WHAT CHALLENGES WILD BEARDED CAPUCHIN MONKEYS (*SAPAJUS LIBIDINOSUS*) IN LEARNING TO CRACK NUTS?

by

NALINA AIEMPICHITKIJKARN

(Under the Direction of Dorothy M. Fragaszy)

ABSTRACT

Young capuchins handle stones and hard-to-access foods for several years until they reach full efficiency at cracking foods with stone hammers. Eight juveniles and seven adult bearded capuchins were followed in three periods from 2011-2013 focusing on their manipulative behavior. I categorized individuals in each collection period into three expertise classes: novice, intermediate and expert. Our results described how manipulative behaviors changed relating to three hypotheses: a) monkeys crack nuts when they are large enough (size driven), b) monkeys initially explore objects and what they can do with them using species-typical actions, and nut-cracking follows a period of learning through practice and exploration (action-perception) and c) monkeys begin to crack nuts using a tool when they reach the necessary cognitive status to understand means-ends relations involved in using a tool (Piagetian). I suggest that consistently positioning the nut is a key feature predicting efficient nut-cracking in young capuchins.

INDEX WORDS: tool use; development; skill acquisition; positioning; action-perception; Piagetian

WHAT CHALLENGES WILD BEARDED CAPUCHIN MONKEYS (*SAPAJUS LIBIDINOSUS*) IN LEARNING TO CRACK NUTS?

by

NALINA AIEMPICHITKIJKARN

BSc, Chulalongkorn University, Thailand, 2014

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2017

WHAT CHALLENGES WILD BEARDED CAPUCHIN MONKEYS (*SAPAJUS LIBIDINOSUS*) IN LEARNING TO CRACK NUTS?

by

NALINA AIEMPICHITKIJKARN

Major Professor: Dorothy M. Fragaszy
Committee: Janet E. Frick
Jaxk Reeves

Electronic Version Approved:

Suzanne Barbour
Dean of the Graduate School
The University of Georgia
August 2017

ACKNOWLEDGEMENTS

Field research for this project was funded by a National Geographic Society Grant CRE 8936-11, a CURO Summer Research Fellowships awarded by the University of Georgia to A. Popp and N. Schwob and Development and Promotion of Science and Technology Talents Project (Royal Government of Thailand scholarship) to me. I would also like to thank my Thesis Advisory Committee, Prof Jaxk Reeves and Prof Janet Frick for their time and support.

For professional guidance, I give special thanks to my advisor, Prof Dorothy Fragaszy, for her critical advice throughout. Thank you to Yonat Eshchar for her wonderful data collection and productive advice. I would like to thank the Statistic Consulting center for helping me on data analysis. Lastly, thank you to EthoCebus colleagues and Oliveira family who helped collect the data and who provided the permission to work on their land.

TABLE OF CONTENTS

LIST OF TABLES

Page

LIST OF FIGURES

CHAPTER 1

INTRODUCTION AND LITERARY REVIEW

Human routinely use objects to augment the functional capabilities of their bodies. For instance, a person using bare limbs alone could not open some encased foods, such as hard nuts. Using a hammer, humans can achieve strikes of greater kinetic energy than they can achieve with hands alone, and at the same time protect the hands from damage. Tools are a universal feature of human behaviour, but individuals of many other species, including elephants, sea otters, birds and other primates, also use tools (Chevalier-Skolnikoff & Liska, 1993; Fujii, Ralls, & Tinker, 2015; Hunt, 1996; Mosley & Haslam, 2016). Psychologists and anthropologists have studied tool use behavior most extensively in non-human primates, with the aim of understanding cognitive and cultural foundations of tool use in humans. The study reported here addresses the development of tool use in wild bearded capuchin monkeys (*Sapajus libidinosus*).

Tool use in primates

Stone tool-use in non-human primates garners specific attention because of its relevance to early hominid stone-use, which is considered to be a precursor of modern technology (Proffitt et al., 2016). Stone tool use is found amongst only three taxa of non-human primates spread across South America, Africa, and Asia: robust capuchins (*Sapajus* spp.), chimpanzees (*Pan troglodytes*), and long-tailed macaques (*Macaca fascicularis*) (Fragaszy, Izar, Visalberghi, Ottoni, & De Oliveira, 2004; Goodall, 1964; Haslam et al., 2009; Malaivijitnond et al., 2007).

In primates, tool use appears relatively late in development (months to years after weaning) although precursors of the effective actions are present before weaning (Fragaszy et al., 2013; Tan, 2017). It requires a long developmental process to reach adult proficiency. The development of nut-cracking by young chimpanzees (*Pan troglodytes*) in Bossou, Guinea was described by Inoue-Nakamura & Matsuzawa (1997). This behavior starts with simple manipulations of a single object at 3-4 month of age, followed by manipulations combining stones and nuts or stones and surfaces at 12-17 month olds. Percussion is the latest-appearing action element, appearing at about 18 months old. Young chimpanzees were first observed succeeding at cracking nuts at 30-42 months old (Brakke, 1989; Inoue-Nakamura & Matsuzawa, 1997).

To achieve the goal of cracking a nut, the necessary kinetic energy should be produced when striking the nut. Body mass is one of the factors that affects the kinetic energy with which the individual can strike the nut (Visalberghi, Sirianni, Fragaszy, & Boesch, 2015). Adult chimpanzees in Taï used stone hammers (5.4 kg average) to crack Panda nuts to get the kernels (Boesch & Boesch, 1984; Visalberghi et al., 2015). Even though the body mass of this wild population has never been measured, body mass of wild adult chimpanzees at Gombe is 39 kg for males and 31.3 kg for female (Pusey, Oehlert, Williams, & Goodall, 2005). Thus, we estimate that hammer stones used by the chimpanzees in Taï constitute around 14-17% of adult body mass.

A similar timeline for development of nut cracking can be observed in capuchin monkeys. Resende, Ottoni and Fragaszy (2008) studied the ontogeny of stone tool use behaviour in a semi-free group of *Sapajus* spp. in Tiête Ecological Park, São Paulo, Brazil. Single manipulations appeared first around 2-3 months of age, following by combinatory actions with two objects (hitting one object with another) at 4-8 months old. Unlike the chimpanzees, young capuchins began to percuss nuts or stones as early as 6-12 months old. The last element in the nut-cracking sequence to appear in capuchins was placing the nut on an anvil surface, and releasing it, leaving it on the anvil (termed "positioning"), which appeared at 19-26 months of age. Individuals' first success in cracking came 1-6 months after "positioning" appeared.

Similar tool-using behavior has been found in wild bearded capuchins (*Sapajus libidinosus*) across semi-arid Caatinga and Caatinga–Cerrado transitional environments of northeastern Brazil (Mendes et al., 2015). The systematic records of body mass collected at one site called Fazenda Boa Vista revealed how proportionally heavy the stones are that the capuchins transport to anvils and lift to crack nuts. Body mass of capuchins at Fazenda Boa Vista ranges from 3.3 - 4.4 kg in adult males and from 1.9 -2.2 kg in adult females (Fragaszy et al., 2016). They normally use hammers weighing on average slightly more than 1 kg, or 25–40% of the average adult body mass; the heaviest hammer found in the study site weighed 2.5 kg, which adult females will sometimes use (Liu et al. 2016).

Long-tailed macaques are the most recently studied primates that habitually use stone tools. Macaques in the "fascicularis" group of macaques (including Japanese; *M. fuscata*, long-tailed; *M. fascicularis*, and rhesus; *M. mulatta*) are often seen handling stones habitually (Li et al., 2009; Nahallage & Huffman, 2008). However, while adult Japanese and rhesus macaques can develop dexterous stone handling patterns (Leca, Gunst, & Huffman, 2008; Nahallage & Huffman, 2012), only some populations of long-tailed macaques develop stone-tool use (Gumert et al., in prep). Unlike capuchins and chimpanzees, that use stone tools in forest environments exclusively on plants, long-tailed macaques mainly crack sessile shellfish in coastal environments, and sometimes sea almonds (the fruit of a coastal-living tree) (Gumert, Hoong, &

Malaivijitnond, 2011; Gumert & Malaivijitnond, 2012). In Gumert et al.'s studies, the macaques used two main types of stone tool, based on the kinds of encased food they were processing. Hand-sized axe hammers were used to pick or chip at oysters attached to boulders or trees, and larger pounding hammers were used to crush sea almonds and unattached shellfish on anvils.

In Khao Sam Roi Yot National Park, Thailand, infant long-tailed macaques begin manipulating single objects at around 1–2 months of age, combining objects from around 6 months old, and begin to crack foods open from 2.5-3.5 years old. The major challenges for long-tailed macaques in learning to crack foods are producing the right order and mastering effective percussion (Tan, 2017).

In Laem Son National Park, macaques use stones up to 3.1 kg. The average weight of an axe hammer was around 87 g, and the average weight of a pounding hammer was around 460 g (Falótico et al., 2017; Gumert, Kluck, & Malaivijitnond, 2009). The body mass of individuals in this population is unknown, but Indochinese long-tailed macaques weigh, on average, 6.83 kg for males and 4.87 kg for females (Hamada, San, & Malaivijitnond, 2016). Therefore, we estimate that axe hammer stones weigh 1- 2 % and pounding hammers weigh 7 - 9% of adult body mass.

Stone tool-use appears facilitated by a propensity for stone manipulation (Tan, 2017). More generally, object manipulation is considered to be one important precursor of tool use (Hayashi, 2015). Repeated exploration allows young individuals to learn the properties of objects, how to relate them to other objects, and the actions that can be performed on them (Myowa-Yamakoshi & Yamakoshi, 2011; Lockman 2000). All three species of nonhuman primates that use stone tools share the basic pattern starting with a dominance of single-object manipulation, then increasingly using combinatory actions, until finally opening an encased food. However, the latest-appearing element in the sequence of actions needed to crack a food item with a stone differs across the species, suggesting that each species arrives at mastery of the problem in a different way.

