavior in a learning context. In a field experiment, wild meerkats (Suricata suricatta) were presented with baited boxes that could be opened in two different ways. Some meerkats (demonstrators) were trained to open the boxes using a particular method. Subsequently, the boxes were presented to all members of the group, and the naive meerkats' interactions with the boxes, as well as when they watched other meerkats opening the boxes, were recorded. The researchers found that individuals were more likely to interact with a box immediately after observing another meerkat interacting with it; the half-life of the effect was 20 s. Young meerkats spend much time with adults in the period when they are learning to forage on the hidden and dangerous scorpions that these animals capture and eat (37). Adults' influence on young individuals in this period is thought to be necessary for meerkats to master their challenging foraging style (38).

We consider the relation in young monkeys between social influence on activity and attentional processes associated with learning. The activity in question relates to using stone hammers to crack nuts, seeds, or other encased foods, a technical tradition in several populations of wild bearded capuchin monkeys (Sapajus libidinosus) (39–42) (Fig. 1). Young capuchin monkeys, like young meerkats, master finding and feeding on hidden and sometimes noxious prey, and like meerkats, they are interested in and affected by others' actions with objects (43). Thus, they are good candidates for studies of the temporal dynamics of social influence on behavior with objects and on the cognitive processes associated with learning traditional tool-using skills.

## Temporal Dynamics of Social Influence as a Window on Sustained Attention

Our objective was to examine temporal dynamics of social influence on young monkeys' behavior in a situation in which the young monkeys were practicing component actions of a traditional manual skill. Temporal dynamics of young monkeys' behavioral coordination with others in this context reflect sustained attention to their own and others' actions. The skill in question is cracking palm nuts using stone hammers, a precursor to the situation facing humans knapping stone (44). Social support in the form of instruction and demonstration aid in the acquisition of knapping, but these actions are not sufficient by themselves for people to learn to knap stone (45). Providing repeated

**Fig. 1.** An adult bearded capuchin monkey has cracked a palm nut using a stone hammer on a log anvil and is removing and eating pieces of the kernel. A young monkey that cannot crack a nut itself watches closely. Image used with permission from Luca Antonio Marino, Roma Tre University (Rome, Italy).

occasions for practice and self-discovery of movement solutions is a crucial dimension of social support for learning this complex perceptuomotor skill and human traditional skills more generally (13, 46).

We measured the temporal rise and fall of social influence on wild young bearded capuchin monkeys (*S. libidinosus*) in the company of adults that were cracking palm nuts by striking them repetitively with stone hammers. These monkeys start to interact with nuts and stones in the first year of life. They handle nuts, percuss nuts directly against a hard surface (hereafter, percuss), and strike nuts or nut shells with stones (hereafter, strike) for several years before they are able to crack palm nuts themselves (47, 48). Thus, young monkeys exhibit remarkable persistence in a foraging activity that they cannot perform effectively. We know that others' cracking nuts is partially responsible for the young monkeys' persistence. In one recent study, while other group members were cracking and eating nuts, monkeys 6 y of age or younger were threefold more likely to be near an anvil, quadrupled their rate of interaction with nuts, and doubled their rate of percussing and striking compared with times when no monkey in the group was cracking nuts. Interactions with objects other than nuts showed the opposite pattern (48).

The data for this report are taken from monkeys 6 y of age or younger belonging to a wild, habituated group of bearded capuchins observed in five periods over 2 y (Table 1). Members of this group of monkeys routinely crack nuts using stone hammers at many anvils scattered across their home range (49–51). In this study, one observer continuously recorded the focal young monkey's behavior. A second observer concurrently recorded at intervals of 1 min the distance from each neighbor (within a 10-m zone) to the focal monkey, the identity and behavior of each neighbor, and the occurrence of cracking nuts (i.e., striking a nut with a stone, producing a sharp cracking noise) by any monkey in the group. The method allowed us to analyze the focal monkey's behavior with nuts and stones and its presence near anvils in relation to the start, continuation, and end of cracking by other members of the group. Data collected while the group was in a frequently visited area with abundant anvils, hammers, and cracked shells, as detailed below, indicated that the temporal pattern of others' influence on young monkeys' activity with nuts and stones and their presence near anvils was associated specifically with the others' activity with nuts (i.e., synchronization was not a byproduct of traveling in a cohesive group). Results are reported for $n = 16$ monkeys, unless otherwise noted.

## Results

**Manipulation of Nuts.** Young monkeys manipulated nuts at the highest rate when others were cracking nuts (i.e., striking nuts with a stone) (median = 8.3 acts per 10 min) and at the lowest rate (median = 0.9 acts per 10 min) during periods when no others were cracking nuts, and had not been cracking nuts for at least 8 min. The difference between these rates was significant (estimate = 1.98, $P < 0.0001$). The onset of the effect of others' cracking nuts was quick: Compared with the minute before others began to crack, the median probability that a young monkey would manipulate a nut doubled in the first minute after others began to crack, and remained doubled or more for at least 5 min when others continued to crack (Fig. 2). Movie S1 provides a video-clip of a young monkey handling a nut while and after another monkey is cracking a nut. During the 7 min after the others stopped cracking, the rate of manipulation of nuts declined exponentially (in $A_t = A_0 * e^{-\beta t}$; estimates: $A = 9.96$, $P < 0.0001$; $\beta = 0.325$, $P = 0.0013$; Fig. 3), where $e$ is the base of the natural logarithm, $\beta$ is the rate by which the dependent variable declines with time, $t$ is the time since cracking in the group stopped, and $A_t$ (the dependent variable) is the rate or percentage

