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RESEARCH ARTICLE

The Physical Characteristics and Usage Patterns of Stone Axe and Pounding Hammers Used by Long-Tailed Macaques in the Andaman Sea Region of Thailand

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Stone hammering in natural conditions has been extensively investigated in chimpanzees and bearded capuchins. In contrast, knowledge of stone tool use in wild Old World monkeys has been limited to anecdotal reports, despite having known for over 120 years that *Macaca fascicularis aurea* use stone tools to process shelled foods from intertidal zones on islands in the Andaman Sea. Our report is the first scientific investigation to look at the stone tools used by these macaques. We observed they were skilled tool users and used stone tools daily. They selected tools with differing qualities for differing food items, and appeared to use at least two types of stone tools. Pounding hammers were used to crush shellfish and nuts on anvils and axe hammers were used to pick or chip at oysters attached to boulders or trees. We found significant physical differences between these two tools. Tools at oyster beds were smaller and exhibited scarring patterns focused more often on the points, whereas tools found at anvils were larger and showed more scarring on the broader surfaces. We also observed grip differences between the two tool types. Lastly, macaques struck targets with axe hammers more rapidly and over a wider range of motion than with pounding hammers. Both our behavioral and lithic data support that axe hammers might be used with greater control and precision than pounding hammers. Hand-sized axe hammers were used for controlled chipping to crack attached oysters, and larger pounding hammers were used to crush nuts and unattached shellfish on anvils. In addition to stones, they also used hand-sized auger shells (*Turritella attenuata*) as picks to axe attached oysters. Pound hammering appears similar to the stone tools used by chimpanzees and capuchins, but axe hammering has not yet been documented in other nonhuman primates in natural conditions. Am. J. Primatol. 71:594–608, 2009.

Key words: long-tailed macaque; stone tool use; stone hammer; Thailand; Andaman Sea

INTRODUCTION

It has been known to the scientific community for over 120 years that long-tailed macaques of the Andaman Sea region of mainland SE Asia (*Macaca fascicularis aurea*) regularly use stone tools on islands in the Mergui Archipelago of Southern Myanmar [Carpenter, 1887]. Curiously, despite wide interest in primate tool use and its relation to the evolution of material culture, this behavior was not explored further. In 2005, this behavior was rediscovered in Thailand after a team of researchers assessed tsunami damage on islands in Laemson National Park, Ranong Province. The finding was approximately 250 km south of the central region of the Mergui Archipelago, and this site is in the southern range of this string of islands scattered all along the western coast of Thailand and Myanmar. After the finding, the team reported that axe-hammering behavior occurred on Piak Nam Yai Island in Laemson National Park [Malaivijitnond et al., 2007]. Later that year, we began the first field study investigating the stone tool use of long-tailed macaques in Laemson National Park. During this study, we have investigated the lithic properties of

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macaque stone tools, and in this report we present the first data on the stone tools used by the long-tailed macaques of the Andaman Sea region.

The customary use [McGrew & Marchant, 1996] of percussive tools (i.e. stone hammers and anvils) by nonhuman primates in natural settings has been investigated in chimpanzees (*Pan troglodytes*) [Boesch & Boesch, 1990; Matsuzawa, 1994; Sugiyama & Koman, 1979] and bearded capuchins (*Cebus libidinosus*) [de A Moura & Lee, 2004; Fragaszy et al., 2004a; Mannu & Ottoni, 2009]. Such tool use appears to represent local traditions or cultures that are not accounted for by biological or environmental conditions alone, but rather are the result of behavioral innovations that are maintained in a local community through the social diffusion of skills [Fragaszy & Perry, 2003; van Schaik et al., 1999; Whiten et al., 1999]. Like chimpanzees and capuchins, the tool use of Andaman long-tailed macaques also involves the regular usage of hammer and anvil stones, and the behavior appears ubiquitous among community members. Stone tool use can be observed daily by all age–sex classes, except infants, on the shores of the island. Consequently, it appears that long-tailed macaque stone tool use is comparable to the tool–use traditions found in other nonhuman primates, and thus investigation of this behavior will provide a useful comparison to work already done on nonhuman primate stone tool traditions.