Developmental theories applied to Tool use

Primates learn to use tools, but exactly how they do so is still debated. Köhler (1925) proposed that learning could occur through insight rather than gradual shaping of behavior by interaction with the environment. He observed one captive chimpanzee solve the problem of retrieving out-of-reach food hung overhead by stacking boxes, so that it could climb up to get the food. In another study, the same chimpanzee that solved the stacked boxes task used different tools sequentially. He used a smaller stick to obtain another longer stick, which he subsequently used to obtain an out-of-reach fruit. In both situations (the stacking problem and the stick-tool problem) there was a period when the animal acted incorrectly, followed by the right action. Köhler summarized that the chimpanzee solved the problems through insight, not trial and error, in line with the Gestalt school of Psychology (Pearce, 2013; Shettleworth, 2012). However, Köhler's interpretations have been questioned because he studied a small number of participants and his experiments had limited control (Birch, 1945; Schiller, 1952). For example, all the apes in his studies were exposed to boxes and sticks prior to his experiments, so that he could not evaluate the effect of prior experience.

Several studies show that previous experience with objects plays an important role in the subsequent appearance of tool use. Birch (1945) tested chimpanzees with a hoe-like tool and food placed out of reach. The chimpanzees who had played with sticks solved the problem by using the stick as the extension of their arms right away, while the others solved it after accidentally causing the stick to move the food. Klüver (1933) presented reaching tasks to a capuchin monkey. The capuchin used a stick to knock down food out of reach. In some case, he even stood on the box to use a stick to reach the food, which could be considered a kind of composite tool use. In Klüver's view, the animal first confronted with a stick and inaccessible food does not perceive a Gestalt, but recognizes a functional relation between its arm, the stick, and the food, and this recognition depends on learning.

Theoretical developments in psychology in the century following Köhler's work have provided alternative explanations for the ontogenetic origins of tool use. In developmental psychology, tool use has usually been presented as indicating that the child understands relations between objects in space and time and how they may be combined to achieve a goal (Kahrs & Lockman, 2014). Piagetian theory offers one perspective on how this understanding develops. The Piagetian perspective posits that the ability to use objects as tools changes in accordance with the organization of behavioral interactions with objects more generally, such as understanding means-ends relations (Case, 1992; Willatts, 1984).

Piaget posited that cognitive development of an individual progresses through a series of discontinuous stages, the first one of which is called the "sensorimotor" stage. In the sensorimotor period, infants bring arms and hands under control and begin to explore the physical world and the actions they can perform in the world. Piaget recognized six distinct substages in the sensorimotor stage. The sensorimotor stage ends, according to Piaget, when the child reaches a different understanding of the world involving reasoning about future events and causal relations, which involve mental representations of objects and actions. The transition to the Concrete operational stage typically occurs at about two years of age, in concert with the onset of language and the use of symbols in other forms (Case, 1992; Siegler, 1991).

Piaget's model of sensorimotor development in humans has been used to guide studies of object manipulation in other primates (Bjorklund & Blasi, 2011; Parker & McKinney, 2012). Some of these studies have been developmental, although the theory is also used descriptively to compare the behavior of adults of other species with human children (e.g., many studies about "object permanence", or memory for a recently-viewed event) (Antinucci, 1989; Blois, 1997; Crystal, 2011; Wood, Moriarty, Gardner, & Gardner, 1980). I focus here on developmental studies using a Piagetian perspective. Various publications reported that great apes develop through the same sensorimotor sequence as human infants, although the social components of the sensorimotor stage in human infants (such as triadic interactions with objects) are essentially absent in apes (Suzanne Chevalier-Skolnikoff, 1983; Potì & Spinozzi, 1994). A cross sectional study with young orangutans (*Pongo pygmaeus*) showed that infants displayed more single object manipulation while juveniles displayed a higher proportion of goal-directed action (Bard, 1995). Natale (1989) reported that young capuchins and long-tailed macaques primarily performed holding and mouthing, which are characteristic of the first substage of sensorimotor development in humans.

According to Piaget, the development of using hand tools should follow the more general developmental sequence of instrumental actions in the sensorimotor stage. Applied to non-human primates learning to crack nuts, actions in nut-cracking would change in accordance with a general developmental change in cognition rather than through learning by discovery. Thus, monkeys would eventually crack nuts only when they reach a particular stage of cognitive development.

Siegler and others challenged Piaget’s stage model of sensorimotor development by claiming that developmental change is more gradual and more variable than Piaget had suggested (Munakata, McClelland, Johnson, & Siegler, 1997; Steinberg, Vandell, & Bornstein, 2010). Siegler's "multiple waves" model suggests that children at a given point in time can vary their approach to a problem, trying a variety of solutions (Chen & Siegler, 2000). Applying Siegler's model to nonhuman primates, monkeys would gradually begin to crack nuts as they grow up. Rather than organizing their behavior with stones and nuts in terms of their understanding of means-ends relations, individual monkeys would explore a variety of strategies to open a nut and gradually narrow them over time to the most effective actions.

Siegler's multiple waves model is compatible with action-perception theory, which suggests that development of tool use is rooted in species-typical perception-action routines. The approach originally was applied to understanding the development of tool use in human children (Lockman, 2000). Rather than ascribing tool use to specific cognitive functioning, a perception-action perspective suggests a common process of affordance learning underlies these adaptive behaviors. Individuals explore producing relations among objects and surfaces and the affordances of such relations (Resende, Ottoni, & Fragaszy, 2008; Fragaszy & Cummins-Sebree, 2005). Through these actions, individuals learn how they can use an object to reach a goal (Gibson, 1986). Thus, the novice who has just begun to perform a certain task should perform differently from the experts - with less fluidity, less competence, and/or more effort. For example, the task is to put the nail into the wall, and there is a hammer nearby. The actor must position the nail on the wall with one hand, pick up the hammer with the other hand, and strike the nail. The expert drives in the nail with one or two quick strikes. The novice may strike at an angle and hit his/her fingers, not strike the nail hard enough or strike too hard, bending the nail, or lose his/her grip on the hammer at impact with the nail.

Using perception-action routines to explore affordances and to practice new variations of familiar routines (e.g., in nut-cracking, striking with more or less force or using a hammer of a different shape or mass) leads to perceptual learning. Behavioral variation, identified by some as "trial and error", is part of perceptual learning and exploration, rather than indicating an absence of insight or representational thinking (Kahrs & Lockman, 2008).

If the individual learns to use an object as a tool through perceptual learning, efficiency should increase with practice. This can be manifest as an increasing proportion of more effective actions and decreasing proportion of less efficient actions. Data supporting this prediction have been presented for all the species of primates that use tools in percussion. Kahrs, Jung, & Lockman (2013) tracked motor actions of infant humans between 6-15 months old. They report that banging changes from an inefficient and variable motor behavior to an efficient and highly consistent one. The older infants eliminated unnecessary hand movements and moved their hands smoothly to accomplish the task (Kahrs & Lockman, 2014). Juvenile capuchins used a variety of manipulations before adopting the more efficient strategy for nut-cracking as they grew up, and the rate of ineffective actions decreased when they concentrated on producing the correct order consistently (Resende, Nagy-Reis, Lacerda, Pagnotta, & Savalli, 2014). Infant chimpanzees showed more variability in actions than adults, including some actions which were not efficient. Inessential actions declined quickly and were not seen after 3.5 years, while essential actions found in the adult repertoire increased with age (Biro, Sousa, & Matsuzawa, 2006)

Study species

Capuchins are long-lived and develop slowly. Bearded capuchins reach one kilogram at around 1.1 years; after that their growth rate slows significantly until they reach full body mass at 7.5 years in females (2.1 kg) and 9.8 years in males (3.5 kg) (Fragaszy et al., 2016). Capuchins have proportionally large brains in relation to body size, and proportionally large cortices, among primates, and generally excel at cognitive tasks (Amici, Aureli, & Call, 2010; Rilling & Insel, 1999; Stephan, Baron, & Frahm, 1988; Visalberghi, 1997). Capuchins are extractive foragers; their diet includes hard-to-access or hard-to-process food (Fragaszy, Visalberghi, & Fedigan, 2004). They produce a great variety of explorative and manipulative behaviors, especially in percussive activity (Adams-Curtis & Fragaszy, 1994).

We followed wild bearded capuchin monkeys, *S. libidinosus*, that use stone tools to crack palm nuts to obtain the kernel (Fragaszy et al., 2004). Among adults, the number of strikes needed to crack open a nut is correlated with body mass (Fragaszy et al., 2010). Heavier monkeys are more efficient than smaller ones at cracking highly resistant nuts, and they need fewer strikes to crack a nut (Fragaszy et al., 2010; Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011). Their persistence and interest in object manipulation are characteristics relevant to tool use (Resende et al., 2014).

The current study

In this paper, we focused on the manipulative behavior during nut cracking sequences of wild bearded capuchin of various ages and skills. Data were procured from an archive in the study by Eshchar, Izar, Visalberghi, Resende, & Fragaszy, 2016 and focused only on cracking bouts. We aimed to evaluate the explanatory value of three (not mutually exclusive) hypotheses about the development of tool use. We analyzed how manipulative behavior changed from the time juveniles started performing strikes with a stone on a nut, to the point when they could crack nuts, until they reached full efficiency with these predictions.

1. Size-driven: the body mass predicts the ability to crack nuts.
2. Perception/action:

   2.1 Rate of manipulative actions should be different among novice, intermediate and expert tool users. The inefficient actions should be most common in novices, while the efficient actions should be most common in expert tool users.