**Table 1. Subjects' date of birth, sex, and body mass at each sampling time point**

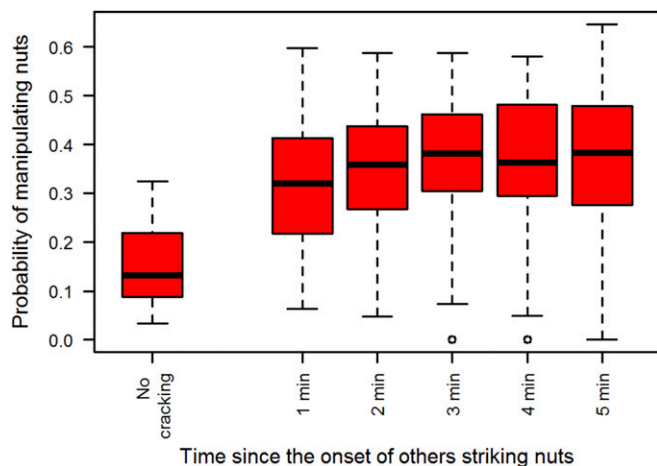| Name | Date of birth (mm/dd/yyyy) | Sex | Body mass in 2011, kg | Body mass in 2012, kg | Body mass in 2013, kg |
|---|---|---|---|---|---|
| Donzela | 01/13/2013 | F | — | — | 0.4 |
| Patricia | 01/11/2013 | F | — | — | 0.5 |
| Titia | 01/03/2013 | F | — | — | 0.7 |
| Divina | 11/07/2012 | F | — | — | — |
| Cachaça | 03/15/2012 | M | — | 0.4 | 1.1 |
| Thais | 02/01/2011 | F | — | 1.1 | 1.3 |
| Presente | 02/15/2011* | M | — | 1.0 | 1.5 |
| Chani | 12/15/2010 | F | — | 1.0 | 1.2 |
| Coco | 07/14/2009 | M | 1.1 | 1.4 | 1.7 |
| Paçoca | 01/01/2009 | F | 1.2 | 1.3 | 1.6 |
| Pamonha | 01/01/2009 | F | 1.2 | 1.4 | 1.6 |
| Doree | 11/09/2007 | F | 1.4 | 1.6 | 1.8 |
| Pati | 11/02/2007 | M | 1.7 | 2.1 | 2.5 |
| Cangaceiro | 09/20/2007 | M | 1.8 | 2.1 | 2.4 |
| Catu | 02/05/2007 | M | 1.8 | 2.1 | 2.5 |
| Tomate | 12/01/2006 | M | 1.8 | 2.0 | 2.3 |

F, female; M, male.
*Estimate.

**Fig. 2.** Probability that a young monkey (*n* = 11) manipulated a nut in the 1 min before the onset of striking a nut performed by another monkey (No cracking) and during each of the 5 min following the onset of striking a nut by another monkey. The boxes display the median and interquartile range, and whiskers indicate minimum and maximum values. The solid line within the box depicts the median. Circles indicate values of outliers.

of time. The output from the model is $A_0$ (the strength of the effect on the dependent variable) and $\beta$. The half-life of the effect was 2.1 min. The rate of nut manipulation during the first to fifth minutes after other monkeys stopped cracking nuts was significantly higher than the rate during periods 8 min or longer after others stopped cracking nuts (i.e., the baseline rate) ($P < 0.0001$ for minutes 1–4 after other monkeys stopped cracking nuts, $P = 0.0146$ for minute 5). The rate of manipulation of nuts during the sixth and seventh minutes after others stopped cracking nuts and the rate during periods 8 min or longer after others stopped cracking nuts did not differ significantly.

The temporal pattern for young monkeys' manipulation of other objects besides nuts was the opposite of their actions with nuts. Young monkeys manipulated other objects at the lowest rate when others were cracking nuts (median = 12.8 per 10 min) and at the highest rate during periods 8 min or longer after others stopped cracking nuts (median = 16.7 per 10 min). The difference between these rates was significant (estimate = 1.29, $P < 0.0001$). From the time when others were cracking nuts through 7 min after they stopped, juveniles' rate of manipulation of other objects increased exponentially (in $A_t = A_0 * e^{-\beta t}$; estimates: $A = 14.2$, $P < 0.0001$; $\beta = -0.03$, $P = 0.015$), although the rate of manipulation of other objects in each of the first 7 min after others stopped cracking nuts did not differ from the rate in baseline periods (i.e., 8 min or longer after other monkeys stopped cracking nuts).

**Percussing Nuts and Striking Nuts with a Stone.** We looked at the rates of two actions that are related to cracking palm nuts: percussing a nut on a hard surface (percuss) and striking a nut placed on a hard surface with a stone (strike). The young monkeys' rate of percussing was highest while others were cracking nuts (median = 1.3 per 10 min) and lowest during periods 8 min or longer after others stopped cracking nuts (median = 0.2 per 10 min). These rates were significantly different (estimate = 6.3, $P < 0.0001$). As was the case for manipulation of nuts, the onset of the effect of others' cracking on young monkeys' percussion was nearly immediate. Compared with the minute before others began to crack nuts, the probability that a young monkey would percuss a nut more than doubled in the first minute after others began to crack nuts (from <0.04 to >0.10) and remained at that level for at least 5 min while others were cracking (Fig. 4). From the time that others stopped cracking nuts, the immature

monkeys' rate of percussion declined exponentially for the next 7 min (in $A_t = A_0 * e^{-\beta t}$; estimates: $A = 8.16$, $P = 0.026$; $\beta = 1.12$, $P = 0.014$; Fig. 5). The half-life of the effect was 0.6 min, less than a third as long as the half-life for manipulation of nuts (2.1 min).

