

From Play to Proficiency: The Ontogeny of Stone-Tool Use in Coastal-Foraging Long-Tailed Macaques (*Macaca fascicularis*) From a Comparative Perception-Action Perspective

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Macaques crack shellfish in coastal environments with specialized stone-hammering techniques. I provide the first examination of skill development from 866 object-manipulation and 7,400 tool-use bouts, collected over 15 months, using longitudinal analyses of infants' object manipulation ($N = 7$) and cross-sectional comparisons of manipulative and tool-use behavior ($N = 69$). I adopt a Perception-action approach, examining how the emergence of actions on objects relate to the spatial-relational and percussive challenges of tool use. Infants begin manipulating single items, particularly stones, at 1–2 months. Combining objects predominates (78%) by 1.5–2.5 years, and bouts involving food and tools but with incorrect spatial relations and action sequences prevail (73%) by 2.5–3.5 years. Placing, precedes rubbing objects on surfaces. Percussion emerges last, as disorganized striking before becoming consistent and targeted. Macaques manipulate combinations of stones and oysters, before stones, anvils, and motile shellfish, but success on either food type is only observed at 2.5–3.5 years. After competence, success rates and strike accuracy improve within 3 months on oysters and 5 months on motile shellfish. Older tool users (>4.5 years) had higher success rates, strike accuracy, strike efficiency, and tool fidelity. Macaque tool-use appears facilitated by a propensity for stone manipulation, but challenged by mastering spatial relations and percussion. I relate my findings to the development of stone-tool use in capuchins and chimpanzees, stone-handling in related macaque species, object play in Old World monkeys, and percussion in children, to further understand how biological propensities, environments, and social influences contribute to perception-action learning across species.

Keywords: ontogeny, skill development, tool use, object manipulation

Long-tailed macaques are the most recently studied primate to habitually use stone tools for extractive foraging (Gumert, Kluck, & Malaivijitnond, 2009; Malaivijitnond et al., 2007) in addition to West African chimpanzees (*Pan troglodytes verus*; Boesch & Boesch, 1981) and robust capuchins (*Sapajus libidinosus* [Fragaszy, Izar, Visalberghi, Ottoni, & Oliveira, 2004]; *Cebus xanthosternos* [Canale, Guidorizzi, Kierulff, & Gatto, 2009]). Unlike capuchins and chimpanzees that carry out stone-tool use in forest environments exclusively on plants (Boesch & Boesch, 1983; Canale et al., 2009; Spagnoletti et al., 2012; Sugiyama & Koman,

1979; Visalberghi et al., 2008) macaques crack animal prey in the form of a wide variety of shelled marine invertebrates in coastal habitats (Gumert & Malaivijitnond, 2012). Macaques select stones of different mass when processing food species that vary in physical properties such as size and shell toughness (Gumert & Malaivijitnond, 2013). They also utilize different techniques according to food type (Gumert et al., 2009; Haslam, Gumert, Biro, Carvalho, & Malaivijitnond, 2013; Tan, Tan, Vyas, Malaivijitnond, & Gumert, 2015). They crack motile shellfish similarly to how capuchins and chimpanzees crack nuts, placing them on anvils and striking them with tool stones, a technique we have termed pound hammering. However, the main food species exploited by macaques are sessile rock oysters that cannot be moved from their growth substrate such as rocks or tree roots. Macaques strike directly at the outward facing valve of the oysters to chip them open. The habitual use of this form of stone-tool use, which we have termed axe hammering, is unique to macaques.

Stone-tool use is a developmental challenge, as it requires recognizing the properties of stones and food items, and then producing and managing actions and spatial relations between objects to accomplish a goal (Visalberghi & Fragaszy, 2006). The act of nut cracking, or cracking of motile shellfish, in which the food item must be placed on an anvil, then struck with a tool, has been termed Level 2 tool use (Matsuzawa, 1996) or second-order relational task (Visalberghi & Fragaszy, 2006), as it entails relating three objects in specific order. Furthermore, it requires managing

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“dynamic” spatial relations (Fragaszy & Cummins-Sebree, 2005), as the food target is movable and the relation between food, anvil, and tool, must be constantly maintained. In terms of managing spatial relations, cracking nuts and motile shellfish is more challenging than cracking sessile oysters, a form of Level 1 tool use or first-order relational task, as the sessile oyster is not movable, and can only be combined with the tool in one way (i.e., hit oyster with tool). However, stone-tool use also involves effective percussion, and cracking sessile oysters requires greater “specificity” or accuracy (Fragaszy & Cummins-Sebree, 2005) than cracking nuts and motile shellfish. Sessile oysters are small targets (~2 cm in diameter) that macaques typically strike with the points of small tools, requiring greater precision than striking with broader faces and edges of larger tools during pound hammering. In addition, sessile oysters can grow at numerous substrate-dependent orientations, and macaques have to strike precisely toward differently angled planes, for example, overhead at oysters under overhanging boulders.

Examinations of the development of stone-tool use by chimpanzees and capuchins have found that both species extensively manipulate tools and foods before competence, but with differences in specific elements within the developmental trajectory (Biro, Sousa, & Matsuzawa, 2006; Frigaszy et al., 2013; Inoue-Nakamura & Matsuzawa, 1997; Resende, Ottoni, & Frigaszy, 2008). Young chimpanzees and capuchins carry out simple actions such as touching and picking up stones and nuts, before combining stones, nuts, and anvils, in various configurations until the correct object combinations and action sequences are achieved to produce first ineffective, then successful tool use. However, the canalization of ineffective exploratory behavior toward successful tool use proceeds differently between the two species. For young capuchins, placing nuts on anvils is most challenging although their percussive actions emerge early in the ontogenetic process (Resende et al., 2008). Conversely, young chimpanzees tended to combine objects by placing, and percussion was the latest emerging element in the developmental sequence (Hirata, Morimura, & Houki, 2009; Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa, 1996; Matsuzawa et al., 2001; Takeshita et al., 2005). These specificities in developmental trajectories have been understood from a Perception-action perspective (Lockman, 2000; Resende et al., 2008).

The Perception-action perspective was originally applied to understanding the development of tool use in human children (Gibson, 1991; Lockman, 2000), and views the development of complex tool use abilities as a continuous process, originating from innate motor routines that animals use to explore their environments, which allow animals to eventually produce biologically relevant activities. For example, the motor changes in infant banging from disorganized movements into consistent and forceful striking actions suitable for tool use occur in play contexts, and preadapt infants for percussive goal-directed actions (Kahrs, Jung, & Lockman, 2012). As young individuals begin to incorporate objects into their perception-action routines, they create opportunities to experience the consequences of combining different objects and surfaces (Takeshita et al., 2005). With regards to learning how to relate objects and surfaces, a key component of tool use, the perception-action theory, therefore, predicts that: (a) simple actions performed on single objects at a time will emerge before routines in which objects and surfaces are combined; (b) earlier

combinatory manipulations will first be carried out with apparent ignorance toward the physical properties of different objects and surfaces, specific spatial orientations between objects, and sequences of actions; and (c) the combinatory actions of immatures will increasingly resemble the adult and effective form, as young individuals first learn object properties and affordances, and then, produce appropriate sequential spatial relations between relevant objects (Kahrs & Lockman, 2014; Lockman, 2000; Resende et al., 2008; Takeshita et al., 2005).

Variation in developmental trajectories are expected, because the environments in which young animals conduct and develop their perception-action routes differ across species, and are likely to be experienced differently by individuals even within species and groups. To explain the differences in the developmental challenges faced by chimpanzees and capuchins for example, an ecological explanation has been proposed. (Resende et al., 2008). Capuchins commonly consume encased plant matter that require percussive extraction even without tools, however, they are arboreal and therefore hesitant to release and risk dropping food, which prevents them from readily letting go of food items to place them on anvils. Chimpanzees are more terrestrial and do not risk losing food items by placing them on ground surfaces, however, they feed predominantly on fleshy fruit that although may require manipulative handling (e.g., Corp & Byrne, 2002), do not require percussion. As opportunities to examine the development of percussive stone-tool use under natural conditions are rare, examining the development of stone-tool use in long-tailed macaques will add a valuable point of comparison to further investigate environmental influences. Other factors are likely to underlie common patterns and variation in the Perception-action development of tool-use skills across species, such as biological propensities, maturational processes, and social influences. An understanding of these influences can be advanced by extending comparisons to the development of related manipulative behavior, such as object play and percussion, across a wider range of species and environmental settings (Huffman & Hirata, 2003; Huffman & Quiatt, 1986).

I report the first analysis of developmental patterns in the ontogeny of stone-tool use in a long-tailed macaque population on Koram Island, Khao Sam Roi Yot National Park, Thailand. Using both quantitative analyses and qualitative descriptions of behavioral observations, I examine the development of stone-tool use in macaques from object manipulation to competency and proficiency. To contribute to comparisons with stone-tool using capuchins and chimpanzees, I derive predictions about the ontogeny of stone-tool use in long-tailed macaques from the Perception-action perspective. Overall, I predict that macaque stone-tool use follows the same general trajectory as capuchins and chimpanzees, where ability to use tools will develop over the first 2 to 3 years of life, during which developing individuals will carry out exploratory object manipulation until successful tool use is achieved. Exploratory object manipulation should proceed from a wide variety of simple actions, to various combinatory manipulations, and action sequences should be carried out in improper configurations, until the correct sequence of actions for successful tool use is produced. Specific to macaques, I examine the order in which the cracking of sessile oysters versus unattached foods on anvils emerge. In addition, I examine the changes to various aspects of tool-use proficiency (e.g., efficiency, accuracy) that continue to occur after the initial tool-use competence is achieved, to further understand the

process of skill refinement in macaques. Using these findings, I identify the challenges faced by macaques in developing percussive tool-use techniques for processing sessile oysters by axe hammering and motile food items by pound hammering. I discuss the ontogeny of stone-tool use in long-tailed macaques in comparison with chimpanzee (Inoue-Nakamura & Matsuzawa, 1997) and capuchin stone-tool use (Resende et al., 2008), and developmental processes of related behaviors such as stone handling in closely related macaque species (Nahallage & Huffman, 2007, 2008, 2012), object play in other Old World monkeys (Fairbanks, 2000), and percussive actions in human infants (Kahrs, Jung, & Lockman, 2013; Kahrs & Lockman, 2014). These comparisons are aimed at broadening perspectives on processes influencing the Perception-action development of tool-use skills.

Method

Ethics Statement

Research protocols were approved by the Nanyang Technological University (NTU) Institutional Animal Care and Use Committee (ARF SBS/NIE-A 0210 AZ). Data collection methods are purely observational, and the macaques are already habituated to close human proximity.

The National Research Council of Thailand (NRCT) permitted research in the Kingdom of Thailand, and the Department of National Parks, Wildlife, and Plant Conservation (DNP) granted permission to conduct research in Khao Sam Roi Yot National Park.

Study Site

Koram Island (N12°14'32," E100°0'17') is located in Khao Sam Roi Yot National Park, Prachuap Khiri Khan province, Thailand, in the Gulf of Thailand, approximately 1 km offshore from the mainland. It is approximately 42 km², with 3.5 km of coastline of limestone cliffs where it faces the open gulf, and rocky shores with small sandy beaches on the side of the coast facing the mainland. It is on these rocky shores and sandy beaches that the macaques carry out tool-aided foraging when marine invertebrates are accessible during low tide.

Observation Periods

I collected data from 17 October 2013 to 2 December 2014, on 227 days in total, for an average of four hours a day corresponding to daily low tide conditions. During the months of November to January, the area experiences annual monsoon conditions that often prevented access to the island, therefore, less data could be collected during these months (monsoon: 5–13 days/month, non-monsoon: 20–25 days/month).

Subjects

The macaques on Koram Island are provisioned and habituated and can be observed at close range. The study group ranged between 65 to 72 individuals during the study. I was able to distinguish each subject according to physical appearance. Sufficient data was collected on 69 individuals for inclusion in developmental analyses.

I divided subjects into seven age groups; Group 1: 0–1.5 years ($N = 11$; 4♀, 6♂), Group 2: 0.5–1.5 years ($N = 9$; 2♀, 7♂), Group 3: 1.5–2.5 years ($N = 9$; 5♀, 4♂), Group 4: 2.5–3.5 years ($N = 5$; 1♀, 4♂), Group 5: 3.5–4.5 years ($N = 6$; 2♀, 4♂), Group 6: 4.5–5.5 years ($N = 5$; 1♀, 4♂), and Group 7: older than 5 years ($N = 24$; 17♀, 7♂). Exact ages are only known for individuals in Group 1, as these infants were born during the study. Group 2 juveniles were existing infants in the group when I began study, and approximately 0.5 years of age based on their size and hair coloration. Three months into the study, in late December 2014, when Group 2 infants were about 9 months of age, a birth peak began, during which, Group 1 infants were born over the several months, with most infants being born in March, 2015 (Dec: 1, Jan: 2, Feb: 1, Mar: 4, Apr: 2, Jun: 1). Therefore, I estimated that Group 2 juveniles were on average, 1 year older than Group 1 infants. Using this method, I determined which individuals belonged to the same age group based on physical characteristics, and estimated that each generation was a year older than the previous. Individuals in Group 6 were adolescents that developed adult physical characteristics during the study (first birth and elongated nipples for females, adult muscularity for males). I corroborated the ages at which these physical characteristics develop with staff from a captive primate facility (Singapore Institute for Clinical Sciences). Individuals in Group 7 were mature adults when I began the study, and I classified them as above 5.5 years of age following from the estimated ages of younger age groups.

Data Collection

I collected behavioral data on object manipulation and tool-use behavior via focal and ad libitum sampling (Altmann, 1974). Observations were either recorded on video or an audio recorder, then transcribed and scored. In focal sampling, I sampled individuals in random order on continuous rotation, for 5-min durations. During focal sampling, I recorded when focal individuals (a) started and ended foraging, resting, locomotive, and social behavior, (b) picked up and dropped tools, (c) started and ended tool-use bouts, and (d) started and ended object manipulation bouts. Because object manipulation and tool use behavior are rare for some individuals, I also recorded all instances of object manipulation that I observed outside of focal sampling, and recorded tool-use behavior if an individual utilized an action pattern or processed a food type that had not been observed during focal sampling.