   2.2 Variability in manipulative behaviors should be greatest in novices and least in expert tool users.
3. Piagetian perspective:

   3.1 A discrete pattern of actions is associated with discrete stages in ability to crack nuts.

   3.2 Any specific manipulation action alone will not predict the cracking outcome.

CHAPTER 2

METHODS

Study site

Our site is located on privately owned land called Fazenda Boa Vista (hereafter, FBV) in the state of Piauí, Brazil (9°39’ S, 45°25’ W). FBV is a flat open woodland at approximately 420 m above sea level, with sandstone ridges, pinnacles, and steep mesas. FBV is in the ecotone between open woodland and semi-arid biomes. The climate in the region is seasonally dry with strong inter-annual variability in precipitation, between 800 and 1600 mm per year (Oliveira & Marquis, 2002).

Capuchins in this study population habitually use heavy hammer stones to crack the fruits (nuts) of Tucum (Astrocaryum spp.), Piassava (Orbignya sp.), and several other local species of palms. The stones used as hammers weigh an average of about 1kg (Visalberghi et al., 2007), and can reach 2kg (Spagnoletti et al., 2011). Cracking is performed on anvils composed of stone or wood (Fragaszy et al., 2004). Tucum is easier to crack with peak-force-at-failure of 5.57 kN compared to 11.5 kN for Piassava (Visalberghi et al., 2008).

Procedure

We followed one group of wild capuchin monkeys in FBV with a specific focus on the juveniles. Data were collected in three discrete collection periods from 2011-2013; each consisted of 6-9 weeks of observations in dry seasons. An observer followed one of the subjects to obtain a continuous focal record of the subject's location and activities for twenty minutes. All observers used hand-held devices with Pocket Observer© software by Noldus Information Technology. Inter-observer 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, & Quera, 2005)

From the corpus of data collected from focal observations, we isolated cracking bouts, defined as sequences of manipulative behavior which included at least one action of striking a nut with a stone. A bout began when the subject started manipulation, direct percussion or striking nuts with a stone and ended when the subject changed his or her behavioral state to either sitting, locomotion or social. Four hundred and fifty-seven cracking bouts from eight juveniles (Age: 1.32- 6.40 yr) and seven adults were collected. The cracking bouts included five manipulative actions (strike with stone, direct percussion, position, tap and other manipulations), two subsequences (nut fly and eat) and a binary outcome for the entire bout, whether the monkey cracked the nut in that bout (see Table 1).

------ Insert Table 1 here -------

We calculated for each variable the average value per subject per collection period. We transformed manipulative actions and outcomes to rate (the sum of the frequency count divided by the total duration of cracking bouts) per ten minutes and transformed the binary outcomes of cracking to the percentage of bouts in which the nut was cracked (*percent crack*).

We categorized monkeys in each data collection period into three classes based on *percent crack*:

Novice: percent success = 0. Four juveniles were in this class (n=5 data points, age: 1.3-4.5 yr);

Intermediate: percent success < 70 (range: 9-44%). Five juveniles were in this class (n=11 data points, age: 3.6-6.3 yr);

Expert: percent success >70 (range: 74-100%), one juvenile (age 4.5 yr) and seven adults were in this class.

------ Insert Tables 2 and 3 here -------

Body mass values used in this study were collected at annual intervals for several consecutive years (Fragaszy et al., 2016). A digital scale was mounted on the trunk of a tree with a water bowl in an area the monkeys visit regularly. We recorded the body mass of all recognized individuals from a digital display placed a few meters away when monkey remained stationary with four limbs on the scale.

Data analysis

Some individuals appeared in more than one data collection period as shown in *Table 2* and *Table 3*. Thus, our data points are not fully independent. However, we treated the data from each individual in different collection periods as independent for analytical purposes, so that the N for analysis exceeds the N of individuals in the study. We adopted this strategy because our N was very low and individuals varied from year to year. We observed that the rate per 10 minutes of our variables did not have individual consistency across years (see *Table 4*). For example, *Figure 7* shows that the rate of percussion scattered from one year to the next for the same individuals. Because we did not notice any pattern of longitudinal change, we determined it was reasonable to treat each data point in different collection periods as independent.

RStudio software was used to create graphs and run the statistics (R Core Team, 2015). Differences in manipulative actions and outcomes across skill classes were examined by box plot and one-way analyses of variance (ANOVAs) or Kruskal-Wallis test. Normally distributed variables, *position and eat,* were analyzed with ANOVAs. Post hoc pairwise comparisons were made between skill classes with Tukey HSD tests when the ANOVAs' results were significant. The remaining variables, which were not normally distributed, were analyzed with a Kruskal-Wallis test. We used a *Dunn* test from the *FSA* package (Ogle, 2012) for the post hoc analysis. To analyze variations of manipulative behaviors by skill class, we calculated the coefficient of variation (CV) for each variable. This measure was used for describing the variance in the context of a mean value. We used the global validation of linear models assumptions (*gvlma)* package for testing the four assumptions of the linear model, that are linearity, homoscedasticity, uncorrelatedness and normality (Pena & Slate, 2014). We created regression lines by using the visualization package called *ggplot2* (Wickham, 2009). We used the Pearson correlation coefficient to explore the association between pairs of variables. After we identified the variables that differentiated cracking skill, we conducted classification analysis to predict skill level based on those predictors.

CHAPTER 3

RESULTS

Size driven hypothesis

We analyzed if there was a relationship between body mass and percentage of bouts ending with cracking. Body mass is positively related to the percentage of bouts ending with cracking (r_{xy} (24)= 0.61, p = 0.0014). We also found significant correlations between body mass and other variables, including direct percussion (r_{xy} (24) = -0.57, p = 0.0036) and position (r_{xy} (24) = 0.49, p = 0.0159), but not strike with stone, tap nor other manipulations (p = 0.9569, 0.9682, 0.1743 respectively).

Perception/Action hypothesis

We looked at the rate of manipulating actions and outcomes by skill classes. As shown in *Figure 1*, the rate of direct percussion dramatically decreased from *Novice* to *Intermediate,* then decreased moderately in *Expert* classes. In contrast, the rate of position increased moderately from *Novice* to *Intermediate* and dramatically increased to *Expert*.

------ Insert Figure 1 here -------

There was a significant effect of skill class on the rate of position at the $p<.05$ level [F(2, 21) = 14.69, p = 0.0001, ηp^2 = 0.583]. Post hoc comparisons using the Tukey HSD test indicated that the mean rate per 10 minutes for the *Expert* (M = 34.33, SD = 6.67) was significantly higher than the *Intermediate* (M = 21.07, SD = 8.83). The *Intermediate* was also significantly higher than the *Novice* (M = 9.01, SD = 9.63). We also found a significant effect of skill class on the mean rate per 10 minutes of eating [$F(2, 21) = 4.05$, $p = 0.0325$, $\eta p^2 = 0.278$]. However, only the mean rate in *Expert* (M = 11.06, SD = 3.98) was significantly higher than those in *Intermediate* (M = 5.65, SD = 5.61). There was a significant difference between each skill class in rate of direct percussion ($H(2) = 19.99$, $p < 0.001$). The mean scores of strike with stone, tap, other manipulations and nut fly in the three skill classes were not found to be significantly different (p=0.3507, 0.5168, 0.2587 and 0.2174 respectively).

We investigated the CV of manipulating actions and found that they varied among skill classes and manipulation actions. As shown in *Figure 2*, we noticed a reducing trend in position, that is, maximum in *Novice* (CV=109.29) that decreased in *Intermediate* (CV=84.44) and *Expert* (CV=74.85) respectively. *Figure 3* shows the proportion of each action for each subject in each skill class arranged from the lowest percent success on the left to the highest percent success on the right.

------ Insert Figure 2 and 3 here -------

Piagetian perspective

According to *Table 2*, we could roughly draw a line to separate skill class based on ages. The monkeys were able to crack their first nuts around three years old and became proficient around six years old. However, there were delayed learners, such as Passoca, who still could not crack nuts at four years of age, or fast learners, such as Tomate, who could successfully crack more than 70% at age five.

A linear model was created to predict the percentage of cracking based on each manipulative action. We performed a single global test to assess the linear model assumptions, and performed specific directional tests designed to detect skewness, kurtosis, nonlinearity, and heteroscedasticity using the *gvlma* package (Pena and Slate, 2014). Only the model using *position* to predict *percent crack* met all assumptions. A significant regression equation was found ($F(1,22)=26.73$, $p<0.001$), with an R^2 of 0.54. The percentage of strikes resulting in a crack increased for each 0.02 position in 10 minutes (see *Figure 4*).

------ Insert Figure 4 here -------

Our results suggested that position is an important action associated with cracking. However, it could be that position is associated with body mass, which is also correlated with tool use expertise. We use the Spearman's rank method to find the correlation between *position* and *body mass*. We found positive correlations between *position* and *body mass* ($r_s = 0.61$, $p = 0.0017$).

------ Insert Figure 5 here -------

For the further analysis, we conducted the classification analysis using *Body mass* and *Position Rate* as the predictors. In classification analysis, one partitions objects into different groups according to specified predictors with a pre-defined number of groups. Here, we partition *skills* into three groups with *Body mass* and *Position Rate* as the predictors. Therefore, if we have the information of *Body mass* and *Position Rate* for a specific capuchin, we can predict which skill level it belongs to. Figure 6 shows the classification results, where the letters in gray indicates the wrong prediction. This indicates that there are only four wrong predictions over the 24 observations, so prediction accuracy rate is 83.3%.

------ Insert Figure 6 here -------

CHAPTER 4

DISCUSSION

We examined the ontogeny of percussive tool use in capuchins, comparing the explanatory power of three approaches to predict when a monkey would master cracking nuts using stone hammers: a) monkeys crack nuts when they are large enough (size driven), b) monkeys initially explore objects and what they can do with them using species-typical actions, and nut-cracking follows a period of learning through practice and exploration (action-perception) and c) monkeys begin to crack nuts using a tool when they reach the necessary cognitive status to understand means-ends relations involved in using a tool (Piagetian). These hypotheses are not mutually exclusive. To sum up, this study supported size driven, perception/action and, partly, the Piagetian perspective.