Four monkeys (all <1 y of age) did not strike a nut with a stone during focal observations, but 12 monkeys (all >1 y of age) did. For the latter monkeys, the rate of striking was highest when others were cracking nuts (median = 1.4 per 10 min) and lowest in periods 8 min or longer after others stopped cracking (median = 0.3 per 10 min; Fig. 6). The difference between these rates was significant (estimate = 4.3, $P < 0.0001$). In the minute after others stopped cracking, the median rate of striking by the young monkeys declined to zero, and for all minutes, the rate of young monkeys' striking was not significantly different from periods 8 min or longer after others stopped cracking. The data did not fit an exponential model of decline.

**Time Spent Near an Anvil.** The percentage of time young monkeys spent near an anvil was highest when others were cracking nuts (median = 13.3%) and lowest during periods 8 min or longer after others stopped cracking (median = 2.6%) (Fig. 7). The difference between these percentages was significant (estimate = 6.06, $P < 0.0001$). When others were cracking until 7 min after all others had stopped cracking, the percentage of time young monkeys spent near an anvil declined 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 was 2.8 min.

## Discussion

**Linking Learning Processes to a Tool-Using Tradition in Monkeys.** Culture in a behavioral sense is present when, aided by social context, individuals consistently learn behaviors exhibited by others in their community (i.e., they have traditions). Culture can extend biology in an evolutionary sense when the traditions in question persist across generations, and when they have selective consequences. In parallel with natural selection, occasional spontaneous behavioral variants (arising from developmental plasticity) that afford some advantage and that are learned by
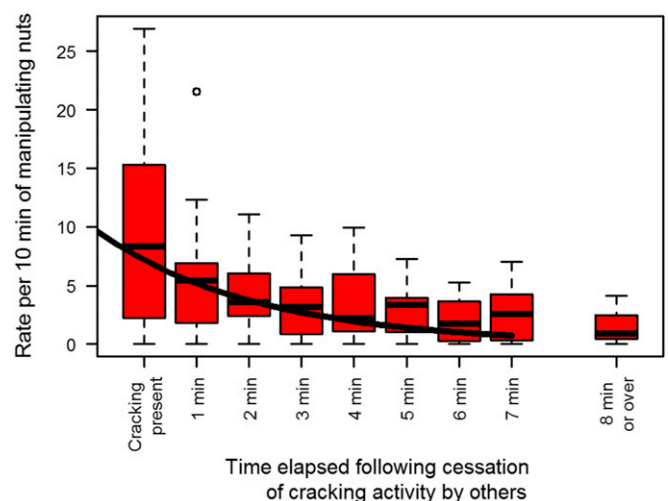


**Fig. 3.** Rate per 10 min of manipulation of nuts by young monkeys (*n* = 16) when one or more other monkeys struck nuts (Cracking present) during each of the 7 min after others stopped striking a nut and in periods 8 min or longer after others stopped striking a nut (8 min or over). The exponential curve generated by model fitting is overlaid. The boxes display the median and interquartile range, and whiskers indicate minimum and maximum values. The solid line within the box depicts the median. Circles indicate values of outliers. The half-life of the decline occurred at 2.1 min.
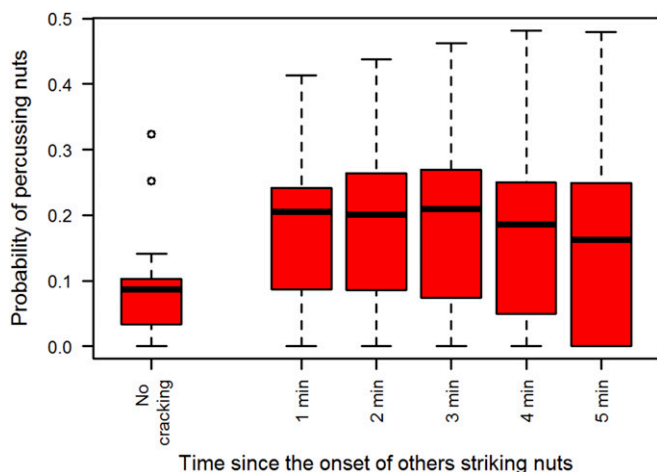
**Fig. 4.** Probability that a young monkey (n = 11) percussed a nut 1 min before the onset of striking a nut performed by another monkey (No cracking) and during each of the 5 min following the onset of striking a nut by another monkey. The boxes display the median and interquartile range, and whiskers indicate minimum and maximum values. The solid line within the box depicts the median. Circles indicate values of outliers.

others can become established as new traditions. Learning a tradition is, by definition, dependent on the social context in which learning takes place, but it is equally dependent on the learning processes of the individual. Here, we draw attention to the power of social partners to influence not just the content of learning a tradition (i.e., how or when to perform a particular behavior) but also how learning itself takes place. Working from findings with humans that sustained attention is developmentally plastic and susceptible to social influence, we examined behavior of young monkeys, seeking evidence that social influences shape attention in young monkeys. Specifically, we examined temporal dynamics of social influence on young monkeys' activity with the materials relevant to the tool-using tradition in their wild group (cracking nuts with stone hammers) to index their sustained attention to this task. Young monkeys were more likely to be near an anvil, and to manipulate, percuss, and strike nuts once others began to strike nuts to crack them (which we call cracking). The higher probability of these actions in young monkeys persisted through 5 min while others cracked nuts (5 min was the longest period for which we had sufficient data for these analyses). They continued to manipulate nuts at higher rates and were more likely to be present near an anvil for minutes after others stopped cracking nuts, with a half-life of more than 2 min for each variable. These findings indicate substantial lingering effects of social influence on young monkeys' interest in nuts and anvils and general exploratory activity directed to nuts. In contrast, these young monkeys decreased manipulation of other objects while other monkeys cracked nuts.