Macaques are not considered to be skilled tool users [Panger, 2007], despite having well-developed hand grip ability [Christel, 1994; Christel & Fragaszy, 2000; Napier & Napier, 1985]. For long-tailed macaques, most studies have focused on the common subspecies, *M. f. fascicularis*, and only limited tool use has been found in these studies. In one case, some captive long-tailed macaques held their tail with their hands to use as an extension to rake objects into their cage [Karrer, 1970]. This shows a potential for using tools, but is not true tool use according to Beck [1980] because the tail is attached to the body. In another case, a captive male learned to use a stick to rake apples into his cage, and this behavior was transmitted to a few others in the group [Zuberbühler et al., 1996]. In Bali, Indonesia, they were found to handle and play with stones, use leaves to rub and clean food items, and even sporadically used stone tools on a few occasions [Fuentes et al., 2005; Wheatley, 1988]. In Lopburi, Thailand, long-tailed macaques were found to use human hair to "tooth-floss" [Watanabe et al., 2007], twigs to pick their teeth, and human-discarded towels to groom one another [Gumert, personal observation]. Tooth-flossing behavior has also been observed in captive long-tailed macaques [Gumert, personal observation]. Lastly, at the Botanical Gardens of Singapore, they used leaves to clean food items and an adolescent male once repeatedly snapped a rubber band against his teeth [Chiang, 1967]. These reports show that long-tailed macaques are capable of tool use, although none of these behaviors have been extensively studied.

The tool use found on Piak Nam Yai Island is far more prolific than the tool use found in the common subspecies of long-tailed macaque (*M.f. fascicularis*). *M. f. aurea* regularly use stone hammers to crack open at least five different types of shelled seafood [Malaivijitnond et al., 2007]. They crack oysters (*Saccostrea cucullata*), sea snails (*Thais tissoti*), clam-like bivalves (*Gafrarium divaricatum*), swimming crabs (*Thalamaita danae*), and rock barnacles (*Semibalanus balanoides*) [Malaivijitnond et al., 2007]. Recently, we have also found them pounding sea almonds (*Terminalia catappa*). Seafood is cracked on the rocky shores and mangroves of the island, whereas nuts are mainly cracked on rocks near the forest edge or inside it at rock outcroppings and streambeds. The variation of food items exploited with stone tools by *M. f. aurea* appears larger than other apes or monkeys, which mainly use stone tools to exploit hard-cased nuts or other hard plant material (e.g. seeds, tubers, and branches). Although there are anecdotes of bearded capuchins pulverizing small vertebrates (e.g. lizards) [de A Moura & Lee, 2004] and of capuchins cracking oysters with stones [in Beck, 1980], *M. f. aurea* is the only primate currently known to customarily use stone tools to process animal food sources.

Not all food items exploited by the macaques of Piak Nam Yai have the same properties, and therefore it is possible that they select tools with properties suitable to the food being processed. Several primates have been shown to clearly discriminate the functional relevance of tools and appear to select tools that are best suited to the goal of the task. Chimpanzees of Taï National Park select tool hardness and weight according to nut shell toughness [Boesch & Boesch, 1983, 1984]. Bearded capuchins in Boa Vista, Brazil, select heavier and harder rocks for hammers [Visalberghi et al., 2007] and also choose differing-sized tools for different-sized seeds [Ferreira & Jerusalinsky, 2008]. Moreover, wild bearded capuchins use stone tools for a wide array of tasks, such as hammering, digging, and extracting secondary tools [Mannu & Ottoni, 2009]. Experimental studies in captivity show tufted capuchins (*C. apella*) discriminate appropriate hammering tools by weight [Schrauf et al., 2008], and several other nonhuman primates select the most appropriate tool for a given task [Evans & Westergaard, 2004; Fragaszy et al., 2004b; Hauser et al., 2002]. Moreover, recent experimental studies in the wild have shown that bearded capuchins actively choose tools based on functional features, such as friability (i.e. potential for tool to break apart) and weight [Visalberghi et al., 2009].

Originally, tool selection by the macaques of the Andaman Sea region was considered to be based on randomly selecting what fits into the hand and not what is functionally relevant as a hammer [Carpenter, 1887]. This is an unlikely assumption given that these macaques exploit a wide range of food sources with tools, and thus probably require tools of differing properties for differing food sources. We therefore hypothesized the characteristics of tools should differ across food items. We predicted that the tools used to crack open oysters should be smaller and show more precise usage patterns than other tools because oysters are attached to a substrate (e.g. boulder) and may require axing or chipping using the smaller surfaces of a tool to break open the top shell. In contrast, unattached shelled foods only need to be crushed between a hard anvil surface and the broad surface of a heavy stone, and therefore less precise control of the tool may be needed. We also predicted that stone tools should show differing qualities than stones not used as tools because we expected that macaques selected tools nonrandomly from the litter of stones available to them along the shores. Lastly, we hypothesized that any differing tool types found should be gripped and used differently.

In order to test these predictions we investigated the stone tools used by long-tailed macaques found on Piak Nam Yai Island in Ranong Province, Thailand. We observed tool use by circling the island with a boat and studied tool use by landing on the island and investigating the stones around tool using sites. We collected tool and nontool stones and measured their lithic properties. We also studied the scarring patterns of tools to determine the manner in which they were used during food processing. Lastly, we used photographs and video to observe how the tools were gripped and used by these macaques.