Data Scoring

Manipulative behavior. From focal samples, I scored manipulative bouts, which consisted of both object-manipulation bouts and tool-use bouts. Object-manipulation bouts are manipulative bouts in which the monkeys manipulated the objects associated with tool use, that is, stones and shell items, in ways that do not constitute tool use. An object-manipulation bout began when the focal individual first contacts a stone or shelled item, and includes all items and actions until the focal individual ceases contact with items for 10 s. Tool-use bouts began when the focal individual began striking, and ended upon the last strike, marked either by the individual consuming the food item, moving on to a different food

item, or ceasing interaction with the food item for 10 s. Tool users sometimes walked with tools in hand while moving from one food item to another. These periods of walking with tools were not included in the durations of manipulative bouts, but were recorded to measure the amounts of time that individuals foraged with tools.

For each manipulative bout, I recorded the objects and the manipulative actions involved, and scored the complexity of the manipulation. I considered only manipulative bouts in which stones, shell items, and anvils were involved. Anvil stones were distinguished from other stones either by being nonmovable stones that are embedded in the ground, or stones that showed signs of use as an anvil (i.e., having food debris or a tool stone placed on it). I distinguished two types of shell items, shelled food items (henceforth referred to as “food”) including unattached foods and sessile oysters, as well as old or empty shells that no longer contained edible contents (henceforth referred to as “shells”). I did not score a manipulative bout where only items that were not stones or shell items, such as pieces of trash, leaves, or twigs, were manipulated, but recorded these items as involved in manipulative bouts if stones and/or shell items were also involved.

I created an ethogram of actions performed on stones, food, shells, and anvils as I scored manipulative behavior, recording, and describing each new action (see Table 1). At any time, macaques may manipulate single stones, food items, shells, and anvils, or manipulate several items simultaneously in various combinations. I classified some actions as Critical Actions, and divided these actions into either Critical-A or Critical-B Actions (see Table 2). Critical-A actions were actions directly involved in an optimal sequence of tool use (cf. Lonsdorf, 2006). For tool use on sessile oysters, these were “pick up stone,” identify oyster (either by “pick at” or “mouth”), and “hit stone on oyster.” For tool use on unattached food items, these were “pick up stone,” “pick up food,” “place food on anvil,” and “hit stone on food.” Critical-B Actions were inaccurate forms of Critical-A Actions that may still represent steps toward mastering the Critical-A Actions for an optimal tool-use sequence, and all hitting actions, as hitting is a key element for cracking foods. I recorded a total of 21 Critical-B Actions.

I coded manipulative bouts according to a mutually exclusive and exhaustive hierarchical classification adapted from Inoue-Nakamura and Matsuzawa's (1997) study on the development of stone-tool use in young chimpanzees, altered to accommodate the cracking of sessile oysters that are unique to macaques (see Table 3). The classification progresses according to the number of objects involved, the number of actions involved, and the relations between objects when multiple objects were manipulated. Manipulative bouts were first split into two classes depending on the number of objects manipulated simultaneously, single object (Class A), or multiple objects (Class B). Class A manipulative bouts were further divided into two classes depending on how many objects were manipulated in total; a single object (Class A-1), or multiple objects (Class A-2). Then, Class A-1 was again divided into two classes, this time based on how many actions were performed on the single object; a single action (Class A-1-i), or multiple actions (Class A-1-ii). Class B manipulative bouts were subdivided according to whether the multiple items being manipulated simultaneously were brought in contact with each other; not combined (Class B-1), and combined (Class B-2). Lastly, manipulative bouts in which macaques carried out the correct object and

action sequences involved in tool use were categorized as Class C. I split Class C manipulations into Class C-S, where macaques produced the tool-use sequence for sessile oysters, and Class C-U, where they produced the tool-use sequence for unattached food items. For Class C manipulations, it did not matter whether the individual was successful in cracking open the food item, as long as the correct object combinations and action sequences were produced.

Tool use. When manipulative bouts were tool use, I further scored the characteristics of tool-use bouts:

- a. *Duration*: The time taken to crack open a food item, measured by the time between the first and last strikes.
- b. *Food type*: Sessile oysters or unattached foods.
- c. *Strike frequency*: The number of strikes used to crack open the food item.
- d. *Strike accuracy*: Accurate strikes were those in which the focal individual managed to make contact with the food item using the tool, and in the case of tool use on unattached foods, the food item did not ricochet from the anvil. In inaccurate strikes, the tool user misses the food item, or causes the food item to ricochet when struck.
- e. *Tool-switching frequency*: The number of times the focal individual switched to a different tool during each bout of tool use.
- f. *Success*: Marked by whether the subject was able to crack and consume the food item.

Tests of intra-rater coding reliability. At the end of the data collection period, and after all collected data had been and scored, I rescored video-taped object-manipulation and tool-use bouts, then examined concordance between the initial and rescored variables by calculating Interclass Correlation Coefficients (ICC) for continuous variables and κ coefficients (Martin & Bateson, 1993) for categorical variables, and the percentage of agreement between the two coding events for all variables. For object manipulation, 43 object-manipulation bouts were video-taped during data collection, and I rescored all bouts. I first recoded the objects and manipulative actions involved in each manipulative bout as described in “Data Scoring—Manipulative Behavior,” then recoded the variables used in analyses which were total number of actions, total number of objects, object category (stones only, shells only, stones and shells, stones/shells and anvils, stone and sessile oyster, and, stone, unattached food and anvil), Hierarchical Class, and whether Critical-A actions and Critical-B were performed. To select tool-use bouts for recoding, I selected 100 focal samples by assigning each focal sample a random sorting number with the RAND function in Microsoft Excel, and selecting the first 100 focal samples. I then recoded all tool-use bouts within these 100 focal samples, which was a total of 339 bouts. Variables of each bout that were analyzed for concordance were number of strikes, accuracy index, number of tool changes, and bout success. For both object manipulation and tool use bouts, I did not recode bout durations as these were based on time stamps from the videos, and not on rater judgment. Consequently, I did not analyze concor-

Table 1

Object-Manipulation Actions on Stones, Unattached Food Items, Sessile Oysters, Empty Shells, and Combinations of These Items

Item	Action	Description
Single-item manipulations		
Stone	Pick up	Lift item off the ground, releasing the item within 2 s.
	Hold	Lift item off the ground, continuing to hold item for >2 s.
	Carry	Pick up and move item from one location to another.
	Manipulate	Move item around in the hands.
	Touch	Makes contact with item using the hand, does not proceed with picking up or manipulating the item.
	Mouth	Makes contact with item using the mouth, includes biting but not ingesting item.
	Sniff	Puts nose close to item.
	Rub on ground	Holds item down on the surface and pushes it around, keeping item in contact with the surface.
	Push off anvil	Nudges an item that is on an anvil with the hands, such that the item falls off the anvil.
	Carry in mouth	Moves item from one location to another by holding it in the mouth.
	Examine	Holds an item in the hand and looks at it intently. May involve some manipulation of the item.
	Hug	Holds item against the body.
	Pick at	Plucks at item usually using either the index finger.
	Hit on ground	Lifts item off the surface and brings it back down onto the surface with some force.
Unattached food	Pick up	
	Carry	
	Mouth	
	Hold	
	Manipulate	
	Carry in mouth	
	Rub on ground	
	Rub on body	
	Hit with hand	Brings hand down onto item with some force.
	Examine	
Sessile oysters	Pick at	
	Mouth	
Empty shells	Pick up	
	Mouth	
	Manipulate	
	Touch	
	Examine	
	Hold	
	Carry	
	Carry in mouth	
Anvil	Mouth	
	Pick at	
Two-item combinations		
Stone/anvil	Place stone on anvil	Takes item from another location (e.g., on the ground), and releases it onto an anvil.
	Rub stone on anvil	
	Swipe stone on anvil	Holds item in one hand, lifting it off and bringing it back onto the anvil surface repeatedly, with a side-to-side U-shaped motion. The item makes contact with the anvil at the bottom of the U-shaped trajectory.
Unattached food/anvil	Hit stone on anvil	
	Place food on anvil	
	Rub food on anvil	
	Swipe food on anvil	
	Hit food on anvil (direct percussion)	
Empty shell/anvil	Place shell on anvil	
	Rub shell on anvil	
	Hit shell on anvil	
Stone/sessile oyster	Rub stone on oysters	
	Swipe stone on oysters	
	Hit stone on oysters (tool use)	
Unattached food/sessile oyster	Rub unattached food on oysters	
	Hit unattached food on oysters	

(table continues)

Table 1 (continued)

Item	Action	Description
Two stones	<u>Combine</u> stone <u>with</u> stone	Hold items in adjacent contact with each other. In “combine with,” items are simultaneously brought together, whereas for “combine above/under” (see below), there appears to be a deliberate order of placing one item in contact with a specific surface of the other item.
Stone/other	Combine stone with other	
Stone/unattached food	Combine unattached food under stone	Holds a stone in one hand and an unattached food item in the other hand, then puts and holds the food item in contact with the underside of the stone.
	Combine unattached food above stone	Holds a stone in one hand and an unattached food item in the other hand, then puts and holds the food item in contact with the top surface of the stone.
Unattached food/other	Combine unattached food with other	
Two unattached foods	Combine food with food	
Unattached food/empty shell	Combine unattached food with shell	
Three-item combinations		
Unattached food/two stones	Combine unattached food with two stones	
Two unattached foods/anvil	Hit unattached food on unattached food placed on anvil	
Two stones/anvil	Hit stone on stone placed on anvil	
Unattached food/shell/anvil	Combine unattached food with shell and hit on anvil	
Stone/unattached food/anvil	Combine food above stone and place combination on anvil	
	Combine food above stone and hit combination on anvil	
	Combine food under stone and hit combination on anvil	
	Hit food on stone placed on anvil	
	Hit stone on food placed on anvil (tool use)	
Four-item combinations		
Unattached food/two stones/anvil	Combine food under stone and hit combination on another stone placed on anvil (B)	

Note. In phrases, the action being described is underlined, and descriptions of actions that are carried out in multiple object categories are not repeated.

dance of strike rates in tool-use bouts, as these were calculated by dividing total strikes by bout duration, and would yield the same results as total strikes. ICCs and κ coefficients indicated perfect or almost perfect concordance between the original and recoded scores for all variables analyzed (cf. Martin & Bateson, 1993; see Table 4).

Analyses

I examined the development of manipulative and tool use behavior using longitudinal and cross-sectional analyses. For manipulative behavior, I carried out longitudinal analyses of object-manipulation bouts by infants born during the study over their first 6 months of development, and cross-sectional analyses of the differences in manipulative behavior between individuals in different age groups. For tool use, I carried out a longitudinal examination of the tool-use characteristics of one juvenile male subject that began to use tools during the study period, over the first 10

months of tool use, and cross-sectional analyses of the differences in tool-use characteristics between individuals in different age groups.

Examining Changes in Manipulative Behavior

Longitudinal analyses of infants’ object manipulation bouts. I examined changes in the proportions of time spent in object-manipulation bouts, and the rates at which infants performed object-manipulation bouts over the first 6 months of development. I included only infants with six full months of data ($N = 7$). I used Friedman tests to test for differences between months, and post hoc tests with Bonferroni corrections to identify months that differed at the $p < .05$ level (two-tailed).
To examine changes in infants’ manipulative behavior after they first start manipulating objects, I analyzed changes in the proportions of infants’ object manipulation bouts in which different characteristics were recorded, over the 6 months after

Table 2
Critical-A Actions That are Directly Involved in an Optimal Sequence of Tool Use, and Their Inaccurate Forms (Critical-B Actions)

Tool-use type	Critical-A actions	Critical-B forms
Sessile oyster	Pick up stone	—
	Identify sessile oyster (pick at/mouth)	—
	Hit stone on sessile oyster	Rub stone on sessile oyster Swipe stone on sessile oyster Hit food on sessile oyster
Unattached food	Pick up stone	—
	Pick up food	—
	Place food on anvil	Place stone on anvil Place shell on anvil Rub food on anvil Swipe food on anvil Hit shell on anvil Hit food on anvil
	Hit food (placed on anvil) with stone	Combine food under stone Combine food above stone Combine food with two stones Hit stone on anvil Hit food on another food placed on anvil Hit stone on another stone placed on anvil Hit food on stone placed on anvil Combine food with shell and hit combination on anvil Combine food above stone and place combination on anvil Combine food above stone and hit combination on anvil Combine food under stone and hit combination on anvil Combine food under stone and hit combination on another stone placed on anvil

infants' first observed object-manipulation bouts. I required that each infant had at least 10 bouts of object-manipulation from which to calculate proportional data in each time period being compared. I divided the first 6 months of each infant's object manipulation behavior into two Time Periods—Time Period 1: 0–3 months, and Time Period 2: 4–6 months, to obtain a sample size of $N = 5$. Because some individuals were not observed to carry out object manipulation until their second month of development, these time periods corresponded to months 2–5, and 6–8 after birth. I included observations from

focal samples and ad libitum observations of all infants to document the emergence of different manipulative actions. [Table 5](#) shows each infant's participation in analyses.

I examined changes between the two time periods in:

- Objects infants manipulated, by calculating (a) the proportions of object manipulation bouts in which each infant manipulated only stones, only shell items, both stones and shell items, and stones and/or shell items and anvils, as well as (b) the average number of objects involved in object-manipulation bouts.

Table 3
Definitions and Examples of Each Hierarchical Class of Manipulative Bouts

Class	Definition
A-1-i: Single action on single object	Subject performed only one action on one object (e.g., touching a stone; mouthing a food item).
A-1-ii: Successive actions on a single object	Subject performed two or more actions, one after another on a single object (e.g., picking at a food item, then mouthing the same food item).
A-2-ii: Successive actions on multiple objects	Subject performed two or more actions, one after another, on two or more objects, but only one object at a time (e.g., picking up a stone, hitting the stone on the ground, then picking at a food item).
B-1: Simultaneous actions on multiple objects while not combining objects	Subject performed two or more actions on two or more objects simultaneously, while not bringing the objects into physical contact (e.g., handling a stone in one hand while picking at a food item with the other).
B-2: Simultaneous actions on multiple objects while combining objects	Subject performed two or more actions on two or more objects either simultaneously, bringing the objects into physical contact (e.g., handling a food item in one hand and a stone in the other, and rubbing the two together).
C-S: Tool-use on sessile oyster	Subject performed the correct sequence of tool use on sessile oyster (i.e., hitting a sessile oyster with a stone).
C-U: Tool-use on unattached foods	Subject performed the correct sequence of tool use on unattached food (i.e., hitting an unattached food that is placed on an anvil surface with a stone).