Key to our argument that attention (and its related process, working memory) can be enhanced by participating in socially supported practice, others' cracking was a strong facilitator of young monkeys' practicing percussion and striking nuts, but only when others were cracking. The young monkeys percussed a nut or struck a nut with a stone much less frequently than they manipulated nuts; moreover, following the end of others' cracking nuts, young monkeys reduced percussion and striking quickly (a half-life of about 37 s for percussion and a median of zero after 1 min for striking).

**Building Sustained Attention for the Least Likely Actions.** These findings illustrate how the frequency and temporal duration of others' actions can influence how young individuals learn a

challenging perceptuomotor skill. When others act in frequent bouts, and when these bouts are long-enduring, they support more frequent performance by young individuals of those actions for which attention is least well maintained and, subsequently, working memory is the most fragile. We provisionally identify this process as social scaffolding for learning attentional skills that support learning the least familiar component(s) of an activity. The socially supported practice of sustained attention in a given context can powerfully support development of longer periods of sustained attention that can be marshalled during other contexts. For example, human infants practice sustained attention while maintaining joint attention with a caregiver, and these common and frequent social interactions influence the development of sustained attention more generally (27). In the case of young bearded capuchin monkeys, we suggest that extending sustained attention for percussive actions with stones and nuts is one outcome of repeated prompting to perform these actions arising from others striking nuts while cracking them. We further suggest that the development of longer sustained attention to their own percussive activity supports the acquisition of nut-cracking using stone hammers, which is a signature tradition of tool use in some groups of bearded capuchin monkeys.

**Socially Tuned Attention and Learning Traditions in Primates and Other Orders.** This line of reasoning leads us to predict that tool-using traditions in nonhuman animals include actions that are infrequent outside of that activity (i.e., traditions are not composed solely of common actions), and to the related predictions that (*i*) the components of tool use traditions that are infrequent in species-typical activity outside of the traditional activity will be performed frequently by proficient tool users, and (*ii*) frequent performance by adults of uncommon actions will support practice of these particular actions by young individuals.

Taxonomic variation in social learning may follow from species-typical variations in attention in combination with temporal dynamics of action. We hypothesize two features of attention and memory distinguish primates from other orders: (*i*) Primates are more likely than other orders to have stronger sustained attention and working memory for actions with objects compared with other kinds of actions, and (*ii*) primates have stronger interest in others' actions with objects than do other orders [although there may be other taxa with strong interest in
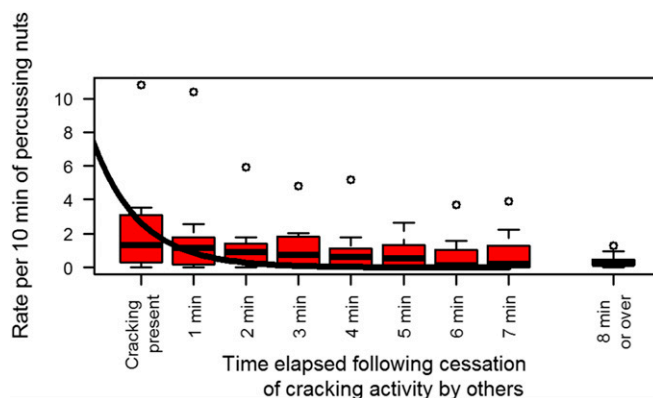


**Fig. 5.** Rate of direct percussion of nuts by young monkeys (n = 16) when one or more other monkeys struck nuts (Cracking present) during the 7 min after other monkeys stopped striking nuts and in periods 8 min or longer after others stopped striking a nut (8 min or over). The boxes display the median and interquartile range; whiskers indicate minimum and maximum values. The solid line depicts the median. Circles indicate values of outliers. The exponential curve generated by model fitting is overlaid. The half-life of the decline occurred at 0.62 min.
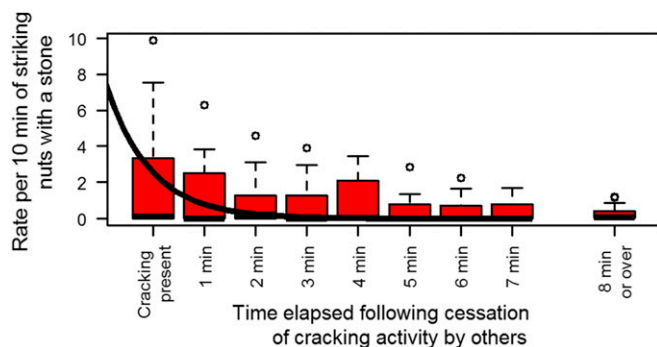
**Fig. 6.** Rate of striking a nut with a stone by young monkeys ($n = 16$) when one or more monkeys in the group struck nuts (Cracking present) during the 7 min after other monkeys stopped striking and in periods 8 min or longer after others stopped striking a nut (8 min or over). The boxes display the median and interquartile range, and whiskers indicate minimum and maximum values. The solid line depicts the median. The exponential curve generated by model fitting is overlaid. Circles indicate values of outliers.

others' actions with objects, such as New Caledonian crows, which also use tools in foraging (52)]. By comparison, some cetacean species (e.g., *Tursiops* and *Orcinus orca*) are more likely than other mammals to have stronger sustained attention to auditory events and more immediate response to others' actions, in keeping with the collaborative nature of their feeding activities and the efficiency of sound transmission in water (7). In general, the social dimension of the developmental niche is likely to contribute to tuning attention, and thus to bias learning, to favor those skills that are commonly practiced by the young individual's social companions.

We hope this work prompts others to develop these ideas and to test them with data from diverse species. Conceptual and empirical work along these lines is needed to integrate developmental and psychological understanding of behavioral variation into theories of cultural evolution, niche construction, and evolutionary biology.