METHODS

Study Site and Observation Periods

Piak Nam Yai Island in Laemson National Park, Ranong Province, Thailand (N9°35′, E98°28′) is a small island with an area of 1.7 km^2 that is located about 750 m off of the mainland of Thailand. The major habitats of the island include rocky shores, mangroves, sandy beaches, fresh water streambeds, and mountainous tropical forest. Surveys to look for evidence of tool use have been conducted in all of these habitat types. We have conducted four short observation periods taking place during December 1st–December 5th, 2007, January 22nd–February 1st, 2008, and February 26th–March 2nd, 2008, December 10th–December 20th, 2008, and one longer study from June 3rd–June 29th, 2008. During these studies, we used a boat to navigate around the island. Whenever a group was encountered we stopped the boat to observe from a distance (i.e. 10–60 m offshore) and recorded the GPS position. Macaque sightings clustered into four areas, indicating that there may be four groups of long-tailed macaques on the island. Rough estimations indicate that the largest group on the island may have consisted of approximately 25–30 individuals, and the other groups appeared to contain 12–25 macaques. After the macaques moved from sight, we landed on the island to observe the tools and shell debris from the cracked food items. We measured the properties of the tools we encountered. During the June 2008 study, more time was spent surveying the island by foot, and thus the majority of our tool data was collected during that survey. All research was conducted in accordance with the legal and ethical requirements for research on wildlife in Thailand and Singapore.

Sampling Techniques

We measured the lithic properties of stones using three methods, ad libitum sampling, zone sampling, and plot sampling. In the first three surveys, we collected and measured stones used as tools ad libitum from recent cracking sites after observing monkeys from the boat and landing on the island. Stones were measured from all groups using this method. A zone sampling method was used during the longer study in June, which was conducted by traversing by foot on the island. Zones were chosen if an area was found where used tools were present. All tools found in these zones were then measured. Only the home range of the largest group was investigated using the zone method. This group's range was chosen because it included all habitat types, was least difficult to traverse, and the group was more habituated than the other groups. The group was more tolerant of being in sight of people because one of the shores they inhabited faced a regularly used boat dock on Piak Nam Noi Island approximately 130 m away. By studying this group we were able to continue to habituate them to a closer presence during stone collection for later behavioral research. Each tool encountered in a zone was marked with a number by using ink markers and then measured. Following measurement, the stone was returned to a marked spot on the anvil where the tool was originally found.

The third method used was plot sampling, also performed in June. We collected plot samples of stones from 1 m^2 areas selected on the shore or in the forest. Four plots were collected, three from the rocky shore and one from inside the forest about 15 m from a freshwater streambed. Plots were selected for having many stones, being easily accessible to the macaques (e.g. a gap between boulders on the rocky shore with numerous stones), and for showing evidence of tool use in the vicinity. All stones in these plots longer than 35 mm and lighter than 5200 g were measured. These parameters were selected as they represented the upper and lower limits of the tools we had previously measured, and thus was a likely representation of the range of stones that were preferred for use by these macaques. We used the plot samples to test whether stones were selected randomly from a range of stones the macaques could handle as tools, or whether they selected tools for particular properties. Stones from the plots were categorized into two groups, tools and nontools. Stones were categorized as tools if they showed tool-like scarring patterns. We considered a stone to have tool-like scarring if it was not likely that the scarring pattern could have occurred from natural tumbling. For example, clear depressions or scarring on small areas of the stone, conspicuous scars on the center of the face of the stone, or flattened or depressed points or edges of the stone. Stones were categorized as nontools if no clear scarring evidence of tool use were found.

Measurement of Stone Characteristics

We used calipers (Marathon Digital 0–150 mm Calipers) to measure the length, width, and thickness of stones under 150 mm and a tape measure for larger stones. We used spring-loaded scales (Economy Spring Scales, Ward's Natural Science) to measure weight. The length measurement was made along the longest line of the stone and then three measurements perpendicular to that length were taken at 1/4, 1/2, and 3/4 the length to measure width and thickness. We used the average measure of width and thickness as our measure of these two dimensions. To measure weight, we placed each stone in an appropriately sized mesh bag. The bag was tiered on the scale and the stone was weighed with a 500 g, 1000 g, or 5000 g scale depending on the stone's size.

In addition to a stone's dimensions, we recorded characteristics of each tool and how it was used. We recorded any kind of shell debris remaining around a tool. Shells were identified as oysters, snails, bivalves, swimming crabs, rock barnacles, or sea almonds. We also noted which surfaces of the stone were scarred. To measure scarring, we delineated three surfaces; points, edges, and faces. Faces were the flat open surfaces of the stone that spanned the full length and width of the stone. Edges were the edges (i.e. sides) along the length of the stones. Points were the edges along the width of the stone or any pointed protrusions. Each surface of the stone was examined during inspection.