Table 4
Interclass Correlation Coefficients and κ Coefficients Indicating Coding Reliability

Manipulative behavior	Variable	% Agreement	Reliability statistic
Object manipulation	Total actions	97.56	ICC = .99
	Total objects	100	ICC = 1.00
	Object category	100	κ = 1.00
	Hierarchical class	100	κ = 1.00
	Presence of Critical-A	100	κ = 1.00
	Presence of Critical-B	97.56	κ = .95
Tool use	Number of strikes	93.81	ICC = .99
	Accuracy index	97.35	ICC = .98
	Number of tool changes	100	ICC = 1.00
	Success	100	κ = 1.00

- Actions performed on objects, by (a) documenting the emergence of different actions across the months of object manipulation, (b) calculating the average numbers of actions each infant carried out during object-manipulation bouts, and (c) the proportions of each infant's object-manipulation bouts in which Critical Actions were performed.
- Complexity of object-manipulation bouts, by calculating the proportions of each infant's object manipulation bouts that fell into each Hierarchical Class.

I used Wilcoxon signed-ranks test to test for differences ($p < .05$, two-tailed) between the two time periods.

Cross-sectional analyses of manipulative behavior. To examine the prevalence of manipulative behavior in each age group, I determined the proportion of individuals in each age group that engaged in manipulative bouts. I then calculated the proportion of total focal time that individuals in each age group spent in manipulative bouts, and the rates at which individuals carried out manipulative bouts per hour of focal time, and tested for differences between individuals in different age groups.

To examine changes in the two types of "correctness" of manipulative behavior tending toward correct tool use across age classes, "object correctness" and "action correctness," I examined differences in the objects and Critical Actions that

individuals involved in manipulation bouts. For object correctness, I calculated the proportion of bouts in which (a) only stones were manipulated, (b) only shell items were manipulated, (c) both stones and shell items were manipulated, and (d) all items necessary for tool use was involved. For tool use on sessile oysters, these items were a stone and a sessile oyster, while for unattached foods, these items were a stone, a food item, and an anvil. For action correctness, I calculated the proportion of bouts in which Critical-A and Critical-B actions were carried out for each individual.

To examine changes in the complexity of manipulative behavior across age classes, I calculated the proportion of bouts in which each Hierarchical Class was scored for each individual. I tested for differences between age groups using Kruskal-Wallis H tests, as the data could not be transformed to fit a normal distribution. I used Dunn post hoc tests to identify which age classes differed. The level of significance was $p < .05$ for all tests.

Examining changes in tool-use behavior. I examined changes in individuals':

- a. Proportion of foraging time spent carrying tools
- b. Rate of tool-use bouts per hour of focal time

Table 5
The Number of Object-Manipulation Bouts Recorded for Each Infant in Its First 3 Months (Time Period 1) and Fourth to Sixth Months (Time Period 2) of Manipulative Activity

ID	No. of bouts			Analysis	
	Time 1	Time 2	Total	Proportion time/rate	Bout characteristics
Dwg ^a	30	—	30		
Sfa ^a	7	—	7		
Waw	39	24	70	X	X
Dat	19	29	52	X	X
Cha	35	5	43	X	
Sai	31	11	45	X	X
Mpr ^a	6	3	9		
Mek	14	27	43	X	X
Gbi	21	8	29	X	
Tpt	31	11	42	X	X
Tup ^a	30	—	30		

Note. X indicates which infants were involved in each analysis.
^a Dwg and Sfa went missing in their third month and Mpr in his fifth month, while Tup was only 5 months old by the end of the data collection period. These infants, therefore, did not have a complete dataset for Time 2.

- c. Strike rate, which is the average number of strikes per second during tool-use bouts
- d. Strike efficiency, measured by the average number of strikes needed to crack food items, with a higher average strike frequency indicating poorer strike efficiency
- e. Strike accuracy, measured by the average proportion of accurate strikes in tool-use bouts
- f. Tool fidelity, measured by the average number of times an individual switched tools during a bout, with more switches being lower fidelity
- g. Tool-use efficiency, measured by the average time taken to crack food items
- h. Tool-use effectiveness, measured by the proportion of successful bouts

Characteristics (a) and (b) measured how much each individual used tools, and characteristics (c) to (h) served as measures of proficiency. I examined changes in tool-use characteristics separately across three food categories, all foods, sessile oysters only and unattached food items only.

Longitudinal analyses of tool-use behavior following first tool use. I calculated tool-use characteristics for the months after first tool use for a juvenile male, Chk, in Age Group 4 (2.5–3.5 years). I calculated each tool-use characteristic for bouts in each 1-month period after Chk's first tool use, up to 10 months when our data collection period ended. Data from months 8 to 10 were pooled because less data was collected during this period because of monsoon weather conditions. Because this was a single-subject analysis, I used 95% confidence intervals (CIs) and visual analyses of graphs to identify significant changes between months (Morgan & Morgan, 2009).

Cross-sectional analyses of tool-use characteristics. In cross-sectional analyses, I included only individuals with more than 10 bouts of tool use in each food category. These analyses involved only individuals from Age Group 4 or older. The number of individuals analyzed in each age class for each food category is listed in Table 6. For analyses of tool-use characteristics on unattached foods, I could not include Age Group 6, as only one individual from that Age Group used tools on unattached food, and post hoc tests could not be run.

To select statistical tests, I first examined if the data for each characteristic was normally distributed using a Shapiro-Wilks test. Then, I applied a square root transformation on characteristics that were found to deviate from a normal distribution, and tested for

normality again. I used one-way between subject analysis of variance (ANOVA) with Tukey post hoc tests for data that was normally distributed, or could be transformed to fit a normal distribution. I used Kruskal-Wallis *H* tests with Dunn post hoc tests for data that could not fit normality. For (f) strike accuracy, (g) tool fidelity, and (h) tool-use effectiveness, I used square root transformed data regardless of whether ANOVA or Kruskal-Wallis *H* tests were used, because the raw data was heavily skewed. The skews were because the macaques were overall very accurate in their strikes, seldom switched tools during bouts, and almost always successful in cracking open food items. In the end, ANOVAs were used to test for differences in bout durations across all food items, strike efficiency for sessile oysters and unattached food, strike rate for all food categories, tool-selection effectiveness across all food categories, and strike accuracy and tool-use effectiveness for unattached foods. Kruskal-Wallis *H* tests were used for all other comparisons.

Results

Changes in Manipulative Behavior

Longitudinal changes in infants' object manipulation behavior.

Prevalence of object manipulation. I obtained 150 hr of total focal time, and recorded 400 object manipulation bouts for all 11 infants across the study period. Infants first manipulated stones and/or shells in their first ($N = 3$), second ($N = 7$), or third ($N = 1$) months of age. Seven infants were included in statistical analyses, contributing 93 hr of focal time across their first 6 months of development, during which I recorded and analyzed 324 object-manipulation bouts. Across all 6 months, the infants spent on average 0.02 (95% CI [0.01, 0.02]) of their focal time engaged in object-manipulation bouts, at an average rate of 0.04 bouts/min (95% CI [0.04, 0.06]). Friedman tests found significant differences in both the proportion of time that infants spent on object manipulation ($\chi^2_{5, N=7} = 20.31, p = .001$, Kendall's $W = 0.58$) and their rates of object manipulation ($\chi^2_{5, N=7} = 16.07, p = .01$, Kendall's $W = 0.46$) over the 6 months (see Figure 1). Wilcoxon's signed-rank post hoc tests revealed that the median proportion of time spent in object manipulation increased significantly from the first month of development ($Mdn = 0.00$) to the fourth ($Mdn = 0.02$), $z = -3.57, p = .01$; fifth ($Mdn = 0.03$), $z = -3.71, p = .003$; and sixth ($Mdn = 0.03$), $z = -3.29, p = .02$, months of development. Post hoc tests also revealed that the median rates of object-manipulation bouts increased significantly from the first month of development ($Mdn = 0.00$ bouts/min) to the third ($Mdn = 0.08$ bouts/min), $z = -3.29, p = .02$; and fourth ($Mdn = 0.09$), $z = -3.36, p = .01$, months of development.

Actions and objects. I observed 34 different actions in the 6 months after infants' ($N = 11$) first recorded object manipulation bouts (see Table 7). Infants with the full 6 months for analyses ($N = 7$) had developed 12 to 19 different actions each ($Mdn = 16$). Different actions emerged in different months for each infant, and there were general patterns in the emergence of different types of actions.

There were changes in the types of objects manipulated by infants over the two 3-month time periods after their first object manipulation. All 11 infants were observed to interact with stones before shell items, with the exception of one infant, Cha. Within

Table 6
Number of Individuals in Each Age Group With More Than 10 Bouts of Tool Use in Each Food Category

Age group	All food	Sessile oysters	Unattached food
4 (2.5–3.5 years)	3	3	3
5 (3.5–4.5 years)	6	6	6
6 (4.5–5.5 years)	5	5	—
7 (>5.5 years)	13	13	8

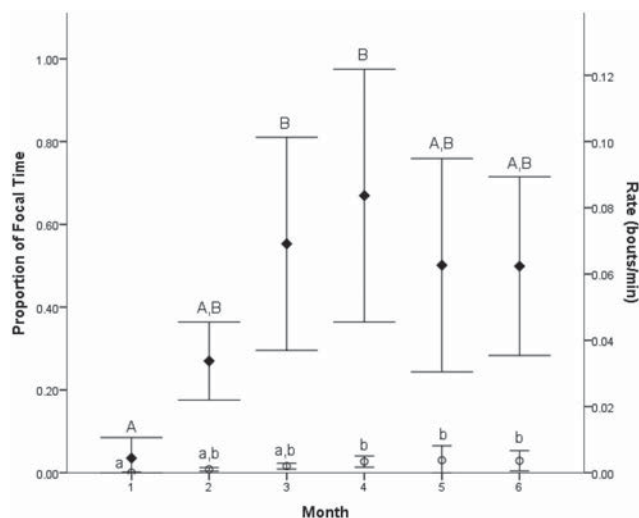


Figure 1. Friedman tests showed that the prevalence of infants' ($N = 7$) object manipulation behavior increased over their first 6 months of age. The median proportion of focal time that infants spent on object manipulation (o) increased significantly from the first to the fourth, fifth, and sixth months, while their rates of carrying out object manipulation bouts (◆) increased from the first, to the third and fourth months of development. Letters (proportion: lower case; rate: UPPER CASE) are used to denote statistical significance, such that significantly different months do not share letters. Error bars represent 95% confident intervals.

shell items, infants interacted with empty shells before they were observed to interact with food. For infants with more than 10 bouts of object manipulation in each time period for analysis ($N = 5$), there was a decrease in the proportion of bouts in which only shells were manipulated. A Wilcoxon signed-ranks test revealed that the median proportion of bouts in which only shell items were manipulated showed a significant decrease from the Time Period 1 ($Mdn = 0.32$) to the Time Period 2 ($Mdn = 0.18$), $z = -2.02$, $p = .04$. I did not find significant differences in the proportions of bouts in which only stones, both stones and shell items, and stones and/or shell items with anvils were manipulated, or in the average number of objects manipulated in each bout. Only one infant, Dat, was observed to carry out an object manipulation bout in which all the objects necessary for tool use on sessile oysters were present (i.e., stone and sessile oyster) in the fourth month after his first object manipulation, but he did not continue to regularly do so. None of the infants performed object manipulation bouts in which all objects necessary for tool use on unattached foods (i.e., stone, food, and anvil) were involved.

There were changes in the numbers of actions performed in object manipulation bouts and the types of actions performed across the months of object manipulation. All five infants showed an increase in the number of actions performed in each object-manipulation bout over the two time periods. A Wilcoxon signed-ranks test revealed that the median number of actions infants carried out during object-manipulation bouts increased significantly from Time Period 1 ($Mdn = 2.00$), to Time Period 2 ($Mdn = 2.18$), $z = 2.02$, $p = .04$.

The proportions of bouts in which infants carried out Critical Actions on objects also increased for all five infants. The median

proportion of bouts in which infants carried out Critical Actions increased significantly from Time Period 1 ($Mdn = 0.42$), to Time Period 2 ($Mdn = 0.64$), $z = 2.02$, $p = .04$. Critical-A actions performed by infants were "pick up stone" ($N = 10$), "pick up food" ($N = 8$), and "pick at oyster" or "mouth oyster" ($N = 11$). Critical-B actions carried out by infants were "place shell" ($N = 1$), "place stone" ($N = 2$), "rub food on anvil" ($N = 1$), "rub stone on oyster" ($N = 1$), "hit food on anvil" ($N = 1$), and "hit stone on anvil" ($N = 1$). The Critical Actions involving "pick up" were the earliest to emerge, followed by those involving "place," then those involving "rub," and lastly, those involving percussive actions.

Lastly, there were changes in the complexity of object-manipulation bouts. All five infants showed an increase in the proportion of bouts that were Hierarchical Class B-2 object-manipulation bouts, that is, object-manipulation bouts in which multiple objects were combined. A Wilcoxon signed-ranks test revealed that the median proportion of bouts that were Hierarchical Class B-2 increased from Time Period 1 ($Mdn = 0.00$), and Time Period 2 ($Mdn = 0.09$), $z = 2.02$, $p = .04$. The first combinatory actions to emerge during the first 6 months of manipulative development were placing objects on anvils, which was carried out by four of the 11 infants (Dat, Sai, Tpt, and Tup) and emerged between the first and fourth months after infants' first object manipulations. The next combinatory actions to emerge were rubbing objects on sand substrate and anvils, carried out by 5 of the 11 infants (Waw, Dat, Sai, Mek, and Tpt) and emerging between the third and fifth months of object manipulation. One infant (Dat) rubbed a stone on a sessile oyster in his fourth month of object manipulation. Percussive actions were the last to emerge, and only observed in two infants. One infant (Sai) interspersed rubbing a *Planaxis sulcatus* snail on an anvil surface with several instances of directly percussing the snail on the surface in his fifth month of manipulative development. Another infant (Dat), hit a stone onto an anvil surface in his sixth month of manipulative development. None of the infants were observed to carry out combinatory manipulations involving more than two objects.

Differences in manipulative behavior between age groups.