## Concluding Remarks

Culture potentially extends biology insofar as the setting of development supports individuals' learning traditions, and occasionally learning behavioral variants of these traditions arising in other individuals that become established as new traditions. Behavioral traditions are learned in social settings, and the attentional and memorial processes that underlie that learning are themselves shaped by social partners. To date, our attention on socially aided learning, traditions, and cultures in nonhuman species has focused on the form and function of traditional behaviors (e.g., foraging skills, social interactional patterns). We argue that we need to include social influences on the learning process itself in the scope of cultural inquiry, as cross-cultural educational psychologists have argued (18). Improving our understanding of the psychological processes supporting socially biased learning, and thus the traditions that animals acquire, must be part of advancing theory in cultural evolution. Working memory and attention are one set of linked cognitive processes available for study with respect to how and when learning occurs, and how the social setting of development influences learning processes.

We have hypothetically linked temporal dynamics of social influence to sustained attention and working memory. These cognitive processes are fundamental to learning, including learning a traditional skill, cracking nuts with a stone hammer in the case of the young monkeys that we studied. We suggested that repeated experiences of performing challenging parts of the action cycle relating to cracking nuts could lead to extended sustained attention and working memory for these actions.

Iterative practice in socially supportive contexts such as we describe for bearded capuchin monkeys characterizes the learning context for culturally acquired instrumental skills in humans and other species (10). Suggestive examples of unlikely actions tightly synchronized with similar actions by another and of more gradual decline of more common actions after others have stopped the activity have been reported in apes. For example, a young chimpanzee, closely watching another chimpanzee cracking a nut with a stone, synchronously raised and lowered its arm (a "striking" action) while the other was striking (53), similar to what we observed with young capuchin monkeys striking nuts in the presence of others cracking nuts. Young orangutans follow peering at others at close range feeding or making nests with higher rates of exploratory actions with the food items handled by others or with nest materials over the next few minutes (54), exhibiting a temporal persistence of social influence on the order of what we report for capuchin monkeys manipulating nuts.

We further suggested that primates exhibit particular attentional biases toward actions with objects. This bias increases the likelihood that they learn about such actions from being with others in concert with practicing themselves. Attentional biases are likely to vary across taxa in accord with, for example, dominant modalities of communication and styles of foraging. Differences in where attentional biases impact learning processes could support taxonomic variation in the content of what the individual learns with others (e.g., songs in some species, food preferences and foraging techniques in other species). The eventual outcome of taxonomic variation in socially biased learning is that traditions develop in varied functional domains, and thus that culture is likely to extend biology in various taxa in different ways.

## Methods

**Study Site.** This study was conducted at Fazenda Boa Vista and adjacent lands in the southern Parnaíba Basin (9°39′S, 45°25′W) in Piauí, Brazil. Palms are abundant in the area, and many produce fruit at ground level. Two species of palm nuts in particular were commonly cracked by the monkeys in this study: tucum (*Astrocaryum campestre*) and piassava (*Orbygnia* spp.). A tucum nut is, on average, 46 mm in length, weighs 15.5 g, and has a 4.1-mm-thick shell, with a peak-force-at-failure of 5.6 kN. An average piassava nut is 61.3 mm long, weighs 50.6 g, and has a thicker and more resistant shell than a tucum nut: 6 mm with a peak-force-at-failure of 11.5 kN (55).

The naturally occurring stones used by the monkeys to crack nuts weigh, on average, 1.1 kg (range: 250 g to 2.5 kg) (56). They are quartz, quartzite,
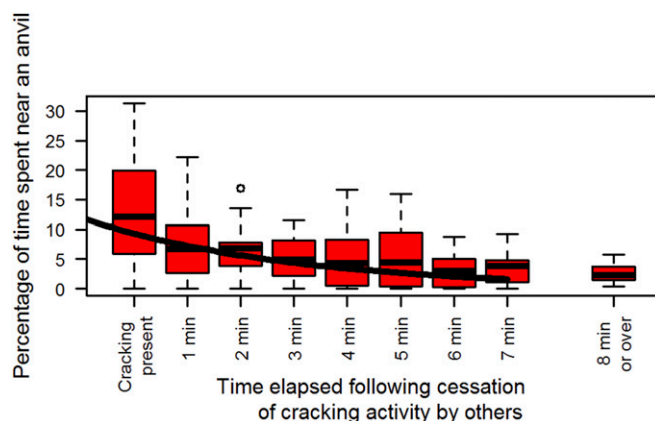


**Fig. 7.** Percentage of time spent within an arm's length of an anvil by young monkeys ($n = 16$) when one or more other monkeys struck nuts (Cracking present) during the 7 min after other monkeys stopped striking and in periods 8 min or longer after others stopped striking a nut (8 min or over). The boxes display the median and interquartile range, and whiskers indicate minimum and maximum values. The solid line depicts the median. The exponential curve generated by model fitting is overlaid. Circles indicate values of outliers. The half-life of the decline occurred at 2.8 min.

siltstone, or harder sandstone. The monkeys cracked nuts on naturally occurring anvils (boulders, exposed stone, or horizontal logs with a flat, or nearly flat, horizontal surface). Anvils are abundant in the region.

**Subjects.** At the beginning of the study, there were 11 immature monkeys in the group, aged from 3 mo to 4.5 y (Table 1). Five more infants were born during the study. At the beginning of the study, none of the subjects could crack open a whole nut of the more resistant palm species. The two oldest juveniles and, to some extent, two others mastered this skill during the study. Apart from the study subjects, the group included three adult males and five adult females. All but one female habitually cracked palm nuts. The body mass of each monkey was obtained as monkeys stood individually on a digital scale to drink from a bowl of water (57).