In June, we added measurements of volume and hardness to our repertoire and these two properties were measured for all stones collected in zone and plot sampling. We measured volume for small stones by placing them into a 1000 ml graduate cylinder filled partially with water and recorded the volume of the displaced water. For larger stones, we used cups or bowls to submerse the stone in water and then measured the amount of water displaced by pouring or draining the displaced water into a 1000 ml graduated cylinder.

We tested a stone's hardness using a Proceq Equotip 2 portable hardness tester loaned to us by Proceq Asia Pte Ltd, Singapore for the month of June 2008. Using a type D impact device, we measured the hardness by taking the average of seven quality strikes in succession on the stone. If during the seven strikes, even one strike was poor (i.e. greatly deviated from the other scores) we repeated the seven strike series until a complete series of seven quality strikes was obtained. The Equotip device measured hardness by comparing the velocity of the small hammer inside the D impact device before impact (V_1) to the velocity after impacting the stone (V_2). This produced a measurement in Leebs, which was equal to $L = V_2/V_1 \times 1000$ and approximated the energy transferred from V_1 to V_2 during each test strike. Harder surfaces transfered more of the initial velocity and softer surfaces absorbed more of the initial impact's energy and thus V_2 was considerably slowed. Therefore, a higher measurement indicated a relatively harder surface.

Comparisons of Stones

During the study we collected 778 stones and 324 of these stones were collected in our four 1 m^2 plot samples. From the total sample, we had 582 tools and 196 nontool stones. All tools were categorized by the surfaces that were scarred. We used the scarring pattern on a tool to judge the degree of precision exerted in using it. Tools were considered to have a precise or coarse pattern of scars. Precision scarring was defined when scarring occurred on only the points of the stone, or on the points and only one other surface, whether faces or edges. Coarse scarring was defined as scarring on only the faces, only the edges, the faces and edges, or a combination of faces, edges, and points. The major distinction drawn in this categorization was that precision scar patterns focused on the points of the tool, whereas coarse scarring focused more on the broad surfaces. Precision tools showed scarring on a smaller surface area, and coarse tools had scarring over a broader surface area, indicating that precision tools may have been used more finely than coarse tools. We defined seven different scar patterns and the patterns were roughly ordered from greater precision to coarser use. P = points only, P,F = points and faces, P,E = points and edges, E = edges only, E,F = edges and faces, P,E,F = points, edges, and faces, and F = faces only.

In our first analysis, we investigated the relationship between scar patterns and the physical properties of a tool. Using a multivariate general linear model (GLM), we tested whether physical dimensions gradually increased from more precisely used tools to more coarsely used tools. The fixed factor of the model was scarring pattern. The dependent variables tested were indicators of size, which included length, width, thickness, weight, and volume. A Wilk's Lamba model was used.

Secondly, we tested whether food type influenced how the tool was used. We compared the proportion of tools with precision or coarse scarring patterns across food groups. We categorized 327 stones with sufficient data into three food type categories, oysters (including barnacles that were rarely cracked), other shellfish (i.e. crabs, snails, and bivalves), and nuts, and then compared the proportion of precision and coarse tools in each category using analysis of variance (ANOVA). Tukey post hoc analyses were used for pair-wise comparison following any significant F values.

Our last analysis of the tools tested whether there were two distinct tool types utilized by these long-tailed macaques, and whether tool samples differed from nontool samples to determine if tools were selected randomly from the stones available. In this analysis, we categorized 38 tools collected around oyster beds as axe hammers and 77 tools found on anvils with shell debris as pounding hammers. We compared these two tools types with our sample of 196 nontools collected from plot samples. Using ANOVA analysis we compared each stone classification and tested length, width, thickness, weight, volume, hardness, and length/width proportion as dependent variables. Tukey post hoc tests were performed following significant F values. All statistical tests in this study were $\alpha \leq 0.05$.

Describing Hand Grip Using Photographs

We investigated photographs to explore the grip patterns of stone tools used by macaques. We assessed 45 photographs of high enough quality to determine the grip patterns being used. From these photographs, we described the grip patterns we observed and attempted to categorize them into the categories of power or precision grips as described by Napier [1980], and compared grips with the more detailed categories established by Jones-Engel and Bard [1996]. We also compared our grips to the classification scheme of Marzke and Wullstein [1996] and Marzke [1997], which focused on precision pinching and power squeezing. We described how the thumb and fingers were use to grasp tools and described to what degree the palm was used in the grip. We used our observations to judge whether macaques gripped different tools in different ways.