As in previous studies, body mass is an important factor for cracking nuts in capuchins at our site. This is related to the proportionally heavy mass of the stones used as hammers by the bearded capuchin monkeys are FBV, in line with the high resistance to fracture of nuts cracked by the monkeys at this site (Visalberghi et al., 2008). Monkeys prefer stones weighing more than a kilogram to crack a resistant palm nut (Liu, Fragaszy, & Visalberghi, 2016). As adult capuchins weigh 1.8 - 4.4 kg (Fragaszy et al., 2016), a stone of 1 kg corresponds to a quarter to more than a half of an adult's body mass. Other nonhuman primates cracking nuts with stones use proportionally lighter stones. We estimate that hammer stones used to crack the most resistant nut (*Panda oleosa*) by chimpanzees at Taï correspond to 14-17% of adult body mass (Boesch & Boesch, 1984; Pusey et al., 2005; Visalberghi et al., 2015). Long-tailed macaques also used relatively small stone, corresponding to 7-9% of body mass for pounding stone and only 1-2% for axe-hammering stone (calculated from; Gumert et al., 2009; Hamada et al., 2016)

Bogy mass alone is not enough to predict the capuchin monkeys' efficiency in cracking. One capuchin in this study that weighed 1.6 Kg did not crack any nuts, pointing that other elements are required. On the other hand, small female monkeys in this population can be very efficient, with no difference in percentage of nuts cracked than larger males (Fragaszy et al., 2010). Still, in general, larger monkeys can produce greater kinetic force at impact, and thus crack larger and/or more resistant nuts. We conclude that strength is a limiting factor for capuchins' nut cracking. Lifting the stones and using them with enough force to crack the nuts requires strength that small juveniles might not possess (Fragaszy et al., 2010; Liu et al., 2016).

Perception–action theory links manipulative development with the onset of tool-using. Tool users should channel their actions toward those that would result in opening up the nut. Variability and inefficient actions, such as direct percussion, should decline as capuchins mature. In contrast, effective actions for cracking should be used more frequently by the more experienced monkeys (Resende et al., 2014).

Even though a study of Jalles-Filho with six captive yellow-breasted capuchin monkeys (*Cebus xanthosternos*) reported no correlation between tool use and the frequency of manipulative events (Jalles-Filho & Grassetto, 2008), the effect of any particular manipulation might be concealed because they combined all manipulation as one variable. Our study found that the rate of position (putting the nut onto the anvil) and direct percussion (striking a nut on a surface) differed significantly among skill classes. In the other words, position predicts tool use, and direct percussion predicts its absence. Unlike chimpanzees where direct percussion of the nut on a surface appears last in the ontogeny of actions related to cracking nuts, the highest rate of direct percussion appears in the early stages of capuchin monkey's actions with nuts, and then declines, whereas positioning the nut tends to increase as the capuchins become more proficient at cracking nuts.

The magnitude of the coefficient of variability for most manipulative actions (strike with stone, direct percussion, tap, and other manipulations) was greatest in the Intermediate group, suggesting that animals in this skill class were exploring how to act with nuts more than the other skills classes. The magnitude of the coefficient of variation in positioning declined from Novice to Intermediate and from Intermediate to Expert group, indicating that the monkeys became more consistent in performing this action when they were able to crack nuts.

Positioning is a necessary manipulative action in nut-cracking. The rate of performing positioning differed among novice, intermediate and expert tool users, with lesser variation in capuchins that were more consistent in cracking nuts. We suggest that consistently positioning the nut is a key feature predicting efficient nut-cracking in young capuchins. This finding corresponds findings from a study with a semi-free ranging group of tufted capuchins (*Sapajus* spp.) (Resende et al., 2008). In that study, as in this one, the rate of positioning increased as the monkeys became more successful in using tools. Positioning required letting go of the object in order to perform the next step of striking with another object. According to a Piagetian perspective, this action involved reasoning about future events and causal relations, which appears after simpler holding and hitting, as per the scales of psychological development of Uzgiris and Hunt (1975; cited by Parker & McKinney, 2012). Our data supported this perspective by showing the highest rate of hitting and other manipulations in young Novice group, and highest rate of position in adult Expert group.

However, given that we also found a positive correlation between position and body mass (itself correlated with chronological age), and body mass is a strong predictor of efficiency

(Fragaszy et al., 2010), it is possible that positioning the nut is be a result of other developmental changes independent of nut-cracking activity. We cannot draw strong conclusions on this issue due to the confounding of body mass and age. Future studies could examine whether the behaviors associated with cracking change with age, independent of practice, or whether they change as a function of practice. These explanations cannot be distinguished in our study.

The study confirms that the manipulative behavior of young capuchins with stones and nuts differed in some features from what has been described for young chimpanzees. Specifically, capuchin monkeys percuss nuts directly on a surface early and often; they position nuts only after much experience with them. Chimpanzees place nuts on a substrate early and often, but only later begin to percuss the nut directly on an anvil. Humans are more similar to capuchins than to chimpanzees in this respect. Human infants start banging against a table with an object at around 7 months, and placing an object on a surface later, at around 10 months (Takeshita et al., 2005).

Capuchins, unlike humans, are arboreal, and releasing a nut might mean losing the nut. The act of positioning a nut challenges young capuchins to inhibit their strong inclination to hold onto the nut rather than place it on the anvil and let go of it. However, the placing action would not be a problem for chimpanzees, that spend more time on the ground than capuchins (Doran & Hunt, 1994; Fragaszy et al., 2004). Human infants place and release an object on a surface in their first year, and do so routinely thereafter (Vauclair & Bard, 1983). While capuchins of all ages commonly bang an object against a substrate (Fragaszy & Adams-Curtis, 1997), this action is uncommon in young chimpanzees (Takeshita et al., 2005). The last element of nut-cracking that chimpanzees master is to strike a stone on a surface. Thus, the most challenging task for chimpanzees was to percuss (Inoue-Nakamura & Matsuzawa, 1997; Takeshita et al., 2005). The same pattern appeared in long-tailed macaques, whose diets consist of food items that do not require percussive extraction. Even though the long-tailed macaque is an arboreal species, they have no trouble placing an object on an anvil, and placing actions are the first combinatory manipulations that macaque infants produce. However, percussive actions were the last to emerge in Tan's (2017) study. The relative challenge of placing a nut on an anvil, compared to the relative challenge of making a percussive action, appears to differ across species, and thus to influence the ontogeny of nut-cracking with a hammer. This may be one feature of percussive tool use that, if influenced by individual experience, varies across populations within species, as well as between species, in accordance with their degree of territoriality and diet.

In conclusion, this work explored the ontogeny of tool-related manipulations in capuchins. As capuchins lack language and do not teach one another, monkeys learn to use tools in other ways. This work shows that young monkeys learn to use tools through discovering and practicing effective positioning and percussive actions; that they must grow to a minimum body mass to use these actions effectively to crack nuts, and that placing and releasing the nut is infrequent when young monkeys have not yet begun to crack nuts, suggesting that this action demands attentional or movement control that develops more slowly than the other components of cracking nuts.

The confounding of age and body mass prevent us from making a strong conclusion about the relation of each of these factors and cracking skill in capuchin monkeys. Furthermore, we did not have enough cases of the same individuals with the same age and body mass, but different in cracking ability, to distinguish the power of specific manipulative behaviors to predict cracking ability. Thus, longitudinal development from the time the juvenile starts performing manipulations to the point of full efficiency should be investigated in future studies.

Eventually we may be able to identify what developmental variables predict variations in tool use performance in adulthood across individuals in the same population.

TABLES

Table 1 Ethogram of manipulative actions, outcomes and cracking results

Manipulative action	
Event	**Description**
Strike with stone	Subject strikes a nut with a stone. Recorded every time the stone hits the nut
Direct percussion	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
Position	Subject puts the nut down and leaves it before striking it
Tap	Subject uses fingertip to tap on rigid surface
Other manipulations	Subject picks up, rubs between the hands or the body, rolls on surface, or manipulates in hands in other ways (including hand/mouth actions). If done continuously, recorded every 3 seconds
Outcome	
Event	**Description**
Nut fly	Nut flies from the surface, usually as a result from striking with stone
Eat	Biting into a food item or putting it in the mouth, could happen from scrounging. If done continuously, recorded every 3 seconds
Cracking result	
Event	**Description**
Nut cracked	Nut shell is broken (determined by the observer hearing or seeing)

Table 2 Subjects and skill class.