Prevalence of manipulative behavior. I obtained 8,266 manipulative bouts consisting of 866 object-manipulation bouts, and 7,400 tool-use bouts from 5,990 focal samples on 69 macaques. This was a total time of about 181 hr of activity with stones and shells, consisting of approximately 72 hr of object manipulation, and 109 hr of tool use from 499 hr of focal sampling.

Altogether, 62 of the 69 macaques, or 90% of individuals were observed to carry out manipulative bouts, during their focal samples. The proportion of individuals that manipulated, total numbers of bouts, proportions of focal time spent on, and rates of manipulative bouts for each age group is given in Table 8.

The proportions of focal time that individuals spent in manipulative behavior ($M = 0.04$, 95% CI [0.03, 0.05]) differed significantly across age groups [$H_6, N = 69 = 18.44$, $p = .01$] (see Figure 2). There was an overall upward trend in the proportion of time that individuals spent in manipulative bouts, but decreasing in the oldest age group. There were significant differences between Age Groups 2 ($Mdn = 0.003$) and 5 ($Mdn = 0.07$), $t = -35.89$, $p = .01$; and Age Groups 2 and 6 ($Mdn = 0.07$), $t = -34.96$, $p = .04$.

Table 7

Actions Recorded in Infants' Object Manipulation Bouts, the Month in Which Each Action was First Recorded for Each Infant, and the Total Number of Individuals Recorded to Perform Each Action

Item	Action	Dwg	Sfa	Waw ^a	Dat ^a	Cha ^a	Sai ^a	Mpr	Gbi ^a	Mek ^a	Tpt ^a	Tup	Total
Single-item manipulations													
Stone	Pick up (A)	2	1	1	2	2	2		2	1	1	1	10
	Hold	2		4	3	3	2		4		1	2	8
	Carry			4	3		3						3
	Manipulate	1	1	1	1	2	2	1	1		1	1	10
	Touch	1	1	1		1	1	2	2		1	1	9
	Mouth	2	1	1		1		2	1	1	1	1	9
	Sniff			2		2	1					1	4
	Rub on ground											2	1
	Push off anvil	2									2		2
	Carry in mouth					2							1
Unattached food	Pick up (A)	2		4		5	2	4	5	1			7
	Carry					5			5	4			3
	Mouth			4		5	2	4	5	1			6
	Manipulate						3	4		4			3
	Carry in mouth	2											1
	Rub on ground									4			1
Sessile oysters	Pick at (A)	2		2	4	2							4
	Mouth (A)	2		2	4	1							4
Empty shells	Pick up			2	1	1	1	5	2	1	1	1	9
	Mouth			2	1	1	1		2	3	1	1	8
	Manipulate			1		2	2			1	3	1	6
	Touch			3									1
	Examine			1				5					2
	Hold			3	3		2		2				4
	Carry			3	2	2			2	5	2		6
	Mouth	1						1	1				3
Anvil													
Two-item combinations													
Stone/anvil	Place stone on anvil (B)			7	2		2				4		4
	Rub stone on anvil			5	3								2
	Hit stone on anvil (B)				6								1
Unattached food/anvil	Rub food on Anvil (B)						3			5			2
	Direct percussion on anvil (B)						5						1
Empty shell/anvil	Place shell on anvil (B)											1	1
	Rub shell on anvil										5		1
Object-manipulation	Rub stone on oysters (B)				4								1
	Total different actions:	11	4	19 ^b	14	16	16	9	13	12	12	11	

^a Data from these infants were used in statistical analyses on the longitudinal changes in object manipulation behavior. ^b This count of actions developed at 6 months of object manipulation excludes the action "Place stone on anvil," which was only recorded in Waw's seventh month of object manipulation.

The rates of carrying out manipulative bouts ($M = 1.71$ bouts/hr, 95% CI [1.20, 2.21]) also differed between age groups ($H_6 = 22.76$, $p = .001$; see Figure 2). The median rate generally increased from younger to older age groups, until the decrease in the oldest age group, with significant differences between Age Groups 2 ($Mdn = 0.08$ bouts/hr) and 5 ($Mdn = 4.34$ bouts/hr), $t = -39.72$, $p = .004$; 2 and 6 ($Mdn = 3.87$ bouts/hr), $t = -35.79$, $p = .03$; and 3 ($Mdn = 0.34$ bouts/hr) and 5, $t = -32.56$, $p = .04$.

Correctness of manipulative behavior.

Object correctness. Overall, 32% of all bouts involved only stones, 22% involved only shell items, and 46% involved both stones and shell items. Bouts corresponding to each object category composed a different proportion of the total bouts for each age group (Figure 3a). I found significant differences in the proportions of manipulative bouts in which individuals in each age group involved only stones [$H_6 = 41.53$, $p < .001$], and both stones and shell items [$H_6 = 34.43$, $p < .001$], but no significant

differences in the proportions of manipulative bouts involving only shell items. In all age groups, there was a lower proportion of manipulative bouts in which individuals handled only shell items as compared with the other two object categories, suggesting that the manipulation of shell items alone was less common in general.

Overall, manipulative bouts involving only stones decreased from younger to older age groups. Differences in the proportions of manipulative bouts involving only stones were significant when comparing between Age Groups 1 ($Mdn = 72\%$) and 5 ($Mdn = 0\%$), $t = 33.68$, $p = .002$; 1 and 6 ($Mdn = 0\%$), $t = 33.68$, $p = .004$; and 1 and 7 ($Mdn = 0\%$), $t = 30.42$, $p < .001$, and well as Age Groups 2 ($Mdn = 60\%$) and 5, $t = 31.94$, $p = .01$; 2 and 6, $t = 31.94$, $p = .01$; and 2 and 7, $t = 28.61$, $p = .001$ (Figure 3b).

Conversely, manipulative bouts involving both stones and shell items increased from younger to older age groups. Differences in the proportions of manipulative bouts involving both stones and shell items, were significant between Age Groups 1 ($Mdn = 2\%$) and 5

Table 8

Number and % of Individuals That Carried out Manipulative Bouts, and the Total Hours and Numbers of Manipulative Bouts Analyzed in Each Age Group

Age group	Total N	n	Hours	Number of manipulative bouts (object manipulation, tool use)
1	11	11 (100%)	18.98	363 (363, 0)
2	9	9 (100%)	2.61	46 (46, 0)
3	9	8 (89%)	20.06	150 (150, 0)
4	5	4 (80%)	21.41	689 (48, 641)
5	6	6 (100%)	23.52	1,465 (23, 1,442)
6	5	5 (100%)	22.17	1,324 (11, 1,313)
7	24	19 (79%)	72.46	4,229 (225, 4,004)
Total	69	62 (90%)	181.21	8,266 (866, 7,400)

(*Mdn* = 99%), $t = 31.88$, $p = .01$; 1 and 6 (*Mdn* = 99%), $t = -34.05$, $p = .01$; and 1 and 7 (*Mdn* = 99%), $t = -21.52$, $p = .03$, as well as Age Groups 2 (*Mdn* = 0%) and 5, $t = -37.06$, $p = .002$; 2 and 6, $t = 39.22$, $p = .002$; and 2 and 7, $t = -26.70$, $p = .004$ (Figure 3b).

The proportions of bouts in which all objects needed for correct tool use also differed for individuals in different age classes [Sessile Oysters: $H_6 = 36.71$, $p < .001$; Unattached Food: $H_6 = 26.07$, $p < .001$]. Recall from the results of the longitudinal analysis on infants, objects needed for correct axe hammering on sessile oysters (i.e., stone and oysters) was first observed on one occasion in one infant (Dat) in his fourth month of manipulative development. However, bouts involving complete objects for axe hammering remained rare, especially in Age Groups 1 and 2. The median propor-

tions of bouts in which stones and sessile oysters were present increased across age classes, and was significantly higher in Age Groups 5 (*Mdn* = 81%), 6 (*Mdn* = 98%) and 7 (*Mdn* = 87%), as compared with Age Group 1 (*Mdn* = 0%); [$t_{(1 \times 5)} = -29.75$, $p = .02$; $t_{(1 \times 6)} = -40.55$, $p = .001$; $t_{(1 \times 7)} = -25.76$, $p = .002$], and Age Group 2 (*Mdn* = 0%); [$t_{(2 \times 5)} = -29.94$, $p = .03$; $t_{(2 \times 6)} = -40.94$, $p = .001$; $t_{(2 \times 7)} = -26.16$, $p = .01$] (Figure 3b). Bouts in which all objects needed for pound hammering of unattached foods (i.e., food, stone, and anvil), emerged later, and was only first observed in 1 juvenile (Pld) in Age Group 3 (1.5–2.5 years). The median proportions of bouts in which stones, unattached foods, and anvils were present was significantly higher in Age Group 5 (*Mdn* = 17%), than Age Groups 1, 2, and 3 (*Mdn* = 0%); [$t_{(1 \times 5)} = -31.92$, $p = .002$; $t_{(2 \times 5)} = -30.50$, $p = .01$; $t_{(3 \times 5)} = -29.96$, $p = .01$]; Figure 3b).

Action correctness. I documented 14 different actions on stones, 10 actions on unattached food items, 2 actions on sessile oysters, 8 actions on shells, and 2 actions on anvils. I also documented 23 two-item, 9 three-item, and 1 four-item combinatory manipulations (see Table 1). The numbers of individuals observed to perform each action and the number of actions observed for each age group varied across age groups (see Table 9). Some actions, that is, picking up, holding, and carrying stones, picking up unattached foods, and picking at and mouthing sessile oysters were ubiquitous across all age groups. Three and four item combinations were not observed in age Groups 0–0.5 years, and 0.5–1.5 years. The number of different actions performed was highest in Age Group 3, and was higher in younger age groups (Age Groups 1, 2, 3, and 4), than older age groups.

The proportions of manipulative bouts in which Critical-A Actions [$H_6 = 54.98$, $p < .001$], and Critical-B Actions [$H_6 = 17.27$, $p = .01$] were performed differed across individuals in different age groups (see Figure 4). The proportion of manipulative bouts in which Critical-A Actions were performed increased from Age Group 1 (*Mdn* = 40%) to Age Group 3 (*Mdn* = 100%), and by Age Groups 4 to 7 Critical-A actions were performed in all bouts. The increase was significant between Age Groups 1 and 3, $t = -25.49$, $p = .01$, 1 and 4, $t = -33.36$, $p = .01$, 1 and 5, $t = -33.36$, $p = .001$, 1 and 6, $t = -33.36$, $p = .002$, and 1 and 7, $t = -33.36$, $p < .001$. The increase in Critical-A actions was also significant between Age Groups 2 (*Mdn* = 67%) and 3, $t = -23.60$, $p = .04$, 2 and 4, $t = -31.44$, $p = .02$, 2 and 5, $t = -31.44$, $p = .003$, 2 and 6, $t = -31.44$, $p = .01$ and 2 and 7, $t = -31.44$, $p < .001$.

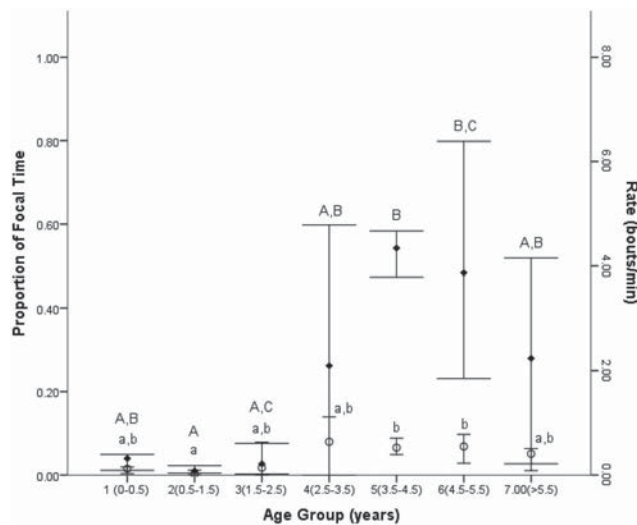


Figure 2. Kruskal-Wallis H tests indicated that macaques in different age groups differed in the median proportions of focal time spent in manipulative activity (○) and rates at which manipulative bouts were carried out (●). These differences were between macaques in age Groups 2 (0.5–1.5 years), and age Groups 5 (3.5–4.5 years) and 6 (4.5–5.5 years) for both proportion of time spent and rate of manipulative activity, and additionally between age Group 3 (1.5–2.5) and age Group 5 for rate of manipulative activity. Letters (proportion: lower case; rate: UPPER CASE) are used to denote statistical significance, such that significantly different months do not share letters. Error bars represent 95% confidence intervals.

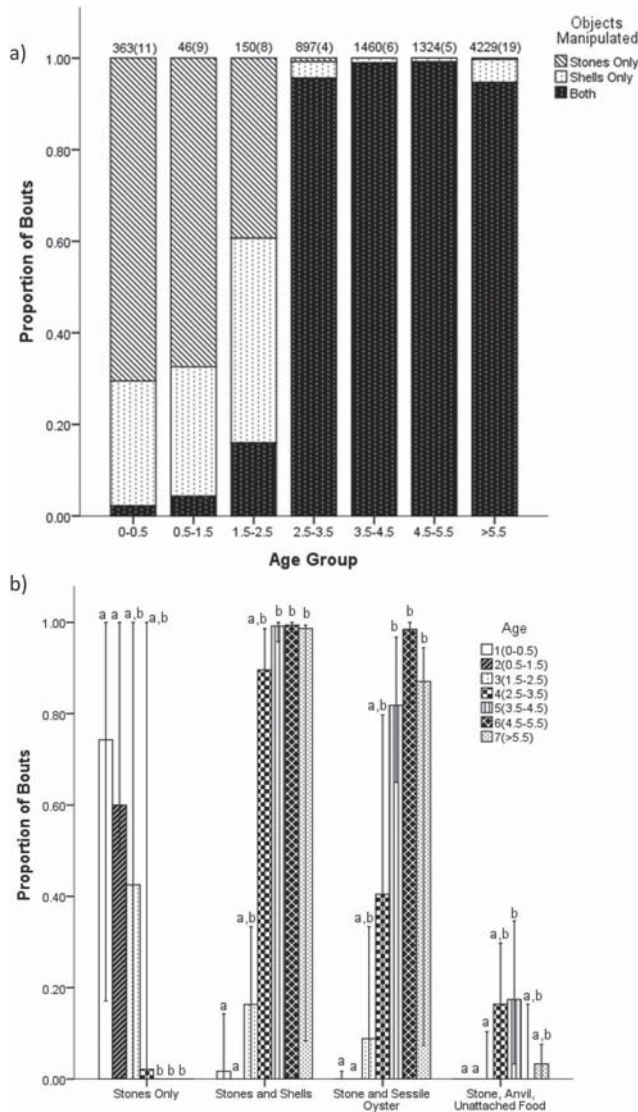


Figure 3. With regards to the types of objects manipulated and object correctness, (a) data showed that different compositions of each age group's total manipulative bouts in which only stones, only shell items, or both stones and shells were involved. Kruskal-Wallis H tests found differences in the median proportions of bouts in which (b) only stones, both stones and shell items, all objects involved in tool use on sessile oysters, that is, a stone and sessile oyster, and all objects involved in tool use on unattached food, that is, stone, anvil, unattached food was involved. Letters are used to denote statistical significance, and significantly different age groups do not share letters. Error bars represent 95% confidence intervals.