Video Analysis of Hammering

We used ad libitum video data to provide a limited behavioral assessment of macaque stone hammering We used this video data to compare to the data we found from the stones in order to test the validity of whether these macaques used two different tools in different ways. We collected several hours of video while surveying the island and used that video to draw 30 axe-hammering and 30 pound-hammering events. Video was collected ad libitum and was affected by the motion of being on a boat at sea, and thus we had to extract observable segments from the video. Therefore, events were not complete hammering bouts, but rather a short sample of time that the subject could be observed clearly on video. For the 30 axe-hammering events, we observed 18 min 25 sec of time and for the 30 pound-hammering events we observed 26 min 14 sec of time. Each video segment was measured for its time in seconds.

We categorized video segments as axe hammering if the macaque used a hand-sized stone to crack attached oysters and as pound hammering if they used a stone to pound on loose food items on an anvil. In each segment, we measured the number of strikes and used that number to measure the rate of striking. In each segment, we also recorded whether the tool was hammered toward a surface on a different or the same plane from where the macaque was seated or standing (Fig. 1). A plane was defined relative to the surface that the macaque was positioned on. We scored striking to the same plane if striking was directed at the same plane the macaque was seated or standing on (e.g. rock or ground surface). We scored striking to a different plane if any other plane other than the plane the macaque was seated or standing on was struck (e.g. rock wall, underside of rock, rock above head, etc.). If in the same segment both the same and a different plane were struck, we scored that event for the striking of a different plane. We used independent t-tests to compare axe hammers to pound hammers for the rate of striking and the proportion of events where different planes were hammered.

RESULTS

Tool Characteristics

We collected 778 stones from the shores, mangroves, streambeds, and forests of Piak Nam Yai Island, of which 582 were tools. 324 stones were collected in four 1 m^2 sample plots, and the remaining 454 stones were collected at cracking sites. Of these 324 stones collected in plots, 128 (39.5%) showed scars and depressions that indicated use as a tool. For the tools collected with clear scarring from usage as a tool, we used a GLM to test the relationship between tool size and the precision of scarring patterns. There was significant variation across scar patterns for length ($F = 6.176$), width ($F = 8.38$), thickness ($F = 6.54$), weight ($F = 5.31$), and volume ($F = 5.40$). For each test df = 6,215 and $P < 0.01$. Smaller tools had more precise scarring (i.e. more scars on the points, points and edges, or points and faces) than larger tools, which showed a coarser pattern of scars (i.e. more scars on faces, edges, edges

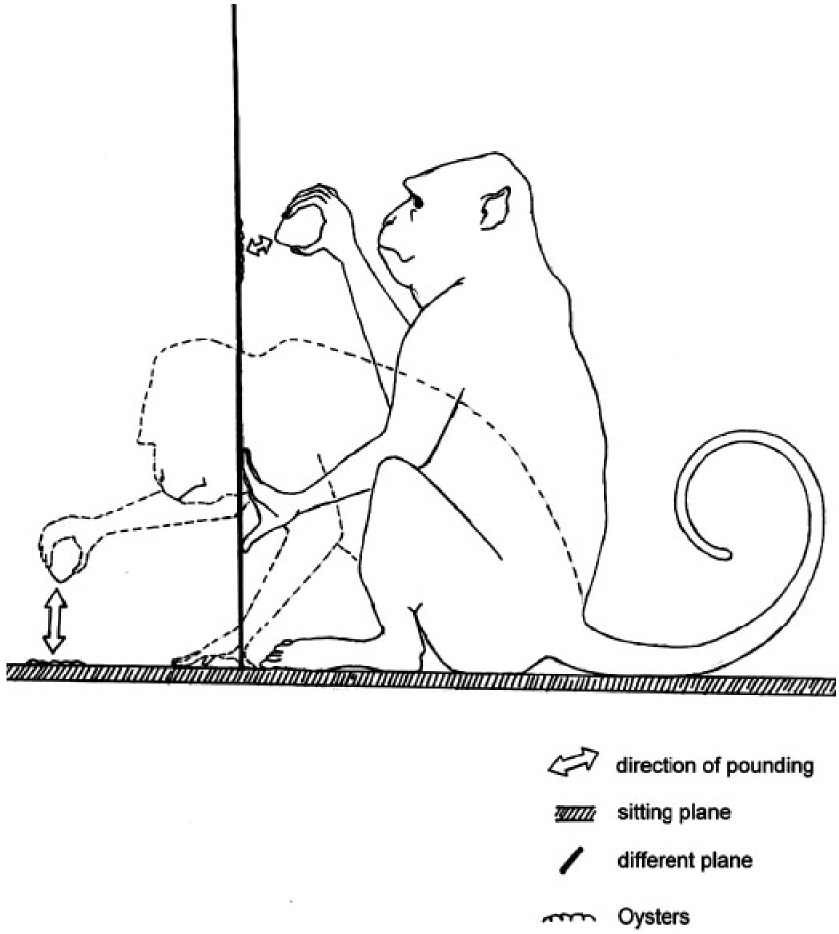

Fig. 1. Macaques struck targets with stone tools on the same planes they were positioned on, as well as striking targets on different planes from where they were seated or standing. Any striking not directed to the same plane they were positioned on was considered striking toward a different plane (drawing by M. Kluck).

and faces, or all three surfaces). There was a clear progressive relationship between the size of a tool and how precise or coarse the scarring pattern on the tool appeared (Fig. 2).