**Data Collection.** Data were collected in five discrete collection periods, each 6 to 9 wk, during three dry seasons (May–July) in 2011, 2012, and 2013 and two wet seasons (January–March) in 2012 and 2013. Observations were collected using two-person teams. One observer followed a focal subject to obtain a continuous record of its activities, including manipulation of nuts and other objects, and locations, specifically if the subject was near an anvil. Concurrently, the other member of the team recorded, as an instantaneous observation every minute, the identity, location, and activity of other monkeys within 10 m of the focal monkey. All observations lasted 20 min, or until the focal subject went out of view and could not be followed. Observations lasting <5 min were discarded.

Observers first learned to identify all members of the group and were subsequently trained in the method with one of the authors (Y.E.). Reliability for focal observations was calculated using Generalized Sequential Querier (GSEQ) software (www2.gsu.edu/~psyrab/gseq/index.html). We used the time unit method, which compares the codes inserted by two observers and defines as a match any instant in which both observers used the same code within a time window of 5 s. For each observer and trainer pair, time unit kappa was at or above 0.7, which is considered highly reliable (58). Reliability for instantaneous observations of other monkeys near the focal monkey was tested separately for each aspect (identity, distance to the focal monkey, activity, and location) until agreement (sum agreement/agreement plus disagreement) was over 80% for each variable for 20 consecutive samples.

The protocol was reviewed and approved by the Institutional Animal Care and Use Committee of the University of Georgia. The study adheres to the code of best practices for field primatology set by the International Primatological Society and all applicable Brazilian regulations for the conduct of field research.

**Data Analysis.** For each subject in each collection period, we collected between 19 and 53 observations, which lasted cumulatively between 5.3 and 27.1 h. Observations were collated by subject for each season. Ten subjects appeared in all five collection periods. Data were collected as the monkeys traveled throughout their home range. The observations were exported from The Observer to GSEQ software to extract the frequency of different events (e.g., manipulation of nuts) at times when others in the group cracked (struck) nuts and at times when they did not.

With respect to change in the young monkeys' activity following cessation of others' cracking, we used general mixed linear models to evaluate the differences in activity under different conditions and exponential models to evaluate the temporal pattern of the effects. SAS/STAT14.2 software was used for the analyses. We examined the rate of manipulation of nuts, manipulation of objects other than nuts, specific actions with nuts, and time spent near an anvil. The data are summarized in Dataset S1.

Our independent variables were the presence of nut-cracking activity (which involved striking nuts with stones) in the group (yes/no) and the time that had elapsed since this activity stopped (e.g., 0–1 min after the activity stopped, 1–2 min after the activity stopped, 2–3 min after the activity stopped). The dependent variables were (*i*) proportion of time the subject spent within an arm's length of an anvil, (*ii*) manipulation of nuts, (*iii*) manipulation of other objects, (*iv*) rate of percussing a nut directly on a surface, and (*v*) rate of striking a nut with a stone. "Total time" is defined as all seconds of observation under a specific condition of the independent variable. For example, the total time of "3 min after activity stopped" includes all observations from 120 to 180 s after all monkeys in the group stopped cracking nuts. Rates for

dependent variables in this period were calculated as the number of events divided by total observation time. The proportion of time near an anvil was calculated as the number of seconds spent there divided by total observation time. In the models, we treated the variables as count variables and used total time as an offset. For variables that did not distribute normally (tested with the Shapiro–Wilk test), the Poisson distribution was used. Subject identification was used as a random factor. Randomization of residuals was used to compensate for overdispersion.

We used the exponential model $A_t = A_0 * e^{-\beta t}$ to describe the dynamics of the dependent variables with time, where $t$ is the time since cracking in the group stopped and $A_t$ (the dependent variable) is the rate or percentage of time. The output from the model is $A_0$ (the strength of the effect on the dependent variable) and $\beta$, from which the half-life can be calculated as $\ln(2)/\beta$. For each variable, we examined the goodness of fit of our data to this exponential model and determined the estimates for $A_0$ and $\beta$, as well as the half-life of the effect. We used the values of the independent variables when monkeys were striking nuts in each of the 7 min after this activity stopped; at times, we also used the values of the independent variables when monkeys were striking nuts 8 min or longer after this activity stopped or during observation that did not include striking at all. Data from all observation periods were used in analyses, except that data from the two wet seasons on young monkeys' direct percussion of the nut and striking the nut with a stone were not used in analyses because these actions occurred very rarely in the data from these seasons.

We examined the effect of the onset of others' cracking by tabulating young monkeys' actions with nuts in the minute before others began cracking and in the 5 min following the onset of others' cracking. The data are presented in Dataset S2. We present these data descriptively. We used 11 monkeys' data for these tallies: 2-y-old, 3-y-old, and 4-y-old monkeys, which our previous analyses had indicated were affected more strongly by others' striking than younger or older immature monkeys.

At each data collection period, one-quarter to one-half of observations were collected while the monkeys visited an area (~30-m diameter) of their home range containing several large boulders, fallen logs, and areas of exposed stone that the monkeys habitually used as anvils to crack nuts. We use this area as our outdoor laboratory. Several hammer stones were present in this area, typically left by the monkeys on or near the anvils. Many other anvils with hammer stones were present within 200 m in the surrounding area. The monkeys were sometimes provisioned in the outdoor laboratory with nuts as part of ongoing experiments (59–62).