Because the Critical Actions "pick up stone," "pick up unattached food," and "pick at sessile oyster" were carried out by all individuals, I also examined differences in the proportion of manipulative bouts in which Critical-A Actions were performed between age groups when these actions were excluded. There continued to be significant differences across age groups in the proportion of bouts in which Critical-A Actions were performed when "pick up stone," "pick up unattached food," and "pick at sessile oyster" were excluded [$H_6 = 38.62, p < .001$]. After this

exclusion, the proportions of individuals' bouts in which Critical-A actions were performed fell to zero in Age Groups 1 and 2, and then increased from Age Groups 3 onward. Increases were significant between Age Groups 1 ($Mdn = 0\%$) and 5 ($Mdn = 99\%$), $t = -33.83, p = .002$; 1 and 6 ($Mdn = 99\%$), $t = -36.00, p = .002$; and 1 and 7 ($Mdn = 99\%$), $t = -24.00, p = .004$, as well as between Age Groups 2 ($Mdn = 0\%$) and 5, $t = -33.83, p = .01$; 2 and 6, $t = -36.00, p = .003$; 2 and 7, $t = -24.00, p = .01$.

Unlike Critical-A Actions, the proportion of manipulative bouts in which Critical-B Actions were performed did not increase linearly across age groups. Instead, Critical-B Actions were performed in the highest proportion of bouts of individuals in Age Group 3, and this difference was significant between Age Groups 3 ($Mdn = 61\%$) and 1 ($Mdn = 3\%$), $t = -26.84, p = .03$; 3 and 2 ($Mdn = 0\%$), $t = -26.56, p = .047$; and 3 and 6 ($Mdn = 1\%$), $t = -35.36, p = .01$.

Complexity of manipulative behavior. The composition of total manipulative bouts that fell into each hierarchical class differed for each age group (see Figure 5). I found significant differences in the proportion of bouts in which individuals carried out manipulations of all Hierarchical Classes, except Class B1, which was not observed in any age group except Age Group 1, meaning that macaques did not often manipulate multiple objects simultaneously without combining them.

Class A-1-i manipulative bouts, single actions on single objects, decreased from Age Groups 1 to 4, and were not recorded for individuals from Age Groups 5 to 7. The median proportions of manipulative bouts that were Class A-1-i differed across age groups [$H_6 = 42.76, p < .001$]. The median proportion of manipulative bouts for individuals in Age Groups 1 ($Mdn = 38\%$) that were Class A-1-i manipulative bouts was significantly higher than in Age Groups 5 ($Mdn = 0\%$), $t = 31.18, p = .001$; 6 ($Mdn = 0\%$), $t = 31.18, p = .003$; and 7 ($Mdn = 0\%$), $t = 31.18, p < .001$. The median proportion of bouts for individuals in Age Group 2 ($Mdn = 36\%$) that were = Class A-1-i was significantly higher than in Age Groups 5, $t = 26.16, p = .03$; and 7, $t = 26.17, p = .001$.

Class A-1-ii manipulative bouts, multiple actions on single objects, decreased from Age Groups 1 to 3, and were not recorded during focal samples for individuals from Age Groups 4 to 7, except for 1 individual in Age Group 7. There were significant differences in the proportions of manipulative bouts that were Class A-1-ii [$H_6 = 42.71, p < .001$]. The proportion of bouts in which individuals in Age Group 1 ($Mdn = 53\%$) carried out Class A-1-ii manipulative bouts was higher than that of individuals in Age Groups 4 ($Mdn = 0\%$), $t = 34.46, p = .004$; 5 ($Mdn = 0\%$), $t = 34.46, p < .001$; 6 ($Mdn = 0\%$), $t = 34.46, p = .001$; and 7 ($Mdn = 0\%$), $t = 32.69, p < .001$.

Class A-2 manipulative bouts were carried out in the highest proportion of bouts by individuals in Age Group 1; only single individuals in Age Groups 2 and 3, and no individuals in Age Groups 4 to 7 carried out Class A-2 manipulative bouts. There were significant differences between age groups in the proportion of manipulative bouts that were Class A-2. The difference was significant between Age Group 1 ($Mdn = 5\%$) and all other age groups ($Mdn = 0\%$), [$t_{(1 \times 2)} = 21.67, p = 0.001$; $t_{(1 \times 3)} = 22.08, p = .002$; $t_{(1 \times 4)} = 25.45, p = .01$; $t_{(1 \times 5)} = 25.46, p = .001$; $t_{(1 \times 6)} = 25.46$; $t_{(1 \times 7)} = 25.45, p = .002$].

Table 9

Numbers of Individuals in Each Age Group Observed to Carry Out Each Manipulative Action, as Well as the Total Number of Individuals Observed to Carry Out Each Action, and the Total Number of Different Actions Observed for Each Age Group

		Number of individuals/age group (N)								
Item	Action	1 (11)	2 (9)	3 (9)	4 (5)	5 (6)	6 (5)	7 (24)	All (69)	
Single-item manipulations										
Stone	Pick up (A)	9	8	7	4	6	5	15	54	
	Hold	6	4	5	3	6	5	15	44	
	Carry	5	2	3	3	6	5	13	37	
	Manipulate	11	6	4					21	
	Touch	10	4	1					15	
	Mouth	11	3	2					16	
	Sniff	6	1	1					8	
	Rub on ground	1	3						4	
	Push off anvil	1	1						2	
	Carry in mouth	3							3	
	Examine			2					2	
	Hug		1						1	
	Pick at			1					1	
	Hit on ground			1					1	
	Unattached food	Pick up (A)	8	3	5	3	6	5	24	54
Carry		4	1	1	1	6	5	24	42	
Mouth		8	4	4		6	5	24	51	
Hold		8	4			6	5	24	47	
Manipulate		6	4	2	1				13	
Carry in mouth		2	3	2					7	
Rub on ground		2	2						4	
Rub on body				1					1	
Hit with hand					1				1	
Examine				1	1				2	
Pick at (A)		4	9	3	2	6	5	24	53	
Mouth		4	9	3	2	6	5	24	53	
Empty shells		Pick up	10	3	1					14
		Mouth	10	1	1					12
		Manipulate	7		1					8
	Touch	1							1	
	Examine	2							2	
	Hold	2							2	
	Carry	5							5	
	Carry in mouth	3							3	
	Anvil	Mouth	3							3
		Pick at			1					1
Two-item combinations										
Stone/anvil	Place stone on anvil (B)	5	2	4	1	1			13	
	Rub stone on anvil	2	3	7					12	
	Swipe stone on anvil		1	1					2	
Unattached food/anvil	Hit stone on anvil (B)			3	3				6	
	Place food on anvil (A)			1	2	6	1	11	21	
	Rub food on Anvil (B)	3	2	5	1	1		1	13	
	Swipe food on anvil (B)			2	1				3	
	Direct percussion on anvil (B)	1		2	3		3	14	23	
Empty shell/anvil	Place shell on anvil (B)	1							1	
	Rub shell on anvil	1							1	
	Hit shell on anvil (B)			1					1	
Stone/sessile oyster	Rub stone on oysters (B)	1		2					3	
	Swipe stone on oysters (B)			2					2	
	Hit stone on oysters (A–tool use)			2	3	6	5	13	29	
Unattached food/sessile oyster	Rub unattached food on oysters			1					1	
	Hit unattached food on oysters (B)			1	1				2	
Two stones	Combine stone with stone		1						1	
Stone/other	Combine stone with other		1						1	
Stone/unattached food	Combine unattached food under stone (B)			1					1	
	Combine unattached food above stone (B)				1				1	
Unattached food/other	Combine unattached food with other			1	1	1			3	
Two unattached foods	Combine food with food			1					1	

Table 9 (continued)

Item	Action	Number of individuals/age group (N)							
		1 (11)	2 (9)	3 (9)	4 (5)	5 (6)	6 (5)	7 (24)	All (69)
Unattached food/empty shell	Combine unattached food with shell			1					1
Three-item combinations									
Unattached food/two stones	Combine unattached food with two stones (B)				1				1
Two unattached foods/anvil	Hit unattached food on unattached food placed on anvil (B)							1	1
Two stones/anvil	Hit stone on stone placed on anvil (B)				1				1
Unattached food/shell/anvil	Combine unattached food with shell and hit on anvil (B)			1					1
Stone/unattached food/anvil	Combine food above stone and place combination on anvil (B)				1				1
	Combine food above stone and hit combination on anvil (B)				1				1
	Combine food under stone and hit combination on anvil (B)				1				1
	Hit food on stone placed on anvil (B)			1	1				2
	Hit stone on food placed on anvil (A=tool use)				3	6	1	9	19
Four-item combinations									
Unattached food/two stones/anvil	Combine food under stone and hit combination on another stone placed on anvil (A)				1				1
Total actions in age class:		35	27	44	28	15	13	15	

Class B-2 manipulative bouts were carried out in the highest proportion of bouts by individuals in Age Group 3. There were differences between age groups in the median proportions of manipulative bouts that were Class B-2 [$H_6 = 24.10$, $p < .001$] and the differences were significant between Age Groups 3 ($Mdn = 80\%$) and 1 ($Mdn = 35\%$), $t = 31.19$, $p = .004$; 3 and 5 ($Mdn = 1\%$), $p = .01$, $t = 34.10$; and 3 and 6 ($Mdn = 1\%$), $t = 37.09$, $p = .01$. In addition, the types of actions in B-2 manipulative bouts were different in different age groups. In Age Groups 1 to 4, individuals carried out a variety of B-2 manipulative actions, such as rubbing or swiping stones, shells, and shelled food items on anvils or other items. For one individual in Age Group 3 (Pld), two B-2 manipulative bouts featured all the actions required for cracking unattached foods, but carried out in erroneous sequence interspersed with other noncritical actions. In one of these bouts, she placed an unattached oyster on top of a stone, and hit both items down onto an anvil. In another bout involving a clam, an empty shell, a stone, and an anvil, she again placed the clam onto the stone and hit both items down onto an anvil, amid other inept actions that were hitting the stone on to the anvil, placing the clam on top of an empty shell and hitting both items onto the anvil, rubbing the clam on the anvil, directly percussing the clam on the anvil, and attempting to bite open the clam. In Age Groups 5 to 7 however, B-2 manipulative actions consisted only of direct percussion of unattached food items onto anvils, with the exceptions of one individual in Age Group 7 that rubs stones on anvils, and another individual in Age Group 7 that rubbed a clam on an anvil.

Opposite to Class A manipulative bouts, Class C-S and Class C-U manipulative bouts, which were those involving the correct action sequences for tool use on sessile oysters and unattached food, respectively, increased from younger to older age groups. There were significant differences between age classes in the

proportion of manipulative bouts that were Class C-S [$H_6 = 38.43$, $p < .001$] and Class C-U [$H_6 = 34.79$, $p < .001$]. Class C-S manipulations were only recorded in individuals from Age Group 3 and older. Two individuals in Age Group 3 (Pld, Fgn) hit sessile oysters with stones, but were not successful on any occasion. Proportions of bouts that were Class C-S were higher in Age Groups 5 ($Mdn = 81\%$), 6 ($Mdn = 98\%$), and 7 ($Mdn = 87\%$), than in Age Group 1 ($Mdn = 0\%$); [$t_{(5 \times 1)} = 28.67$, $p = .02$; $t_{(6 \times 1)} = 40.30$, $p < .001$; $t_{(7 \times 1)} = 25.21$, $p = .002$], and Age Group 2 ($Mdn = 0\%$); [$t_{(5 \times 2)} = 28.68$, $p = .03$; $t_{(6 \times 2)} = 40.30$, $p < .001$; $t_{(7 \times 2)} = 25.21$, $p = .01$], and also higher in Age Group 6 than in Age Group 3 ($Mdn = 1\%$); $t = 31.68$, $p = .02$. Class C-U manipulations emerged later than Class C-S, and were only recorded in individuals in Age Group 4 and older. The proportion of bouts that were Class C-U was higher in Age Group 5 ($Mdn = 17\%$) than in Age Groups 3, 2, and 1 ($Mdn = 0\%$); [$t_{(5 \times 3)} = 33.50$, $p = .002$; $t_{(5 \times 2)} = 33.50$, $p = .001$; $t_{(5 \times 1)} = 33.50$, $p = .001$]. The proportion of bouts that were Class C-U were also higher in Age Groups 4 ($Mdn = 18\%$) and 7 ($Mdn = 3\%$) than in Age Group 1 [$t_{(4 \times 1)} = 27.50$, $p = .05$; $t_{(7 \times 1)} = 18.16$, $p = .046$].