As tools of different size showed different scarring patterns, it was possible that tools were used differently for differing food sources. We tested this hypothesis on 327 tools that had sufficient data on food type by determining if tool characteristics were different for three categories of food, oyster, other shellfish (i.e. snails, bivalves, and crabs), and nuts. There was significant variation between these groups in how tools were used (one-way ANOVA: df = 2,325, $F = 25.92$, $P < 0.001$) (Fig. 3). Tukey post hoc analysis ($P < 0.05$) showed that oyster tools had more precise scarring patterns that focused on the points of the tool (Fig. 5d), and tools for nuts and other shellfish showed more coarse scarring patterns that indicated use of the broad surfaces (Fig. 5c). We considered that tools that showed use on the points required greater precision of use in order to direct the point at the food item than tools with scars on larger surfaces or over all surfaces. Consequently, our results indicate two basic utilization styles for tools; a precision tool for axing oysters, and a more coarsely used smashing tool for pounding shellfish and nuts.

Comparison of Hammer Types and Non-Hammer Stones

Having found two distinct tool types, we further investigated whether the physical characteristics of these two tool types were different, and whether tools differed from a random sample of stones suitable to fit into the hands of the macaques. We started this analysis by categorizing tools left on anvils with debris of shellfish or nuts in one group and tools left by oyster beds or with oyster debris into a second grouping of tools. These two types of tools were compared with a sample of nontools collected from plot samples of stones. These three categories varied in length (ANOVA: df = 2,308, $F = 17.547$, $P < 0.001$), width (df = 2,308, $F = 21.11$, $P < 0.001$), thickness (df = 2,308, $F = 19.981$, $P < 0.001$), weight (df = 2,306, $F = 7.93$, $P < 0.001$),

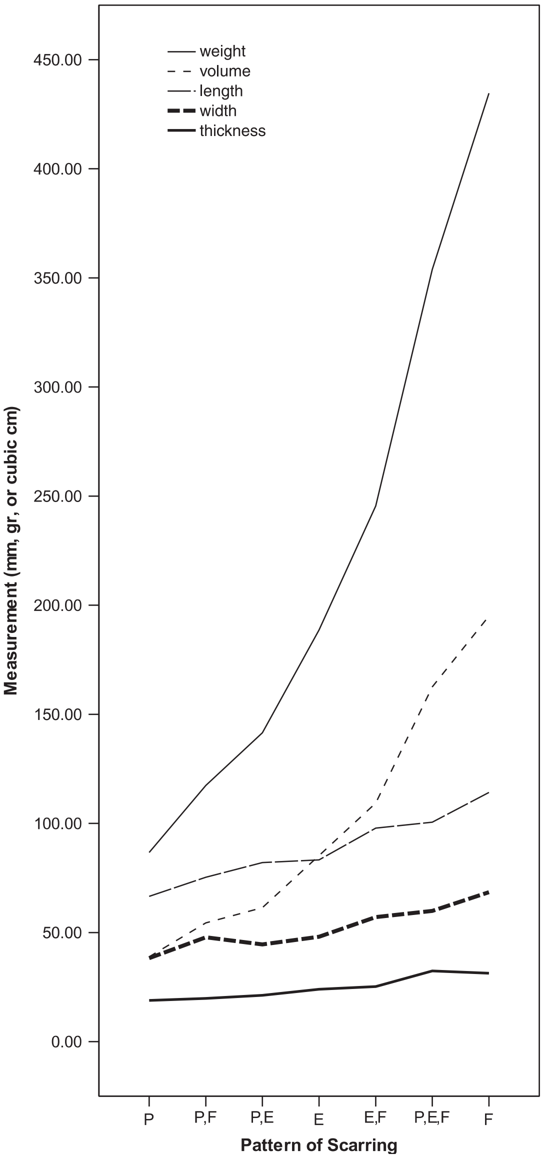

Fig. 2. The relationship between the size of a stone tool and its scarring pattern. The left side of the x-axis represents more precise scarring, and the right side represents coarser scarring. Scarring patterns are labelled as P = points only, P,F = points and faces, P,E = points and edges, E = edges only, E,F = edges and faces, P,E,F = points, edges, and faces, F = faces only. Precision use includes P, P,E, and P,F, and coarse use includes all other patterns.