The table shows subjects by age (on the top) and skill classes: N for Novice, I for Intermediate and E for Expert

Subject \ Age (yr)	1	2	3	4	5	6	Adult
Cachaca	N						
Thais	N						
Coco	N	N	I				
Doree			I	I	I		
Pati			I	I	I		
Passoca				N			
Tomate				I	E		
Catu				I	I	I	
Jatoba							E
Chuchu							E
Masinho							E
Dita							E
Piassava							E
Teimoso							E
Teninha							E

Table 3 Subjects, gender, skill class, age, body mass(kg) and duration of bouts (sec)
The shading shows skill classes: light for N(Novice), medium for I (Intermediate) and dark for E(Expert)

Subject	Gender	Skill class	Age (years)	Body Mass (kg)	Number of bouts	Total duration of bouts (sec)	Average bout (average duration per session)	% Cracked
Cachassa	M	N	1.3	0.4	4	338	84.5	0
Thais	F	N	1.4	1.1	3	61	20.3	0
Coco	M	N	2.0	1.1	11	1546	140.6	0
Coco	M	N	2.9	1.4	12	810	67.5	0
Coco	M	I	3.9	1.7	6	1638	273.0	17
Doree	F	I	3.6	1.4	12	3390	282.5	8
Doree	F	I	4.6	1.6	8	585	73.1	13
Doree	F	I	5.6	1.8	14	4785	341.8	29
Pati	M	I	3.6	1.7	40	6251	88.0	43
Pati	M	I	4.6	2.1	75	6598	156.3	36
Pati	M	I	5.7	2.5	9	4515	501.7	44
Passoca	F	N	4.5	1.6	3	449	149.7	0
Tomate	M	I	4.5	1.8	23	6031	262.2	13
Tomate	M	E	5.4	2.0	17	1325	77.9	100
Catu	M	I	4.4	1.8	18	2566	64.1	22
Catu	M	I	5.4	2.1	22	1411	142.6	9
Catu	M	I	6.4	2.5	3	734	244.7	33
Jatoba	M	E	A	4.1	50	3032	60.6	74
Chuchu	F	E	A	2.0	26	2148	82.6	81
Masinho	M	E	A	3.5	16	891	55.7	81
Dita	F	E	A	2.0	20	808	40.4	95
Piassava	F	E	A	1.9	27	2329	86.3	96
Teimoso	M	E	A	3.5	16	645	40.3	100
Teninha	F	E	A	2.0	22	1554	70.6	100

Table 4 Rate of actions and consequences per 10 minutes.
Any capuchin who is observed for two or three years are shaded in gray

Subject	Age	Skill	Strike with	Direct	Position	Tap	Other	Nut fly	Eat
Cachassa	1.32	N	15.98	21.3	0	1.78	19.53	0	12.43
Catu	4.37	I	63.13	25.49	25.95	1.87	13.09	0.94	3.51
Catu	5.41	I	55.71	4.25	23.81	0.43	19.56	0.43	14.46
Catu	6.4	I	54.77	1.63	31.88	0	15.53	1.63	2.45
Chuchu	A	E	32.4	0.28	32.68	1.68	14.53	0.84	6.98
Coco	1.97	N	39.2	26.39	7.37	1.55	22.9	0.78	6.21
Coco	2.93	N	34.81	7.41	16.3	0	28.15	2.22	9.63
Coco	3.92	I	32.97	14.65	10.62	0.37	12.09	0	2.93
Dita	A	E	77.97	0.74	44.55	0	26.73	0.74	15.59
Doree	3.61	I	70.62	13.98	19.47	0.88	13.98	0.35	3.01
Doree	4.61	I	51.28	2.05	31.79	0	31.79	0	9.23
Doree	5.64	I	28.34	1.63	14.67	0	9.78	1.25	1.88
Jatoba	A	E	42.94	0.2	26.12	0.99	15.44	0.59	13.06
Masinho	A	E	45.79	0	28.28	0.67	16.16	3.37	10.77
Passoca	4.52	N	24.05	9.35	21.38	0	10.69	0	0
Pati	3.64	I	52.79	11.33	12.77	1.15	23.9	0.77	7.29
Pati	4.64	I	57.47	3.91	33.1	0.45	25.19	0.73	10
Pati	5.66	I	24.85	1.86	18.6	0.4	7.84	0.4	5.05
Piassava	A	E	70.33	0.26	43.02	3.09	17.52	0.77	7.73
Teimoso	A	E	55.81	0.93	29.77	1.86	20.47	0	17.67
Teninha	A	E	57.14	0	33.98	0	22.39	4.63	8.49
Thais	1.37	N	118.03	39.34	0	0	49.18	0	0
Tomate	4.48	I	33.03	31.44	9.05	2.29	13.23	0.4	2.39
Tomate	5.4	E	43.02	0.45	36.23	0.91	21.28	1.81	8.15

FIGURES

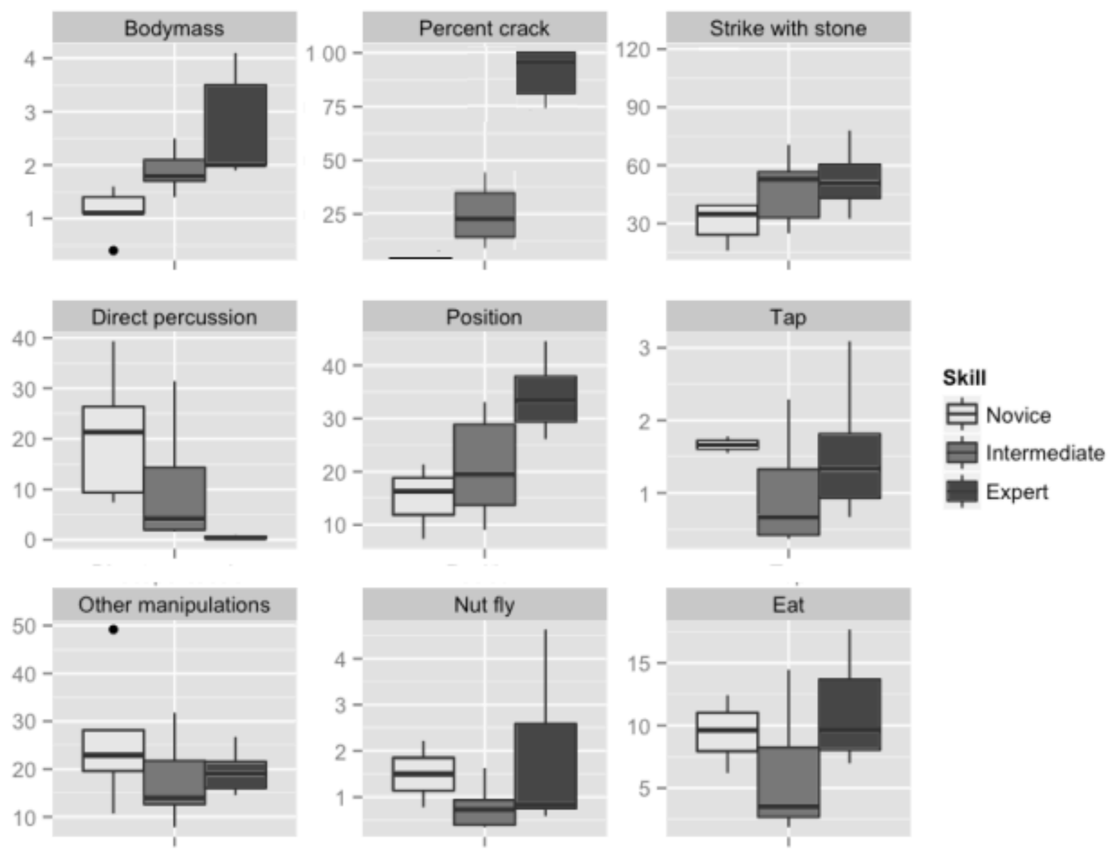

Figure 1 Boxplots showing body mass (kg), percent crack, and the rate per 10 min of all variables across skill classes

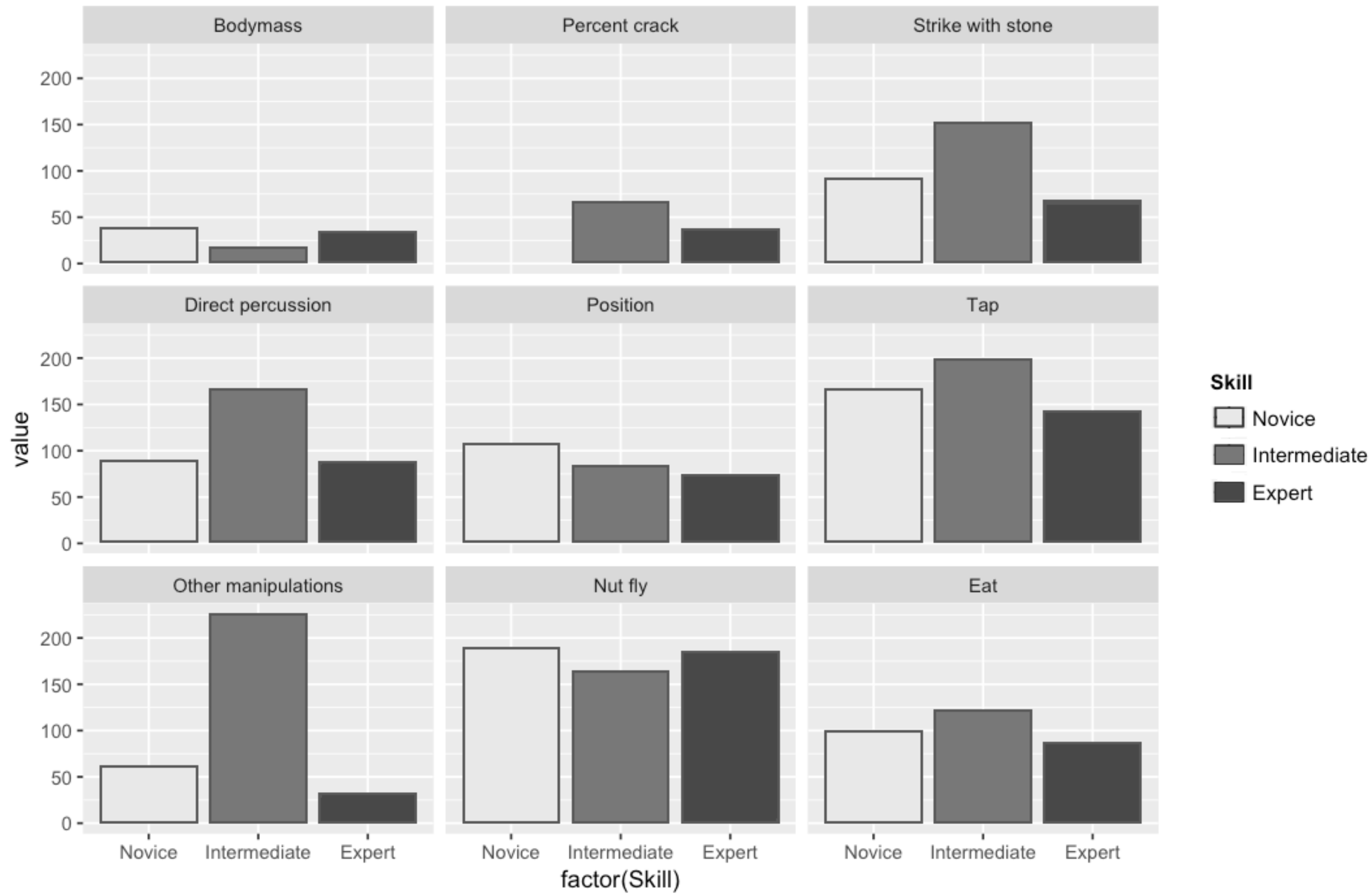

Figure 2 Bar graphs showing the coefficient of variation of manipulating actions among skill classes