In Age Group 4, two individuals that carried out Class-C manipulation bouts sometimes also carried out Class B-2 manipulations, amid the correct tool use sequences. One individual (Chk), carried out erroneous object combinations and action sequences, in several bouts where he also produced the correct object-action sequences to crack a *Planaxis sulcatus* snail. These erroneous sequences were placing the snail either on top of the tool or under the tool and hitting both items on the anvil simultaneously, placing the tool on the anvil and hitting it with the snail, manipulating the tool and snail while holding them in contact with each other but not relating them to the anvil, and placing the snail on the anvil but striking at another location on

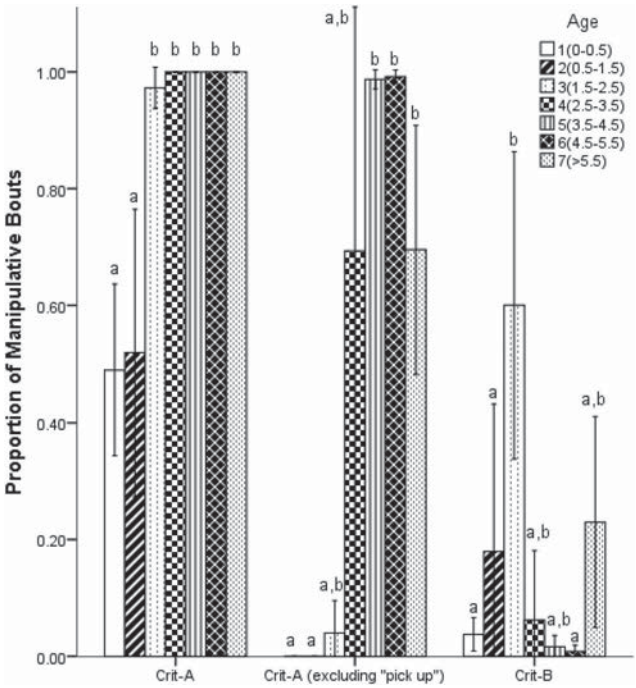


Figure 4. With regards to action correctness, Kruskal-Wallis H tests found significant differences in the median proportions of bouts in which Critical-A actions were performed, including when the more ubiquitous actions of “pick up stone” and “pick up food” were excluded, as well as in the proportion of bouts in which Critical-B actions were performed. Letters are used to denote statistical significance, and significantly different age groups do not share letters. Error bars represent 95% confidence intervals.

the anvil with the tool. Another individual (Moo) picked up a stone and hit it on a blank rock surface (without sessile oyster coverage), before carrying the stone a short distance and using it to strike oysters. These superfluous action sequences were not observed in the Class C manipulations, that is, tool use, of individuals in Age Group 5 and older.

Changes in tool-use characteristics.

Longitudinal changes following first successful tool use. I observed one juvenile male, Chk, carry out his first successful tool use on an unattached food item (*Planaxis sulcatus*) on 5th February 2015, and observed him successfully cracking sessile oysters on February 22, 2015. In all food categories, Chk’s average bout duration, strike frequency, and rate of tool changes decreased (i.e., tool fidelity increased) over the months following first tool use, while strike rate, strike accuracy index, and proportion of successful bouts increased (Figure 6a and 6b). Some changes appeared gradual with no significant change between months, however, by the third month of his first tool use, Chk’s overall proportion of successful tool use bouts across sessile oysters and unattached foods increased beyond the 95% confidence limits of his first 2 months of tool use (Figure 6a vi and 6b vi). Strike accuracy also saw significant increases, with the strike accuracy index of the third month higher than the 95% confidence limit of the first two months for tool use on sessile oysters (Figure 6a iv). Strike accuracy took longer to improve for tool use on unattached food, with the difference only apparent from the fifth month (Figure 6b

iv). For tool use on sessile food, strike rate was significantly higher from the second month of tool use (Figure 6a iii), but this change was not observed for tool use on unattached food.

Differences in tool-use characteristics between age groups.

Prevalence of tool use. Overall, tool users spent 57% of their foraging time with a tool in hand, and carried out 1.30 bouts of tool use per minute of foraging time. These values increase from juvenile tool users (Age Group 4: $M_{prop} = 0.49$, 95% CI [0.30, 0.68]; $M_{rate} = 1.18$ bouts/min, 95% CI [0.54, 1.81]) into adolescence (Age Group 5: $M_{prop} = 0.55$, 95% CI [0.47, 0.63]; $M_{rate} = 1.26$ bouts/min, 95% CI [1.06, 1.46]) and early adulthood (Age Group 6: $M_{prop} = 0.61$, 95% CI [0.44, 0.77]; $M_{rate} = 1.45$ bouts/min, 95% CI [0.76, 2.15]), and fall slightly in mature adulthood (Age Group 7: $M_{prop} = 0.58$, 95% CI [0.48, 0.69]; $M_{rate} = 1.28$ bouts/min, 95% CI [0.96, 1.60]), but these differences did not reach statistical significance in ANOVA tests.

Changes in proficiency measures. The means and SDs of proficiency measures in different age classes are listed in Table 10. I found significant differences between age classes for some proficiency measures of tool use analyzed across all foods and on sessile oysters only, but no significant differences between age classes for tool use on unattached foods only. Results are described below, and test statistics provided in Table 11 (ANOVA or Kruskal-Wallis H tests) and Table 12 (post hoc tests).

There were significant differences between age groups in strike efficiency when tool use was analyzed across both food types (Figure 7a), and sessile oysters only (Figure 7b). Strike efficiency increased (i.e., average strike frequency decreased) from younger to older age groups and differences were significant between Age Groups 4 and 7.

There were also significant differences between age groups in strike accuracy analyzed across both food types. Strike accuracy

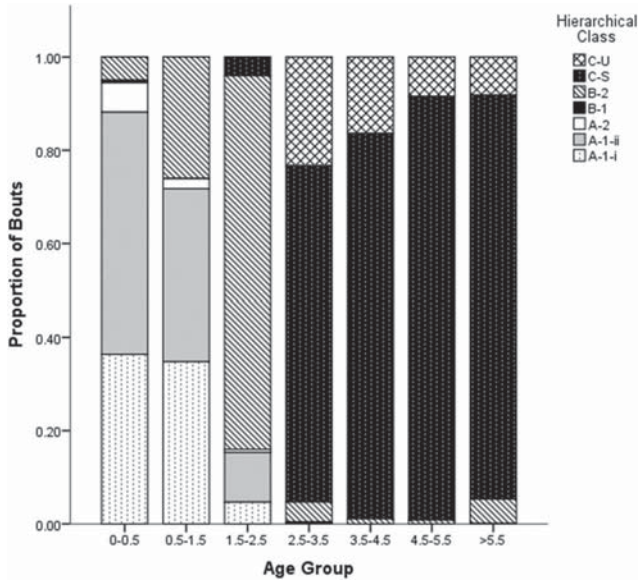


Figure 5. With regards to the complexity of manipulative behavior across age groups, data showed different compositions of each age group’s total manipulative bouts that fell into each hierarchical class.

a) Sessile Oysters

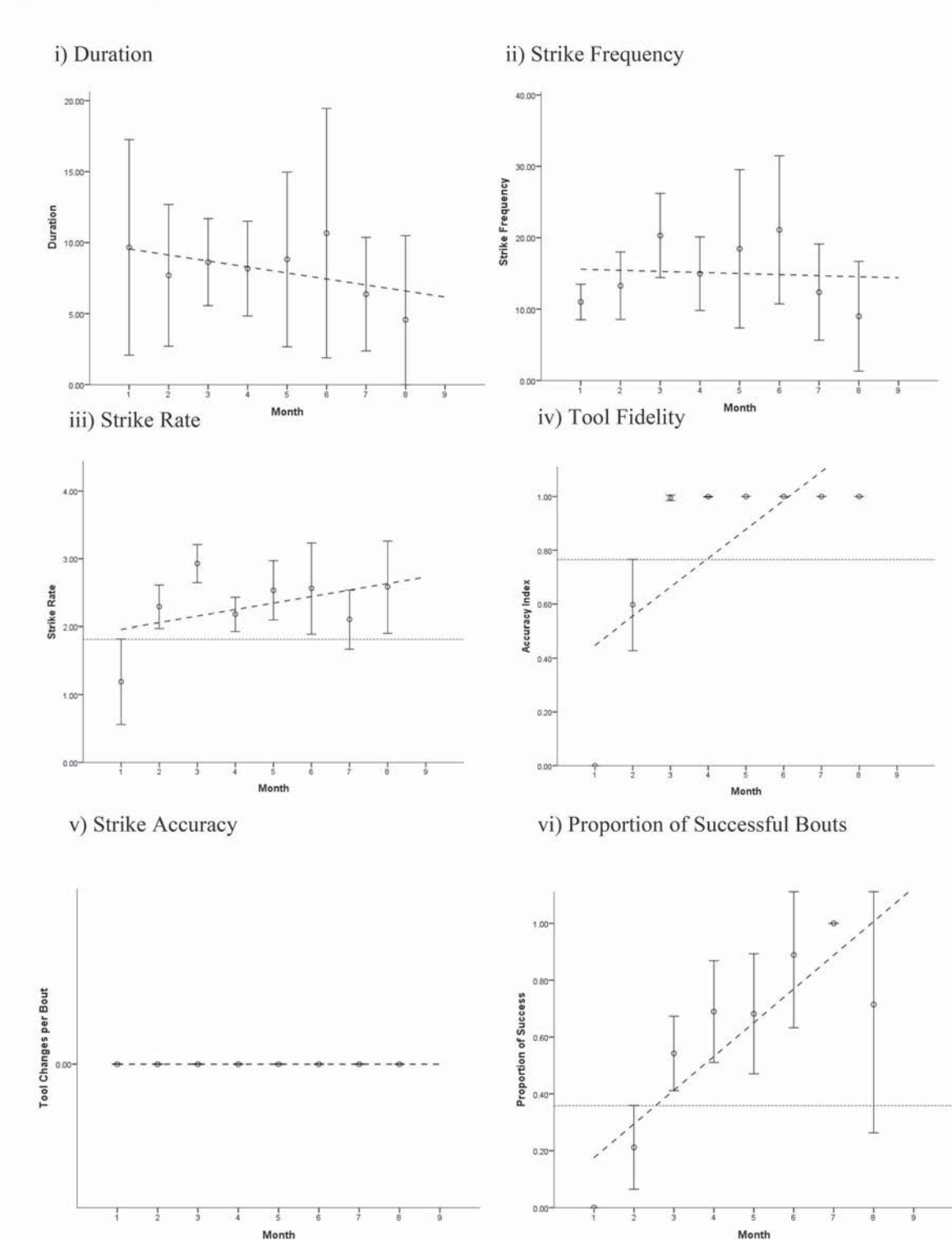


Figure 6. Chk's average bout duration, strike frequency, strike rate, strike accuracy index, rate of tool change, and proportion of successful bouts showed changes over the months following first tool use on (a) sessile oysters, and (b) unattached food. Error bars represent 95% confidence intervals of the means of each month's data, and red dotted lines indicate significant changes.

b) Unattached Food

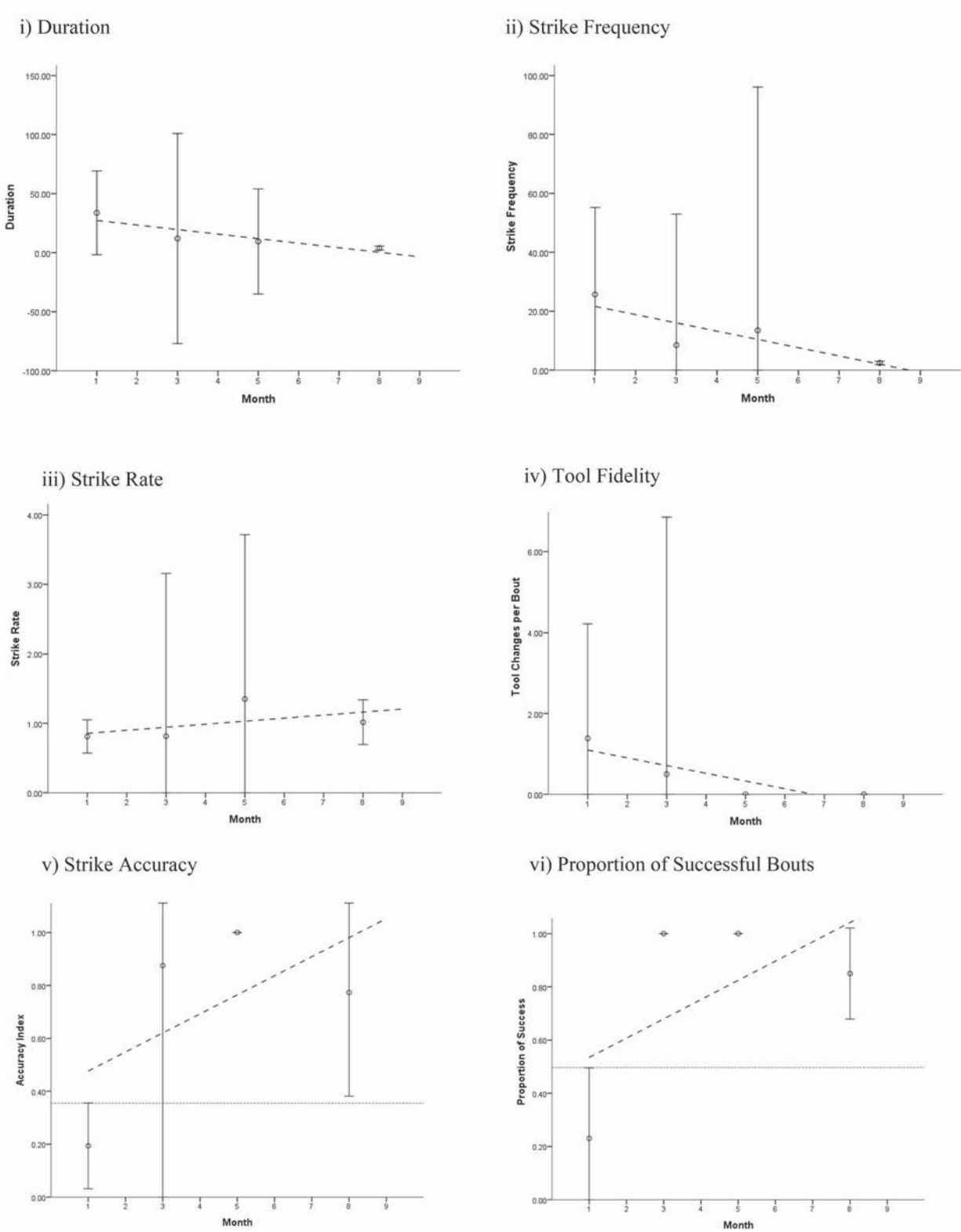


Figure 6. (Continued)

Table 10
Means and 95% Confidence Intervals of Each Individuals' Tool-Use Characteristics Across Age Groups