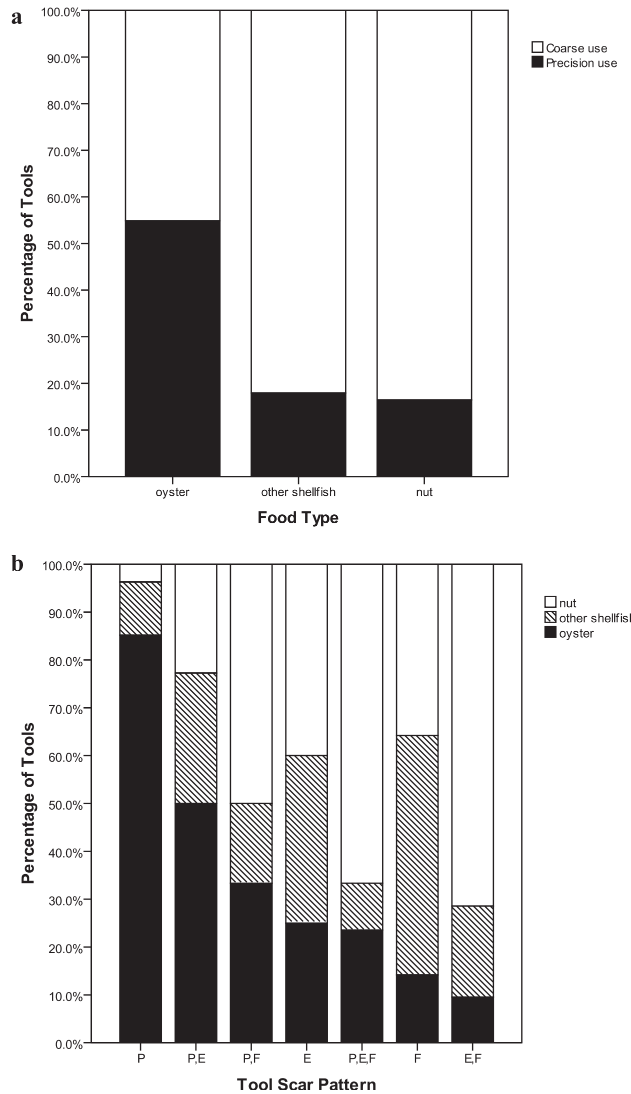

Fig. 3. (**a**) The percentage of stone tools showing precision or coarse scarring patterns for three different food items; oysters, other shellfish (i.e. snails, bivalves, and crab), and nuts. (**b**) The percentage of stone tools used in each of the three food categories across different scarring patterns. Scarring patterns are labelled as P = points only, P,E = points and edges, P,F = points and faces, E = edges only, P,E,F = points, edges, and faces, F = faces only, E,F = edges and faces. Precision use includes P, P,E, and P,F, and coarse use includes all other patterns.

volume (df = 2.292, $F = 8.69$, $P < 0.001$), hardness (df = 2,302, $F = 17.61$, $P < 0.001$), and length/width proportion (df = 2,308, $F = 3.64$, $P < 0.03$), and so there were significant difference between the three groups of stones.

After running Tukey post hoc tests ($P < 0.05$), we found that oyster tools were smaller than nontools and tools left on anvils were larger than nontools (Fig. 4a). Anvil tools were longer, wider, thicker, and heavier than nontool stones, which were longer, wider, thicker, and heavier than oyster tools. Furthermore, anvil tools were more voluminous than nontools, which were marginally more voluminous than oyster tools ($P < 0.053$). Anvil tools were also harder than both oyster tools and nontools, indicating hardness may be more important for pounding than axing (Fig. 4b). Lastly, oyster tools had significantly smaller length-to-width ratios than nontools, and this might indicate a preference for a uniform-sized stone over oblong, narrow rocks when selecting an oyster tool, possibly because it is more suitable for fitting the hand for axing. Overall, there seemed to be a clear distinction between small tools