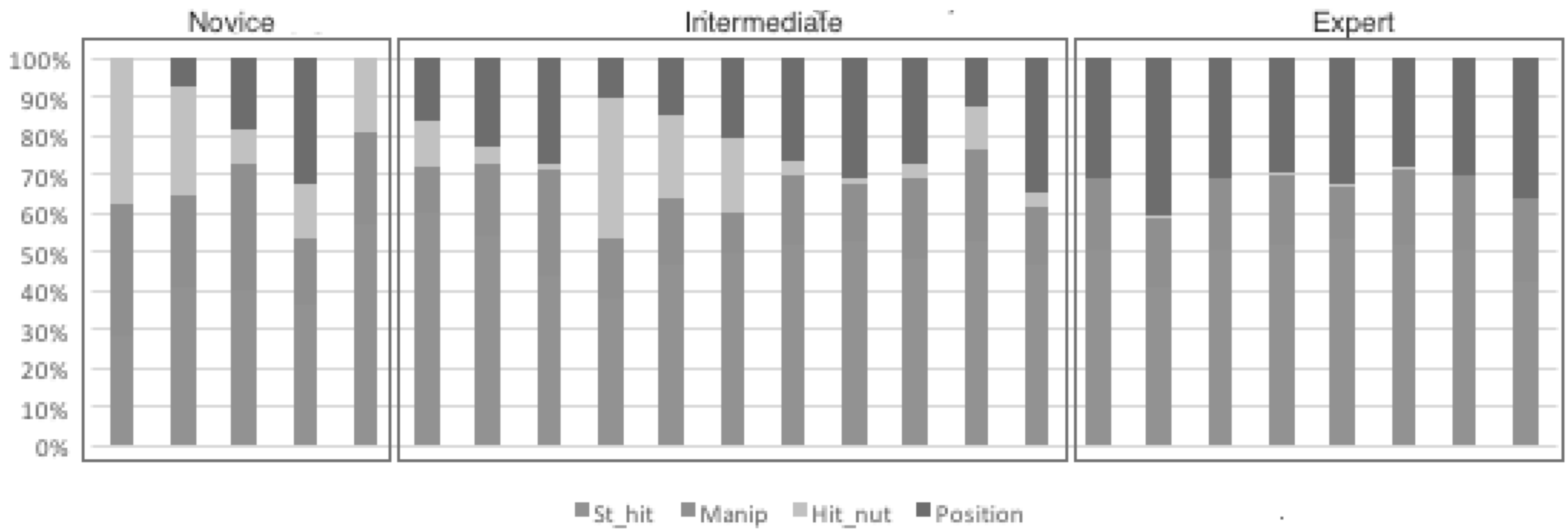

Figure 3 Bar graphs showing the proportion of each action for each subject in each skill class arranged from the lowest percent success on the left to the highest percent success on the right.

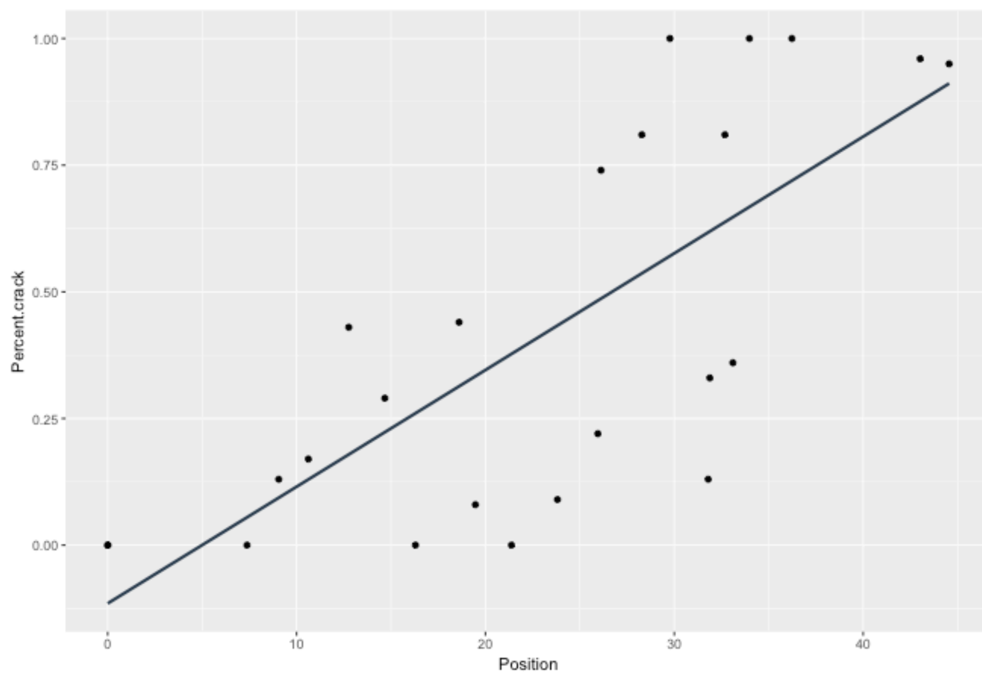

Figure 4 The simple linear regression for predicting the percentage of results in cracking based on the rate of positioning per 10 minutes. y=-0.12 + 0.02x

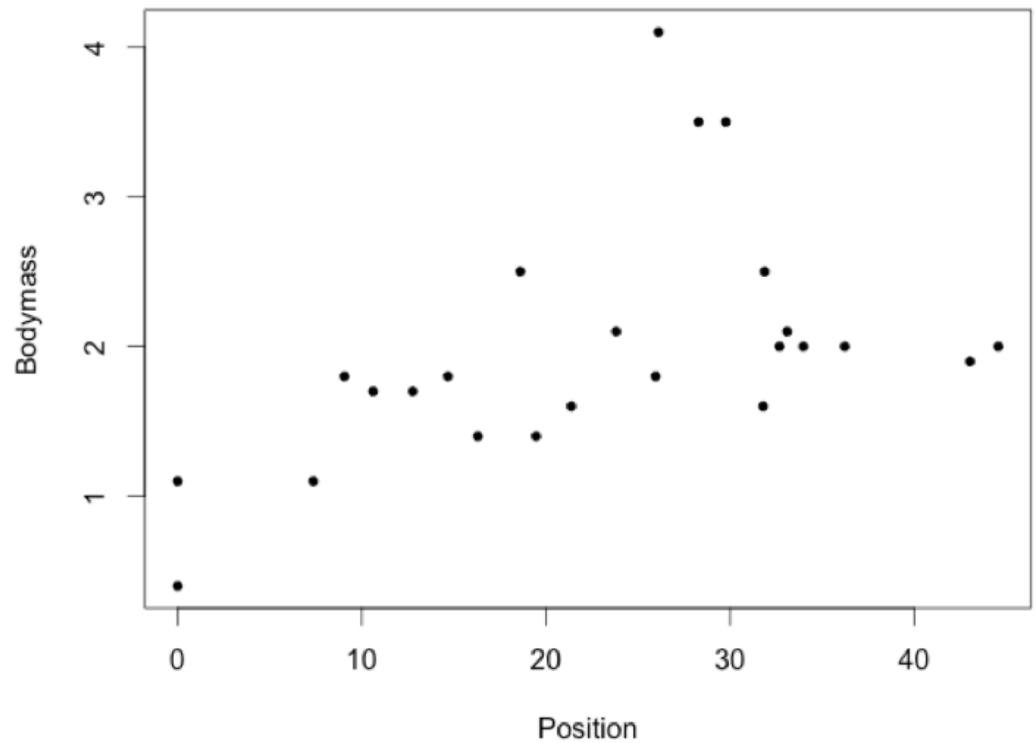

Figure 5 The correlation of rate of position (per 10 minutes) and body mass (kg)