Characteristic	Age group	M [95% CI]		
		All food	Sessile	Unattached
Duration	2.5–3.5 years	7.59 [1.17, 14.01]	7.21 [1.29, 13.14]	9.34 [–3.42, 22.09]
	3.5–4.5 years	5.58 [4.34, 6.82]	5.30 [3.84, 6.68]	12.01 [1.12, 22.90]
	4.5–5.5 years	5.42 [3.52, 7.32]	5.41 [3.50, 7.32]	5.64 [n.a.]
	>5.5 years	5.20 [4.35, 6.05]	4.93 [4.13, 5.73]	6.19 [4.39, 8.00]
	Total	5.59 [4.95, 6.23]	5.37 [4.74, 6.00]	8.63 [5.32, 11.93]
Strike frequency	2.5–3.5 years	12.95 [4.24, 21.65]	13.87 [5.01, 22.75]	8.73 [.90, 16.55]
	3.5–4.5 years	9.38 [7.13, 11.63]	10.09 [8.20, 11.98]	6.92 [2.59, 11.25]
	4.5–5.5 years	11.38 [7.79, 14.97]	11.4 [8.12, 14.82]	4.27 [n.a.]
	>5.5 years	8.78 [7.64, 9.93]	9.28 [8.31, 10.26]	6.42 [4.11, 8.72]
	Total	9.86 [8.82, 10.90]	10.42 [9.41, 11.42]	6.85 [5.35, 8.46]
Strike rate	2.5–3.5 years	2.13 [1.56, 2.69]	2.32 [1.56, 3.08]	1.23 [.63, 1.83]
	3.5–4.5 years	2.16 [1.54, 2.79]	2.34 [1.78, 2.92]	.93 [.71, 1.15]
	4.5–5.5 years	2.51 [1.72, 3.30]	2.53 [1.78, 3.27]	1.08 [n.a.]
	>5.5 years	2.11 [1.78, 2.45]	2.19 [1.95, 2.43]	1.26 [1.03, 1.49]
	Total	2.20 [1.98, 2.41]	2.31 [2.13, 2.49]	1.14 [1.00, 1.27]
Accuracy index	2.5–3.5 years	.93 [.78, 1.07]	.96 [.83, 1.09]	.74 [.39, 1.10]
	3.5–4.5 years	.96 [.93, .99]	.99 [.97, 1.01]	.71 [.46, .95]
	4.5–5.5 years	1.00 [.99, 1.00]	1.00 [1.00, 1.00]	.91 [n.a.]
	>5.5 years	.97 [.96, 1.00]	.99 [.99, 1.00]	.89 [.80, .98]
	Total	.97 [.96, .99]	.99 [.98, 1.00]	.81 [.72, .89]
Tool change rate	2.5–3.5 years	.05 [–.04, .14]	.03 [–.02, .09]	.18 [–.55, .90]
	3.5–4.5 years	.02 [.004, .03]	.01 [–.004, .03]	.11 [–.04, .25]
	4.5–5.5 years	.01 [–.02, .03]	.01 [–.02, .04]	.02 [n.a.]
	>5.5 years	.01 [.0006, .02]	.01 [–.003, .01]	.03 [.01, .05]
	Total	.02 [.01, .02]	.01 [.003, .02]	.08 [.01, .15]
Proportion of success	2.5–3.5 years	.72 [.39, 1.08]	.73 [.36, 1.10]	.75 [.51, 1.00]
	3.5–4.5 years	.83 [.78, .87]	.84 [.80, .89]	.74 [.58, .89]
	4.5–5.5 years	.86 [.82, .93]	.88 [.81, .94]	.95 [n.a.]
	>5.5 years	.88 [.84, .90]	.88 [.85, .91]	.84 [.75, .93]
	Total	.85 [.82, .89]	.85 [.82, .88]	.81 [.73, .86]

increased from younger to older age groups (Figure 7a ii). Macaques in Age Groups 6 and 7 had significantly higher median strike accuracy than those in Age Group 4 and Age Group 5.

Tool fidelity also differed between age groups when analyzed across all foods. Tool fidelity increased, that is, the number of times the macaques changed tools per bout decreased, from younger to older age groups (Figure 7a iii). Tool fidelity was significantly higher in Age Groups 6 and 7 than in Age Group 4.

Lastly, tool-use effectiveness differed between age groups when analyzed across all foods. Tool-use effectiveness, measured by the proportion of successful bouts, increased across age groups (Figure 7a iv); however, these differences did not reach statistical significance in pairwise comparisons between groups.

Discussion

This study provides the first description of the ontogeny of stone-tool use in long-tailed macaques. Overall, results support predictions made from the Perception-action perspective that tool use would develop over several years and that naïve macaques would first carry out simple manipulations, then a wide variety of nonfunctional combinatory manipulations, before manipulative behavior is channeled toward the actions and object combinations necessary for tool use, that are then produced in various permutations until effective tool-use sequences are produced. The ontogeny of object manipulation and tool use in long-tailed macaques

provides a new point of reference for comparison with the only two other nonhuman primate stone-tool users—chimpanzees (Biro et al., 2006; Inoue-Nakamura & Matsuzawa, 1997) and capuchins (Resende et al., 2008, 2014). Extending comparisons to patterns of development of stone-handling in closely related macaque species (Nahallage & Huffman, 2007, 2008, 2012), manipulative object play in other Old World monkeys (Fairbanks, 2000), and object percussion in human children (Fragaszy, Simpson, Cummins-Sebree, & Brakke, 2016; Kahrs, Jung, & Lockman, 2012, 2013), provides further insight into biological propensities (Huffman, 1996; Huffman & Hirata, 2003) and processes that underlie developmental similarities in different organisms. Conversely, differences in the processes and outcomes of manipulative development between species, populations, and individuals, highlight areas where environmental and social influences interact with developmentally flexible behavior. This augments our understanding of behavioral phenomenon viewed from the perception-action perspective of tool-use development.

Before achieving tool use, young macaques carry out a wide variety of exploratory manipulations with the objects involved in tool use that change in frequency and form over the acquisition period. Macaque infants begin exploratory manipulation between their first and third months of development. In terms of the objects that infants manipulate, all but one infant first manipulated stones before shell items, and in older juveniles, single-item object ma-

Table 11
Results of Either One-Way Between Subject ANOVAs or Kruskal-Wallis H Tests Found Significant Differences Between Age Groups in Several Tool-Use Characteristics

Food type	Characteristic	$F_{(2, 23)}$	$H_{(3, N = 27)}$	p	η^2
All	Duration	1.53		.23	.17
	Strike frequency	3.49		.03	.31
	Strike rate	.63		.60	.08
	Accuracy index		13.55	.004	
	Tool fidelity (tool changes/bout)	4.86		.01	.39
	Proportion of success		7.99	.05	
Sessile oysters	Duration		1.97	.58	
	Strike frequency	3.20		.04	.29
	Strike rate	.90		.46	.11
	Accuracy index		6.12	.11	
	Tool fidelity (tool changes/bout)		3.67	.30	
	Proportion of success		6.14	.11	
Unattached food	Duration		1.21	.75	
	Strike frequency	.52		.61	.11
	Strike rate	3.24		.07	.32
	Accuracy index	2.21		.15	.26
	Tool fidelity (tool changes/bout)		.39	.94	
	Proportion of success	1.37		.29	.24

Note. Effect size η^2 is only reported for one-way between subject analyses of variances (ANOVAs). For analyses utilizing Kruskal-Wallis H tests, the effect sizes of significant pairwise comparisons in Mann-Whitney U tests are reported as z scores (Table 12).

nipulation more commonly involved only stones rather than food items. This is interesting because macaque tool use is adapted for extractive foraging, but infants' early exploratory manipulations appear not to be goal-directed or motivated by the potential to obtain food, but by an intrinsic motivation to manipulate stones that alone offer no possibilities for food rewards.

The propensity for macaques to manipulate stones might have a phylogenetic explanation. Stone handling as a form of object play has been recorded in all macaque subspecies belonging to the *fascicularis* taxonomic subgroup of macaques (Nahallage & Huffman, 2008; Nahallage, Leca, & Huffman, 2016), and the two behaviors share similar developmental trajectories (Nahallage & Huffman, 2007, 2008). Like long-tailed macaques, stone-handling Japanese and rhesus macaques begin manipulating stones with simple exploratory manipulations (e.g., picking up, biting) within their first to third months of age, and the variety and complexity of their manipulative actions increase to a peak between 2 and 4 years of age. These observations suggest that at least in macaques, a

phylogenetically linked biological tendency to stone handle may be a key factor in the emergence of the earliest perception-action exploratory routines on stones, that can develop into tool use under the right conditions (Huffman & Hirata, 2003; Huffman & Quiatt, 1986). However, while adult Japanese and rhesus macaques develop sound-producing and other manually dexterous stone-handling patterns, only long-tailed macaques develop stone-tool use. In addition, this appears limited to coastal-living long-tailed macaques as temple populations of long-tailed macaques have also been observed to stone handle (Nahallage et al., 2016), but not develop stone-tool use, highlighting the importance of environmental influences on the outcomes of developmentally labile behavior. Through their natural tendencies to stone handle, macaques could be discovering the properties of stones and how they can interact with their environments, such as being hard and allowing one to strike other surfaces and objects (Huffman & Quiatt, 1986; Lockman, 2000; Resende et al., 2008; Visalberghi & Frigaszy, 2006). In coastal-living long-tailed macaques, these perceptual

Table 12
Tukey HSD (for ANOVAs) or Mann-Whitney U (for Kruskal Wallis) Post Hoc Tests Indicated Which Age Groups Differed

Food type	Characteristic	Age Group A	Age Group B	Tukey HSD	Mann-Whitney U
All	Strike frequency	2.5–3.5	>5.5	$p = .047$, 95% CI [.43, 8.27]	
	Tool fidelity	2.5–3.5	4.5–5.5	$p = .01$, 95% CI [.03, .32]	
			>5.5	$p = .02$, 95% CI [.02, .28]	
	Accuracy index	2.5–3.5	4.5–5.5		$U = .00$, $z = -2.29$, $p = .02$
			>5.5		$U = 4.00$, $z = -2.09$, $p = .04$
		3.5–4.5	4.5–5.5		$U = .00$, $z = -2.76$, $p = .01$
Sessile	Proportion success	2.5–3.5	4.5–5.5		$U = 1.00$, $z = -2.55$, $p = .01$
			>5.5		$U = .00$, $z = 2.34$, $p = .03$
		3.5–4.5	4.5–5.5		$U = 4.00$, $z = -2.09$, $p = .04$
	Strike frequency	2.5–3.5	>5.5	$p = .04$, 95% CI [.29, 1.21]	$U = 4.00$, $z = -2.00$, $p = .045$

Note. HSD = honest significant difference; ANOVA = analysis of variance.

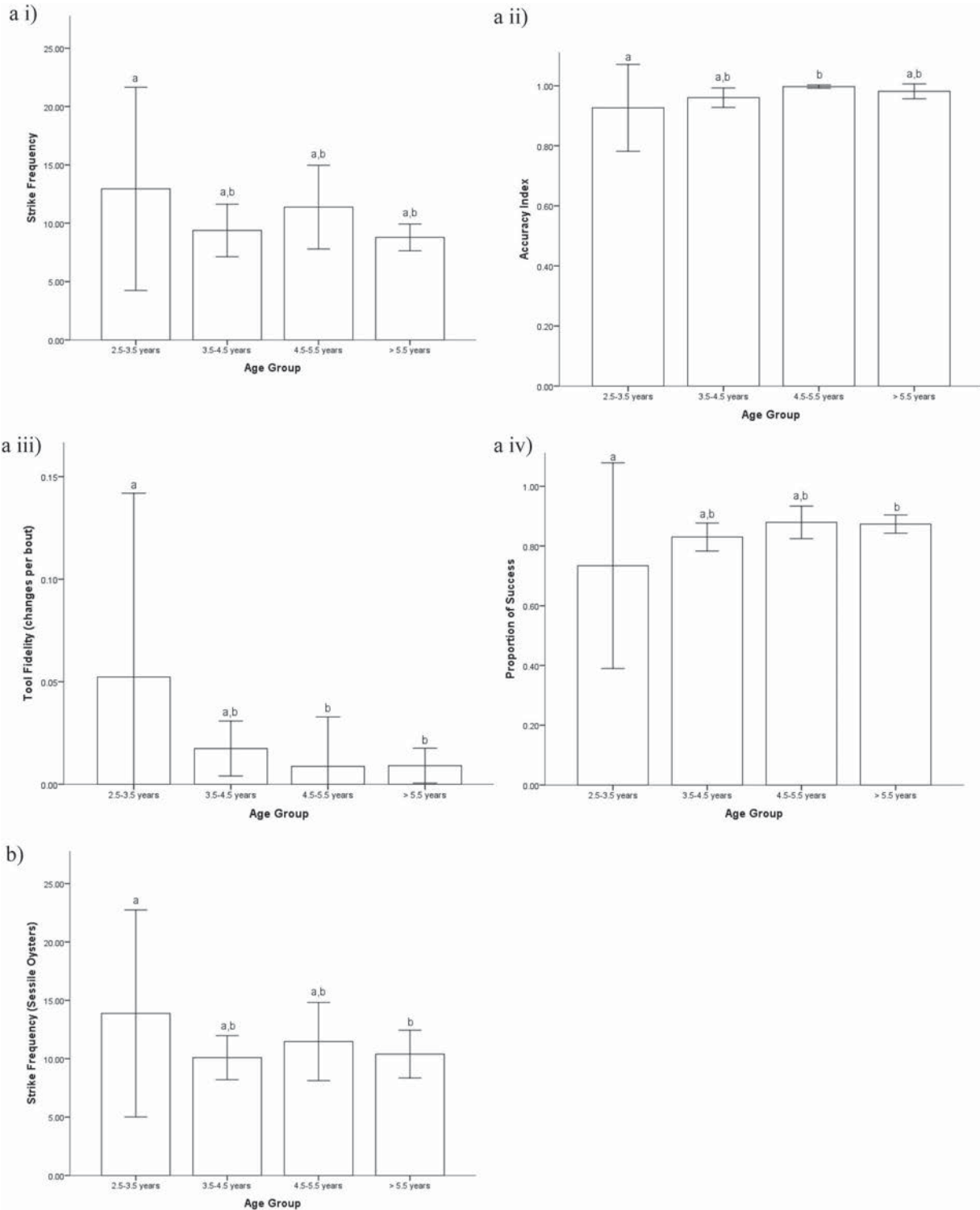


Figure 7. One-way between-subjects analysis of variances (ANOVAs) or Kruskal-Wallis H tests found differences in the (ai) strike frequencies, (a ii) strike accuracies, (a iii) rate of tool changes, and (a iv) proportion of successful bouts of macaques in different age groups when analyzed across both food types, and in their (b) strike frequencies when analyzed within tool-use on sessile oysters. Letters are used to denote statistical significance, and thus significantly different age groups do not share letters. Error bars represent 95% confidence intervals of the mean.

experiences occur in environments enriched with encased foods, facilitating the development of tool use as young macaques incorporate their stone handling predispositions into foraging routines.