When in the outdoor laboratory, young monkeys had ample opportunity to spend time near anvils handling stones and nut shells independent of other monkeys' activity. The influence of others in the group cracking nuts in their vicinity on the rate of manipulating nuts and on proximity to anvils by our subjects in the outdoor laboratory is approximately the same (manipulation: $P = 0.0406$, estimate = 2.33; proximity to anvils: $P < 0.0001$, estimate = 8.4) as in the full sample collected over the entire home range (estimate = 1.98 for manipulation, estimate = 6.06 for proximity to anvil). Young monkeys approached anvils and handled nuts most often while adults were cracking nuts, although anvils were available, and nut shells and hammer stones were equally present and available, when others were not cracking. They showed the opposite pattern for manipulating other objects. We conclude that the fine temporal influence of others' nut-cracking on young monkeys' activity with nuts and presence near anvils reported here is not a byproduct of synchronized travel of a cohesive group.

1. Fragaszy DM, Perry S (2003) Towards a biology of traditions. *Traditions in Nonhuman Animals: Models and Evidence*, eds Fragaszy D, Perry S (Cambridge Univ Press, Cambridge, UK), pp 1–32.
2. Perry SE, Barrett BJ, Godoy I (2017) Older, sociable capuchins (*Cebus capucinus*) invent more social behaviors, but younger monkeys innovate more in other contexts. *Proc Natl Acad Sci USA*, 10.1073/pnas.1620739114.
3. West-Eberhard MJ (2003) *Developmental Plasticity and Evolution* (Oxford Univ Press, Oxford).
4. Laland KN, et al. (2015) The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proc Biol Sci* 282:20151019.
5. Fragaszy DM, Perry S (2003) *The Biology of Traditions: Models and Evidence* (Cambridge Univ Press, Cambridge, UK).