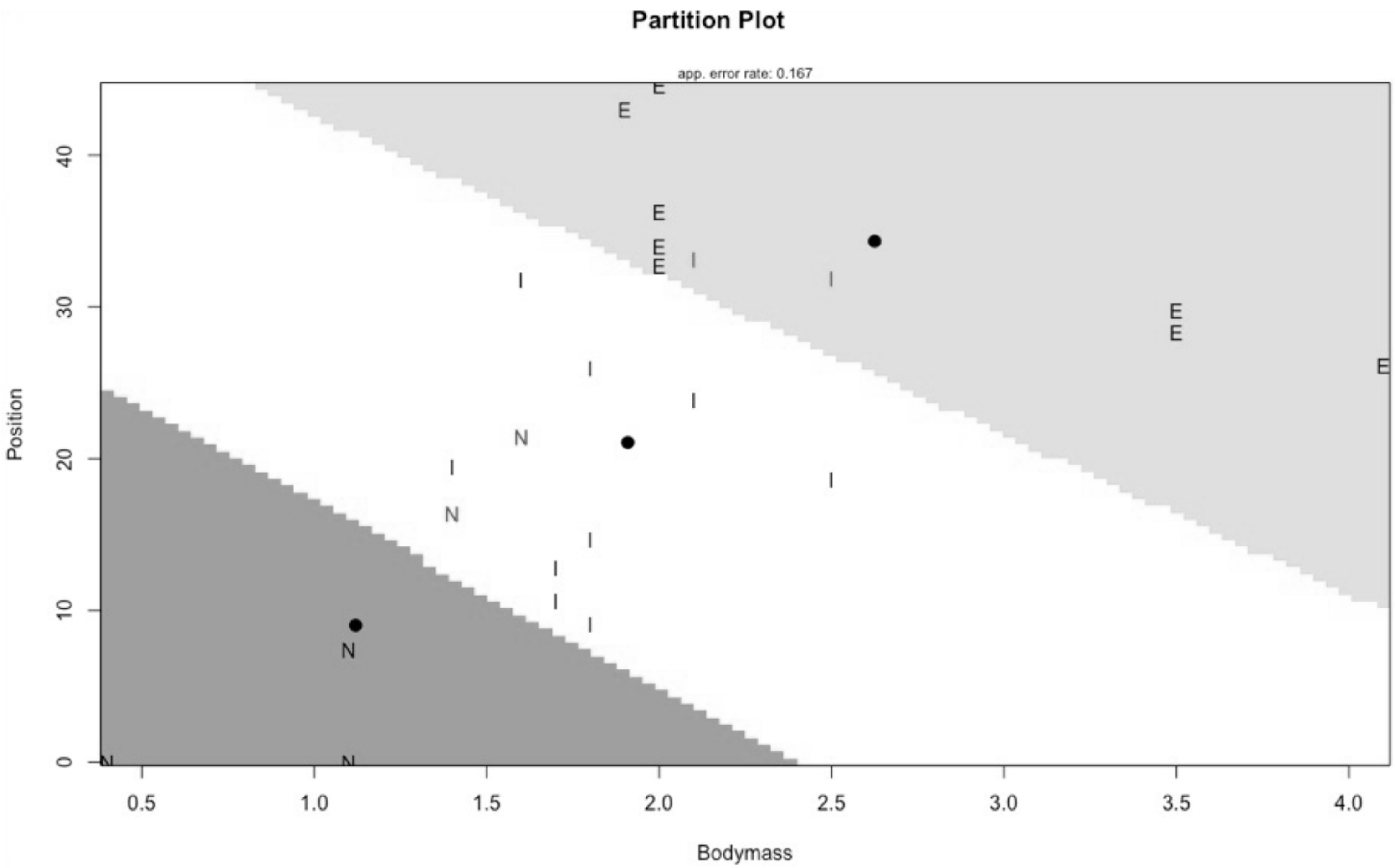

Figure 6 The classification analysis to predict skill level based on body mass (kg) and the rate of percussion per 10 min. The letters in gray indicates the wrong prediction

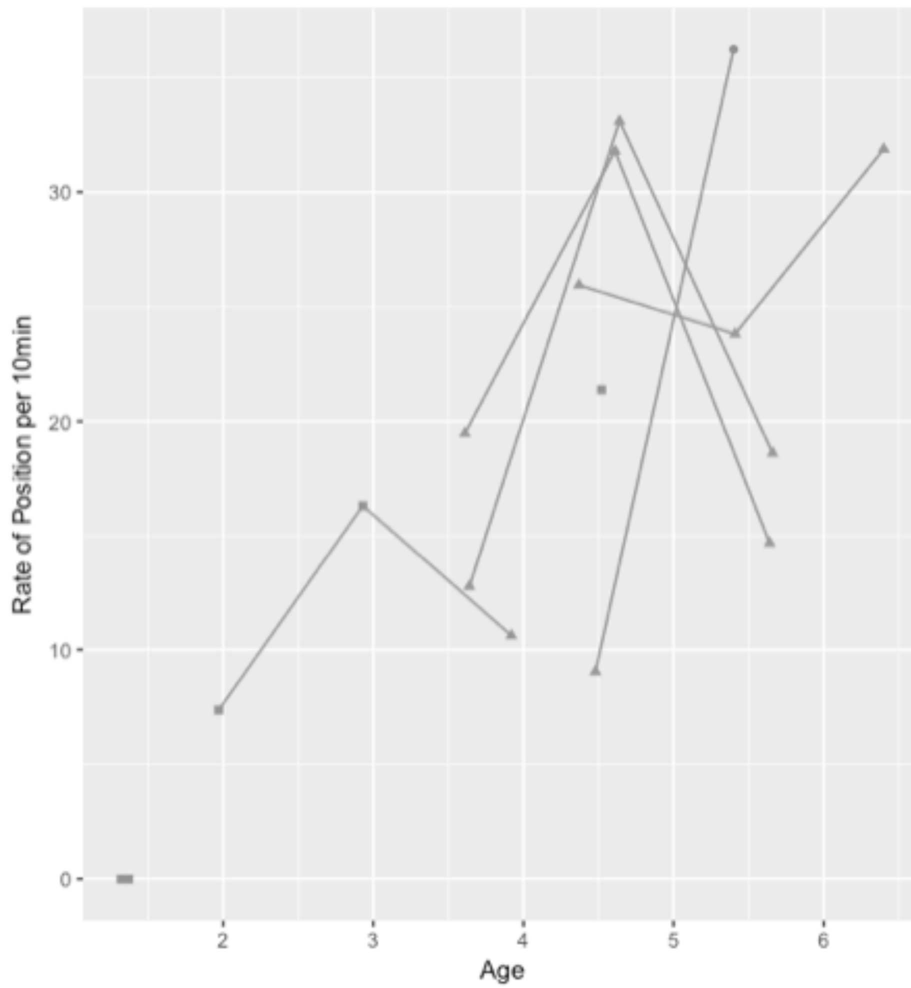

Figure 7 The rate of position per 10 min across age for capuchins in our sample. A circle is an Expert skill capuchin, 11 triangles are Intermediate skill capuchins, and 5 squares are Novice skill capuchins. Any capuchin who is observed for two or three years has his/her values connected by lines. Note that we exclude adults for which we did not have data on age

REFERENCES

Adams-Curtis, L. E., & Fragaszy, D. M. (1994). Development of manipulation in capuchin monkeys during the first 6 months. *Developmental Psychobiology*, *27*(2), 123–136.

Amici, F., Aureli, F., & Call, J. (2010). Monkeys and apes: are their cognitive skills really so different? *American Journal of Physical Anthropology*, *143*, 188–197.

Antinucci, F. (1989). *Cognitive structure and development in nonhuman primates.* Lawrence Erlbaum Associates, Inc.

Bard, K. A. (1995). Sensorimotor cognition in young feral orangutans (*Pongo pygmaeus*). *Primates*, *36*(3), 297–321.

Birch, H. G. (1945). The relation of previous experience to insightful problem-solving. *Journal of Comparative and Physiological Psychology*, *38*(6), 367–383.

Biro, D., Sousa, C., & Matsuzawa, T. (2006). Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: Case studies in nut cracking and leaf folding. In *Cognitive development in chimpanzees* (pp. 476–508). Springer.

Bjorklund, D., & Blasi, C. H. (2011). *Child and adolescent development: An integrated approach*. Nelson Education.

Blois, S. T. De. (1997). Object permanence in three species of primates: Rhesus monkeys (*Macaca mulatta*), squirrel monkeys (*Saimiri sciureus*), and orangutans (*Pongo pygmaeus*). University of Massachusetts Amherst.

Boesch, C., & Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, *13*(5), 415–440.

Brakke, K. (1989). The comparative development of postural competence and object manipulation in bonobo (*Pan paniscus*) and chimpanzee (*Pan troglodytes*). Georgia State University.

Case, R. (1992). *The mind's staircase: Exploring the conceptual underpinnings of children's thought and knowledge*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Chen, Z., & Siegler, R. S. (2000). II. Overlapping Waves Theory. *Monographs of the Society for Research in Child Development*, *65*(2), 7–11.

Chevalier-Skolnikoff, S. (1983). Sensorimotor development in orang-utans and other primates. *Journal of Human Evolution*, *12*(6), 545–561.

Chevalier-Skolnikoff, S., & Liska, J. (1993). Tool use by wild and captive elephants. *Animal Behaviour*.

Crystal, J. D. (2011). Comparative Cognition: Comparing Human and Monkey Memory. *Current Biology*, *21*(11), R432–R434.

De Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): A Perception-action perspective. *Developmental Science*, *11*(6), 828–840.

Doran, D. M., & Hunt, K. D. (1994). Comparative locomotor behavior of chimpanzees and bonobos. *Chimpanzee Cultures*, 93–108.

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*). *Animal Cognition*, *19*(3), 605–618.

Falótico, T., Spagnoletti, N., Haslam, M., Luncz, L. V, Malaivijitnond, S., & Gumert, M. (2017). Analysis of sea almond (*Terminalia catappa*) cracking sites used by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*). *American Journal of Primatology*.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., & De Oliveira, M. G. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, *64*(4), 359–366.

Fragaszy, D. M., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., & Visalberghi, E. (2013). The fourth dimension of tool use: temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *368*(1630).

Fragaszy, D. M., & Cummins-Sebree, S. E. (2005). Relational spatial reasoning by a nonhuman: the example of capuchin monkeys. *Behavioral and Cognitive Neuroscience Reviews*, *4*(4), 282–306.

Fragaszy, D. M., Izar, P., Liu, Q., Eshchar, Y., Young, L. A., & Visalberghi, E. (2016). Body mass in wild bearded capuchins, (*Sapajus libidinosus*): Ontogeny and sexual dimorphism. *American Journal of Primatology*, *78*(4), 473–484.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. M. (2004). *The Complete Capuchin: The Biology of the Genus Cebus*. *Reading*.

Fragaszy, D., Pickering, T., Liu, Q., Izar, P., Ottoni, E., & Visalberghi, E. (2010). Bearded capuchin monkeys' and a human's efficiency at cracking palm nuts with stone tools: field experiments. *Animal Behaviour*, *79*(2), 321–332.