In accordance with Perception-action theory, macaques' early manipulative behavior comprised simple actions that do not involve combining objects, and were not instrumental to tool-use sequences. Infants touch or pick up objects, manipulate them in the hands or mouth, or carry them over short distances. Infants later began to combine objects into their exploratory manipulations, although actions combining objects were rare below 1.5 years of age. At 1.5–2.5 years, actions combining objects rise sharply, and comprise on average 80% of juveniles' manipulation bouts. In addition to the replacement of simple manipulations with combinatory manipulations, juveniles in this age group perform the widest variety of different manipulative actions and increased percussive activity. Early percussive actions appeared to lack the goal-directedness of tool use, and most commonly, juveniles hit stones into anvil surfaces with no possibility for obtaining food rewards. Also between 1.5–2.5 years of age, manipulative behavior later begins to resemble tool use, although at this stage, sequences were often erroneous and all attempts were unsuccessful, until some individuals achieve competence at 2.5–3.5 years of age. Newly competent tool users still performed inept actions in their early tool use bouts; however, they no longer performed simple manipulations such as picking up, and manipulating stones and food items out of the contexts of tool use or trying to obtain food rewards from their actions. The effect of this is that the wide variety of manipulative actions observed before competence is sharply reduced and restricted to tool use behavior.

An additional pattern observed within the developmental trajectory, is that object manipulation is simple, but relatively higher during the first 6 months, then appears to decline between 6 months to 1.5 years, before a re-emergent rise in activity between 1.5–2.5 years, where manipulative complexity also increases noticeably. Furthermore, macaques above Age Group 4 ceased manipulative activity regardless of whether or not they were able to use tools, suggesting that the period of development up to around 3.5 years represents a critical period of learning, after which macaques do not develop tool-use skills under natural conditions. These patterns of developmental peaks and depressions in behavioral prevalence and variability, and critical periods for skill acquisition, have also been reported in other species, suggesting underlying biological processes that influence the ontogeny of perception-action routines. Similar to macaques, early emerging combinatory manipulations by captive chimpanzees remained rare until a sharp increase at 1.5 years of age (Hayashi, Mizuno, & Matsuzawa, 2005), and a critical age for nut-cracking skill acquisition up to 5 years of age has also been reported (Biro et al., 2003). In human children, declines in manipulative performance between 16 to 18 months of age is attributed to Piaget's observations that as infants progress through sensorimotor developmental stages, behaviors from earlier stages often persist temporarily into later stages (Kopp, Sigman, & Parmelee, 1974). This has parallels with the wide variety of manipulative actions seen in macaques aged 1.5–2.5 years, which may be a product of the overlap between the decline of simple actions and the increase in combinatory manipulations involving percussion, as well as with the errors that persist within the early tool use successes of juveniles.

Comparisons with ontogenetic trajectories of object play of other Old World monkeys suggest that maturing neural and motor systems underlie periods of change in developmental trajectories, and that young individuals' experiences during periods of neural maturation affect developmental outcomes, providing a mechanism for differences across species, groups, and individuals to emerge (Bourgeois & Rakic, 1993, 1996; Fairbanks, 2000; Jacobs et al., 1995; Rakic, Bourgeois, Eckenhoff, Zecevic, & Goldman-Rakic, 1986; Zecevic, Bourgeois, & Rakic, 1989). In vervet monkeys and rhesus macaques, peaks in frequencies of object play occur when the formation of synaptic connections between the cerebral cortices and motor neurons are increasing exponentially between 3 to 6 months of age, until rates of dendritic pruning overtakes growth at 6 months. Conversely, play declines with the myelination of neurons in the central nervous system (Armand, Olivier, Edgley, & Lemon, 1997; Gibson, 1991). This process is developmentally complete at 3.5 years, and renders neurons less plastic and responsive to behavioral experiences. This could, therefore, underlie the observation of the end of the critical learning period at 3.5 years, where some macaques no longer acquire tool use skills, and those who have restrict manipulative activities to the tool use patterns they have acquired.

These comparisons suggest that perception-action routines of object manipulation in infancy coincides with a period where the developing neural and motor systems are most amenable to experiential feedback (Fairbanks, 2000). Sensory input from the types of manipulations that infants practice at this stage, affect which motor-neural connections are strengthened or lost over development (e.g., Bourgeois & Rakic, 1996). Infants' behaviors are in turn influenced by the physical environments and social contexts surrounding their development, giving rise to individual differences in behavioral outcomes. The effects of environmental factors on manipulative outcomes might be most apparent in species and population level differences. For example, although macaque species within the *fascicularis* taxonomic subgroup share a propensity for stone manipulation (Nahallage & Huffman, 2008, 2012), stone-handling emerges only in some populations where the macaques are provisioned. Infants in these groups can afford more time for stone play, reinforcing motor-neural connections and allowing the behavior to be maintained into maturity. In long-tailed macaques, stone-tool use emerges only in some coastal populations. Coastal environments provide greater opportunities for infants to manipulate stones in conjunction with hard-shelled food items, channeling manipulative experience toward those that prime motor-neural systems for the acquisition of tool use.

The influence of species-typical environments and natural histories on the outcomes of perception-action routines, may also be seen in comparisons of the developmental challenges encountered by different species in mastering stone-tool use. Young macaques appear to face two major challenges in achieving competent and effective tool use—producing spatial relations between objects in the right order for carrying out tool use, and mastering effective percussion. The challenge of managing multiple spatial relations is evidenced by the later emergence of tool-use sequences for cracking motile organisms on anvils, compared with cracking sessile oysters. At 1.5–2.5 years, one juvenile (Pld) began to manipulate all the objects involved in cracking food items, but combined the objects and actions in various incorrect permutations. These errors in producing effective spatial relations between anvils, tools, and

food items persist for at least another year before the proper sequence is achieved as they were still committed in the early tool-use bouts of the juvenile (Chk) who carried out his first successful tool use on motile items between 2.5–3.5 years of age. In contrast, three juveniles in the same age group were already hitting stones onto sessile oysters, expressing the correct action sequence. However, none of them were successful and their failure likely reflects the second apparent challenge for young macaques in mastering effective percussion, with percussive actions being the latest emerging combinatory actions.

Comparing the challenges that macaques face with capuchins and chimpanzees reveals that juveniles of all three species face difficulty in managing tool-use sequences for cracking food items on anvils (Hayashi et al., 2005; Inoue-Nakamura & Matsuzawa, 1997; Matsuzawa et al., 2001; Resende et al., 2008), with long periods of errors before juveniles are able to produce sequence of taking a food item, placing it on an anvil, then striking it effectively with a tool. Closer examinations, however, have revealed that the source of difficulty in this aspect of tool use differs across species. In addition to managing multiple spatial relations, capuchins are hindered from producing tool use sequences because of their apparent difficulty in performing the second action in the sequence, which is placing nuts on anvils (Resende et al., 2008). In contrast, infant chimpanzees develop placing actions early in combinatory manipulation (Inoue-Nakamura & Matsuzawa, 1997; Takeshita et al., 2005) and we have seen the same pattern in macaques. Instead, macaques and chimpanzees both face difficulties in producing percussive actions. This is not an issue for capuchins as percussion is a general feature of their foraging behavior (Fragaszy et al., 2004), and emerges reliably in early development (Fragaszy & Adams-Curtis, 1997; Resende et al., 2008).

The pattern of readiness to place objects but difficulty in percussion shared between macaques and chimpanzees support the explanation proposed by Resende et al. (2008), that natural foraging ecologies influence the types of actions that animals are predisposed to. For capuchins, percussion is a general feature of their foraging behavior (Fragaszy et al., 2004) as they commonly consume encased plant matter that require percussive extraction even without tools. However, they are arboreal and, therefore, hesitant to let go of and risk dropping food, possibly inhibiting placing actions that involve releasing food items onto anvil surfaces. Chimpanzees are more terrestrial and do not risk losing food items by placing them on ground surfaces, however, although the fruits they commonly feed on may require manipulative handling for example, (Corp & Byrne, 2002), percussion is rarely necessary. In addition, young chimpanzees are inclined to carry out “inserting” in their early combinatory manipulation even in captivity, and this is thought to reflect the higher proportion of food and drink resources in their natural habitats that require extraction by inserting a tool into a cavity (e.g., termite fishing, ant dipping, and leaf sponging; Hayashi et al., 2005). With the exception of these coastal populations that subsist on a high proportion of shelled marine organisms, long-tailed macaques are generally frugivorous, and their diets consist of food items that do not require percussive extraction (Gumert & Malaivijitnond, 2012).

In addition to being a late-emerging element in the manipulative behavior of macaques, initial percussive actions differed qualitatively from the motor actions required for tool use. Early percus-

sive actions involved “swiping,” where objects were swung using lateral and roughly U-shaped motions, and would strike the substrate at the bottom of the U-shaped trajectory without particular precision. This resembled an action that looks intermediate between the side-to-side rubbing actions that juveniles develop before percussion, and the striking actions used in effective tool use, which utilized a more fixed up-down motion perpendicular to the plane on which the target object was oriented, and accurately hitting the same point with reliability. This again accords with the perception-action perspective’s prediction that eventual tool-use actions (proper striking), reflects earlier exploratory actions (rubbing items on surfaces).

The early percussive actions in developing macaque tool users resemble the early inept and inconsistent strike trajectories of human infants’ object banging (Kahrs, Jung, & Lockman, 2012, 2013; Kahrs & Lockman, 2014). Over development, infants’ banging actions during object play changed from varying widely in velocity, object displacement, strike angles, and strike trajectories that often involved lateral rather than up-down motions resulting from a lack of control over distal arm joints, to more consistently straighter strike trajectories, and perpendicular strike angles, that would enable greater accuracy and efficient force delivery should these exploratory percussive actions develop into tool use (Kahrs et al., 2012, 2013). In human infants, this developmental stage has been linked to a lack of control over postural stability and the distal arm joints (Fragaszy, Simpson, Cummins-Sebree, & Brakke, 2014; Kahrs et al., 2013). The developmental changes from disorganized and ineffective striking actions to consistent and accurate strike motions appear similar children and young macaques, suggesting that the two species may face similar biological constraints on the development of effective percussion from exploratory perception-action routines.

In summary, the current examination of the ontogeny of stone-tool use by long-tailed macaques has supported further understanding of tool-use skill development from a Perception-action perspective. Corroborating earlier research on the development of stone-tool use in capuchins and chimpanzees, the acquisition of tool use in macaques is a lengthy and gradual process, in which skills develop from the simple exploratory manipulative behavior first observed in infancy, increasing in complexity and resemblance to tool use as young macaques gain perceptual knowledge through their actions. In addition to physical maturational processes in the motor-neural systems, Perception-action processes are influenced by species-typical biological and environmental characteristics, giving rise to variation in the emergence of various elements of tool-skill development. For example, our observations and extended cross-species comparisons to stone-handling in closely related macaque species, suggest that biological propensity to stone handle is a factor in emergence of stone-tool use, and this might be unique to long-tailed macaques, as habitual stone handling is not reported in capuchins and chimpanzees. In other species, stone-tool use might originate from other biological predispositions that relate to their unique natural histories, for example, a percussive tendency in capuchins that is driven by feeding ecology (Fragaszy, Visalberghi, & Fedigan, 2004). These differences also relate to cross-species variation observed throughout the developmental process, evident in the different challenges that young macaques, chimpanzees, and capuchins face in mastering the same tool-use tasks.

While global patterns in the normative developmental trajectories of tool-use skills have been illuminative in regards to how ecological and biological influences contribute to unique perception-action learning across species, there is substantial individual variation within species that also calls for further investigation. From current observations, long-tailed macaques vary widely in the frequency at which they carry out manipulative and tool use behavior, and in their ability to overcome the difficulties of producing spatial relations and mastering percussion generally faced by their species. In relation to producing action sequences for cracking shellfish on anvils, one individual, Nms, carries out tool use in an action pattern that appears to reflect incomplete development. Recall that juveniles attempt the sequence of pound hammering (take food and stone, place food on anvil, crack with stone) in several erroneous ways during development, one of which being taking a stone and food item, placing the food item in contact with the underside of the handheld stone, and attempting to bring both objects down onto the anvil simultaneously. While other individuals develop the typical sequence, Nms always cracks unattached foods using this action pattern, but appears to have refined it such that she is effective with this technique. With regards to mastering percussion, while many juveniles did not yet percuss items at 1.5–2.5 years, or carried out percussive actions with improper “swiping” actions, direct percussion of a food item onto a rock surface with the typical vertically oriented striking motions was recorded as early as the fifth month of manipulative development for infant Sai. Most illustrative of this variation in percussive behavior is that only 76% of the macaques on Koram Island above 2.5 years old, developed tool use, and 88% of adults and adolescents at the other studied location, Piak Nam Yai Island. Among the nontool users, some carried out direct percussion of food items on hard substrate, some rubbed food items on substrate but never percussed them, and yet others were never observed to process food items in combination with any other object or substrate. These variations in individual macaques’ ontogenetic trajectories highlight that tool-use learning is subject to other influences apart from biological predispositions and maturation of physical, neurological, and cognitive systems. One possible source of individual variation for further study, is the social interactions and influences that occur during development (Biro et al., 2003, 2006; Coelho et al., 2015; Matsuzawa et al., 2001; Ottoni, Resende, & Izar, 2005; Resende, Izar, & Ottoni, 2004). Examining how social influences affect developmental processes is of interest to understanding both human and nonhuman primate cognition for example, (Call, 2013; Heyes, 1994), as well as the cultural maintenance and evolution of skilled technological traditions across species (Fragaszy & Perry, 2003; Mesoudi, Whiten, & Laland, 2006).

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