6. McGrew W (2004) *The Cultured Chimpanzee: Reflections on Cultural Primatology* (Cambridge Univ Press, Cambridge, UK).
7. Whitehead H, Rendell L (2015) *The Cultural Lives of Dolphins and Whales* (Univ of Chicago Press, Chicago).
8. Mesoudi A (2011) *Cultural Evolution* (Univ of Chicago Press, Chicago).
9. Mesoudi A (2017) Pursuing Darwin's curious parallel: Prospects for a science of cultural evolution. *Proc Natl Acad Sci USA*, 10.1073/pnas.1620741114.
10. Whiten A (2017) Culture extends the scope of evolutionary biology in the great apes. *Proc Natl Acad Sci USA*, 10.1073/pnas.1620733114.
11. van de Waal E, Bshary R, Whiten A (2014) Field experiments show wild vervet monkey infants acquire maternal food-processing techniques. *Anim Behav* 90:41–45.
12. Perry S (2011) Social traditions and social learning in capuchin monkeys (*Cebus*). *Philos Trans R Soc Lond B Biol Sci* 366:988–996.
13. Stout D, Hecht EE (2017) Evolutionary neuroscience of cumulative culture. *Proc Natl Acad Sci USA*, 10.1073/pnas.1620738114.
14. Lotem A, Halpern JY, Edelman S, Kolodny O (2017) The evolution of cognitive mechanisms in response to cultural innovations. *Proc Natl Acad Sci USA*, 10.1073/pnas.1620742114.
15. Jablonka E, Lamb M (2014) *Evolution in Four Dimensions* (MIT Press, Cambridge, MA), 2nd Ed.
16. Flynn EG, Laland KN, Kendal RL, Kendal JR (2013) Target article with commentaries: Developmental niche construction. *Dev Sci* 16:296–313.
17. Rogoff B (1991) *Apprenticeship in Thinking* (Oxford Univ Press, Oxford).
18. Li J (2012) *Cultural Foundations of Learning: East and West* (Cambridge Univ Press, Cambridge, UK).
19. Yates FA (1966) *The Art of Memory* (Chicago Univ Press, Chicago).
20. Carruthers P (2013) Evolution of working memory. *Proc Natl Acad Sci USA* 110:10371–10378.
21. Atkinson RC, Schiffrin RM (1968) Human memory: A proposed system and its control processes. *Psychol Learn Motiv* 2:89–195.
22. O'Connell RG, et al. (2008) Self-alert training: Volitional modulation of autonomic arousal improves sustained attention. *Neuropsychologia* 46:1379–1390.
23. Fragaszy DM, et al. (2013) The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. *Philos Trans R Soc Lond B Biol Sci* 368:20120410.
24. Thompson B, Kirby S, Smith K (2016) Culture shapes the evolution of cognition. *Proc Natl Acad Sci USA* 113:4530–4535.
25. Reynolds GD, Romano AC (2016) The development of attention systems and working memory in infancy. *Front Syst Neurosci* 10:15.
26. Pasternak T, Greenlee MW (2005) Working memory in primate sensory systems. *Nat Rev Neurosci* 6:97–107.
27. Yu C, Smith LB (2016) The social origins of sustained attention in one-year-old human infants. *Curr Biol* 26:1235–1240.
28. Fausey CM, Jayaraman S, Smith LB (2016) From faces to hands: Changing visual input in the first two years. *Cognition* 152:101–107.
29. Myowa-Yamakoshi M, Matsuzawa T (2000) Imitation of intentional manipulatory actions in chimpanzees (*Pan troglodytes*). *J Comp Psychol* 114:381–391.
30. Fragaszy DM, Deputte B, Cooper EJ, Colbert-White EN, Hémery C (2011) When and how well can human-socialized capuchins match actions demonstrated by a familiar human? *Am J Primatol* 73:643–654.
31. Rizzolatti G, Sinigaglia C (2008) *Mirrors in the Brain: How Our Minds Share Actions, Emotions and Experience* (Oxford Univ Press, Oxford).
32. Fragaszy DM, Crast J (2016) Functions of the hand in primates. *The Evolution of the Primate Hand, Perspectives from Anatomical, Developmental, Functional, and Paleontological Evidence*, eds Kivell T, Schmitt D, Lemelin P (Springer, New York), Vol 2, pp 313–344.
33. Davis RT (1974) Monkeys as perceivers. *Primate Behavior: Developments in Field and Laboratory Research*, ed Rosenblum L (Academic, New York), Vol 3.
34. Treves A (2000) Theory and method in studies of vigilance and aggregation. *Anim Behav* 60:711–722.
35. Heyes C (2012) What's social about social learning? *J Comp Psychol* 126:193–202.
36. Hoppitt W, Samson J, Laland KN, Thornton A (2012) Identification of learning mechanisms in a wild meerkat population. *PLoS One* 7:e42044.
37. Thornton A, Hodge S (2008) The development of foraging microhabitat preferences in meerkats. *Behav Ecol* 20:103–110.
38. Thornton A, McAuliffe K (2006) Teaching in wild meerkats. *Science* 313:227–229.
39. Visalberghi E, Fragaszy DM (2013) The EthoCebus project. Stone tool use by wild capuchin monkeys. *Tool Use in Animals. Cognition and Ecology*, eds Sanz C, Call J, Boesch C (Cambridge Univ Press, Cambridge, UK), pp 203–222.
40. Ferreira RG, et al. (2009) On the occurrence of *Cebus flavius* (Schreber 1774) in the Caatinga, and the use of semi-arid environments by *Cebus* species in the Brazilian state of Rio Grande do Norte. *Primates* 50:357–362.
41. Canale GR, Guidorizzi CE, Kierulff MC, Gatto CA (2009) First record of tool use by wild populations of the yellow-breasted capuchin monkey (*Cebus xanthosternos*) and new records for the bearded capuchin (*Cebus libidinosus*). *Am J Primatol* 71:366–372.
42. Falotico T, Ottoni E (2016) The manifold use of pounding stone tools by wild capuchin monkeys of Serra da Capivara National Park, Brazil. *Behav* 153:421–442.
43. Fragaszy DM, Visalberghi E, Fedigan L (2004) *The Complete Capuchin* (Cambridge Univ Press, Cambridge, UK).
44. Mangalam M, Izar P, Visalberghi E, Fragaszy DM (2016) Task-specific temporal organization of percussive movements in wild bearded capuchin monkeys. *Anim Behav* 114:129–137.
45. Stout D, Khreisheh N (2015) Skill learning and human brain evolution: An experimental approach. *Camb Archaeol J* 25:867–875.
46. Whiten A (2015) Experimental studies illuminate the cultural transmission of percussive technologies in *Homo* and *Pan*. *Philos Trans R Soc Lond B Biol Sci* 370:20140359.
47. de Resende BD, Ottoni EB, Fragaszy DM (2008) Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): A perception-action perspective. *Dev Sci* 11:828–840.
48. Eshchar Y, Izar P, Visalberghi E, Resende B, Fragaszy D (2016) When and where to practice: Social influences on the development of nut-cracking in bearded capuchins (*Sapajus libidinosus*). *Anim Cogn* 19:605–618.
49. Spagnoletti N, Visalberghi E, Ottoni E, Izar P, Fragaszy D (2011) Stone tool use by adult wild bearded capuchin monkeys (*Cebus libidinosus*). Frequency, efficiency and tool selectivity. *J Hum Evol* 61:97–107.
50. Verderane MP, Izar P, Visalberghi E, Fragaszy DM (2013) Socioecology of wild bearded capuchin monkeys (*Sapajus libidinosus*): An analysis of social relationships among female primates that use tools in feeding. *Behaviour* 150:659–689.
51. Howard AM, Nibbelink N, Bernardes S, Fragaszy DM, Madden M (2015) Remote sensing and habitat mapping for (*Sapajus libidinosus*): Landscapes for the use of stone tools. *J Appl Remote Sens* 9:096020–096020.
52. Holzhaider J, Hunt G, Gray D (2010) The development of pandanus tool manufacture in wild New Caledonian crows. *Behaviour* 147:553–586.
53. Fuhrmann D, Ravignani A, Marshall-Pescini S, Whiten A (2014) Synchrony and motor mimicking in chimpanzee observational learning. *Sci Rep* 4:5283.
54. Schuppli C, et al. (2016) Observational social learning and socially induced practice of routine skills in immature wild orangutans. *Anim Behav* 119:87–98.
55. Visalberghi E, et al. (2008) Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *Am J Primatol* 70:884–891.
56. Visalberghi E, et al. (2007) Characteristics of hammer stones and anvils used by wild bearded capuchin monkeys (*Cebus libidinosus*) to crack open palm nuts. *Am J Phys Anthropol* 132:426–444.
57. Fragaszy DM, et al. (2016) Body mass in wild bearded capuchins, (*Sapajus libidinosus*): Ontogeny and sexual dimorphism. *Am J Primatol* 78:389–484.
58. Bakeman R, Deckner DF, Quera V (2005) Analysis of behavioral streams. *Handbook of Research Methods in Developmental Science*, ed Teti DM (Wiley, New York), pp 394–420.
59. Massaro L, Liu Q, Visalberghi E, Fragaszy D (2012) Wild bearded capuchin (*Sapajus libidinosus*) select hammer tools on the basis of both stone mass and distance from the anvil. *Anim Cogn* 15:1065–1074.
60. Fragaszy DM, Liu Q, Wright BW, Allen A, Brown CW (2013) Wild bearded capuchin monkeys (*Sapajus libidinosus*) strategically place nuts in a stable position during nut-cracking. *PLoS One* 8:E56182.
61. Hanna JB, et al. (2015) Kinetics of bipedal locomotion during load carrying in capuchin monkeys. *J Hum Evol* 85:149–156.
62. Liu Q, Fragaszy DM, Visalberghi E (2016) Wild capuchin monkeys spontaneously adjust actions when using hammer stones of different mass to crack nuts of different resistance. *Am J Phys Anthropol* 161:53–61, 1.