Fujii, J. A., Ralls, K., & Tinker, M. T. (2015). Ecological drivers of variation in tool-use frequency across sea otter populations. *Behavioral Ecology*, *26*(2), 519–526.

Gibson, J. J. (1986). Gibson Theory of Affordances.pdf. *Chapter Eight The Theory of Affordances*.

Goodall, J. (1964). Tool-Using and Aimed Throwing in a Community of Free-Living Chimpanzees. *Nature*, *201*(4926), 1264–1266.

Gumert, M. D., Hoong, L. K., & Malaivijitnond, S. (2011). Sex differences in the stone tool-use behavior of a wild population of burmese long-tailed macaques (Macaca fascicularis aurea). *American Journal of Primatology*, *73*(12), 1239–1249.

Gumert, M. D., Kluck, M., & Malaivijitnond, S. (2009). The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman sea region of Thailand. *American Journal of Primatology*, *71*(7), 594–608.

Gumert, M. D., & Malaivijitnond, S. (2012). Marine prey processed with stone tools by burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. *American Journal of Physical Anthropology*, *149*(3), 447–457.

Hamada, Y., San, A. M., & Malaivijitnond, S. (2016). Assessment of the hybridization between rhesus (*Macaca mulatta*) and long-tailed macaques (*M. fascicularis*) based on morphological characters. *American Journal of Physical Anthropology*, *159*(2), 189–198.

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., … Warren, R. (2009). Primate archaeology. *Nature*, *460*(7253), 339–344.

Hayashi, M. (2015). Perspectives on object manipulation and action grammar for percussive actions in primates. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1682), 20140350.

Hidaka, H., Kojima, H., Kawabata, T., Nakamura, T., Konaka, K., Kashiwagi, A., … Shigeta, Y. (1995). Effects of an HMG-CoA reductase inhibitor, pravastatin, and bile sequestering resin, cholestyramine, on plasma plant sterol levels in hypercholesterolemic subjects. *Journal of Atherosclerosis and Thrombosis*, *2*(1), 60–65.

Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, *379*(6562), 249–251.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*.

Jalles-Filho, E., & Da Cunha, R. G. T. (2008). Manipulation and Tool Use in captive Yellow-Breasted Capuchin Monkeys (*Cebus xanthosternos*). *International Journal of Comparative Psychology*, *21*, 12–18.

Jalles-Filho, E., Da Cunha, R. G. T., & Salm, R. A. (2001). Transport of tools and mental representation: is capuchin monkey tool behaviour a useful model of Plio-Pleistocene hominid technology? *Journal of Human Evolution*, *40*(5), 365–377.

Kahrs, A., & Lockman, J. J. (2014). Tool using, *8*(4), 231–236.

Kahrs, B. A., Jung, W. P., & Lockman, J. J. (2013). Motor Origins of Tool Use. *Child Development*, *84*(3), 810–816.

Kahrs, B. A., & Lockman, J. J. (2008). Building tool use from object manipulation: A perception–action perspective. *Computer*, *144*(5), 724–732.

Leca, J. B., Gunst, N., & Huffman, M. A. (2008). Of stones and monkeys: Testing ecological constraints on stone handling, a behavioral tradition in Japanese macaques. *American Journal of Physical Anthropology*, *135*(2), 233–244.

Li, J., Han, K., Xing, J., Kim, H.-S., Rogers, J., Ryder, O. A., … Batzer, M. A. (2009). Phylogeny of the macaques (Cercopithecidae: *Macaca*) based on Alu elements. *Gene*, *448*(2), 242–249.

Liu, Q., Fragaszy, D. M., & Visalberghi, E. (2016). Wild capuchin monkeys spontaneously adjust actions when using hammer stones of different mass to crack nuts of different resistance. *American Journal of Physical Anthropology*, *161*(1), 53–61.

Lockman, J. J. (2000). A perception–action perspective on tool use development. *Child Development*, *71*(1), 137–144.

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, *69*(2), 227–233.

Mendes, F. D. C., Cardoso, R. M., Ottoni, E. B., Izar, P., Villar, D. N. A., & Marquezan, R. F. (2015). Diversity of nutcracking tool sites used by *Sapajus libidinosus* in Brazilian Cerrado. *American Journal of Primatology*, *77*(5), 535–546.

Mosley, H., & Haslam, M. (2016). Extending material cognition to primate tool use. *Quaternary International*, *405*, 70–77.

Munakata, Y., McClelland, J. L., Johnson, M. H., & Siegler, R. S. (1997). Rethinking infant knowledge: toward an adaptive process account of successes and failures in object permanence tasks. *Psychological Review*, *104*(4), 686–713.

Myowa-Yamakoshi, M., & Yamakoshi, G. (2011). Play behaviors involving the use of objects in young chimpanzees at Bossou. In *The Chimpanzees of Bossou and Nimba* (pp. 231–240). Springer.

Nahallage, C. A. D., & Huffman, M. A. (2008). Comparison of stone handling behavior in two macaque species: Implications for the role of phylogeny and environment in primate cultural variation. *American Journal of Primatology*, *70*(12), 1124–1132.

Nahallage, C. A. D., & Huffman, M. A. (2012). Stone handling behavior in rhesus macaques (*Macaca mulatta*), a behavioral propensity for solitary object play shared with Japanese macaques. *Primates*, *53*(1), 71–78.

Ogle, D. H. (2012). FSA: fisheries stock analysis. *R Package Version 0.2–8*.

Parker, S. T., & McKinney, M. L. (2012). *Origins of intelligence: The evolution of cognitive development in monkeys, apes, and humans*. JHU Press.

Pearce, J. M. (2013). *Animal Learning and Cognition, 3rd Edition: An Introduction*.

Pena, E. A., & Slate, E. H. (2014). gvlma: Global Validation of Linear Models Assumptions. *R Package Version 1.0. 0.2*.

Potì, P., & Spinozzi, G. (1994). Early sensorimotor development in chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *108*(1), 93–103.

Proffitt, T., Luncz, L. V., Falótico, T., Ottoni, E. B., de la Torre, I., & Haslam, M. (2016). Wild monkeys flake stone tools. *Nature*, *539*(7627), 85–88.

Pusey, A. E., Oehlert, G. W., Williams, J. M., & Goodall, J. (2005). Influence of ecological and social factors on body mass of wild chimpanzees. *International Journal of Primatology*, *26*(1), 3–31.

Resende, B. D., Nagy-Reis, M. B., Lacerda, F. N., Pagnotta, M., & Savalli, C. (2014). Tufted capuchin monkeys (*Sapajus* sp) learning how to crack nuts: Does variability decline throughout development? *Behavioural Processes*, *109*(Part A), 89–94.

Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): A Perception-action perspective. *Developmental Science*, *11*(6), 828–840.

Rilling, J. K., & Insel, T. R. (1999). The primate neocortex in comparative perspective using magnetic resonance imaging. *Journal of Human Evolution*, *37*(2), 191–223.

Schiller, P. H. (1952). Innate constituents of complex responses in primates. *Psychological Review*, *59*(3), 177–191.

Shettleworth, S. J. (2012). Do animals have insight, and what is insight anyway? *Canadian Journal of Experimental Psychology/Revue Canadienne de Psychologie Expérimentale*, *66*(4), 217–226.

Siegler, R. S. (1991). *Children's thinking*. Prentice-Hall, Inc.

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. *Journal of Human Evolution*, *61*(1), 97–107.

Steinberg, L., Vandell, D. L., & Bornstein, M. H. (2010). *Development: Infancy Through Adolescence*. Cengage Learning.

Stephan, H., Baron, G., & Frahm, H. D. (1988). Comparative size of brains and brain components. In *Comparative Primate Biology, Vol 4* (pp. 1–38). A.R. Liss.

Takeshita, H., Fragaszy, D., Mizuno, Y., Matsuzawa, T., Tomonaga, M., & Tanaka, M. (2005). Exploring by doing: how young chimpanzees discover surfaces through actions with objects. *Infant Behavior and Development*, *28*(3), 316–328.

Tan, A. W. (2017). From Play to Proficiency: The Ontogeny of Stone-Tool Use in Coastal-Foraging Long-Tailed Macaques (*Macaca fascicularis*) From a Comparative Perception-Action Perspective. *Journal of Comparative Psychology (Washington, DC: 1983)*.

Tan, A. W. Y. (2017). From Play to Proficiency: The Ontogeny of Stone-Tool Use in Coastal-Foraging Long-Tailed Macaques (Macaca fascicularis) From a Comparative Perception-Action Perspective. *Journal of Comparative Psychology*, (March).

Vauclair, J., & Bard, K. A. (1983). Development of manipulations with objects in ape and human infants. *Journal of Human Evolution*, *12*(7), 631–645.

Visalberghi, E. (1997). Success and Understanding in Cognitive Tasks: A Comparison Between *Cebus apella* and *Pan troglodytes*. *International Journal of Primatology*, *18*(5), 811–830.

Visalberghi, E., Sabbatini, G., Spagnoletti, N., Andrade, F. R. D. de, Ottoni, E., Izar, P., & Fragaszy, D. (2008). Physical properties of palm fruits processed with tools by wild bearded capuchins (*Cebus libidinosus*). *American Journal of Primatology*, *70*(9), 884–891.

Visalberghi, E., Sirianni, G., Fragaszy, D., & Boesch, C. (2015). Percussive tool use by Taï Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: a comparison. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *370*(1682), 20140351.

Wickham, H. (2009). ggplot2: Elegant Graphics for Data Analysis Springer-Verlag. *New York*.

Willatts, P. (1984). The stage-IV infant's solution of problems requiring the use of supports. *Infant Behavior and Development*, *7*(2), 125–134.

Wood, S., Moriarty, K. M., Gardner, B. T., & Gardner, R. A. (1980). Object permanence in child and chimpanzee. *Animal Learning & Behavior*, *8*(1), 3–9.