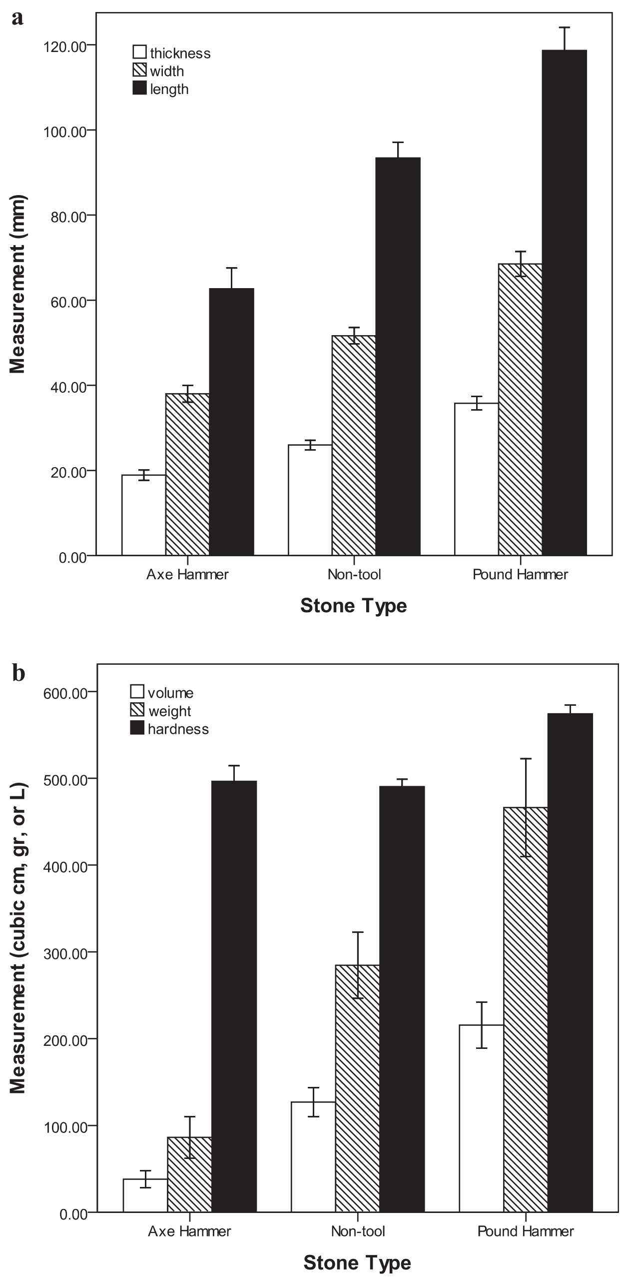

Fig. 4. (**a**) The differences in the size of axe hammers, pounding hammers, and nontools measured in mm of length, width, and thickness of the stone. (**b**) The differences in size and hardness of the three stone types. Weight measured in g, volume measured in cm^3, and hardness measured in Leebs (L).

for axing open oysters and larger tools for pounding food item on anvils.

Differences Between Axing and Pounding

We used photographic and video analysis to explore for other distinctions between the axing tools used for oysters and the pounding tools used at anvils. Overall, we found that axe hammers were small hand-sized stones that were rapidly hammered to chip oysters attached to boulders or trees (Fig. 5b), and that pounding hammers were larger stones that were collected and used to pound loose food items placed on an anvil (Fig. 5a). The hammer was raised with one or two hands and brought down forcefully onto the food item. Most pounding stones were completely lifted off the anvil's surface, but for very heavy stones only one side was lifted, thus using one side as a fulcrum.

We observed in 45 close-up photographs that the macaques typically held tools using all fingers, the palm, and the thumb. We found that grip patterns were consistent with minor variations over two similar patterns that were noticeably different between axe and pound hammering. Macaques typically held axe hammers by gripping or pinching a hand-sized tool tightly between all fingers and the thumb, with the tool passively supported by the palm (Fig. 6a,b,c). This grip was also occasionally used for one-handed pounding of items on anvils, but the tool was larger than the hand and appeared under less control (see supplemental video). This hand grip did not fall clearly into the categories described by Napier [1980] or Jones-Engel and Bard [1996]. Rather, it was best described as a finger-to-thumb/passive palm grip, such as the cup grip in chimpanzees or the cradle grip in humans [Marzke, 1997; Marzke & Wullstein, 1996]. We considered the grip to have a high degree of finger-to-thumb pinching as in the human cradle grip, but there was no evidence of an ability to translate or rotate the tool [Marzke & Wullstein, 1996]. We also observed that macaques held very small axe hammers with a precision grip between fingers and the thumb without any clear contact to the palm (Fig. 6d).

Macaques typically held pounding tools differently, with the exception noted above of occasionally using the cradle-like grip for one-handed pounding tools. Typically though, one-handed pounding tools were gripped between the fingers and palm, with the thumb slightly outstretched (Fig. 7a). When using two-handed pounding, both hands used the same grip. They gripped tools with fingers on one side, securing the tool into the palm, with the thumb slightly outstretched and supporting the tool (Fig. 7b) or with the thumb tightly adducted toward the rest of the fingers (Fig. 7c). These grips appeared to be a form of power-finger/active palm grip, which might be comparable to what Marzke and Wullstein's [1996] termed the squeeze grip. In addition, we also observed grips with the two hands being used to manually squeeze the tool between two hands, placing pressure from the fingers, palm, and thumb to clasp the tool between both hands (Fig. 7d).

We observed a difference in grip between the two tool types. During axe hammering, there was greater reliance on gripping between fingers and thumb and the palm acted as a stabilizing buttress. In contrast, during pound hammering there was more reliance on

Fig. 5. (**a**) An adult male pound hammers a shellfish that he carried and placed onto this anvil. He strikes onto the same plane he is seated. (**b**) An adolescent male axe hammers attached oysters. He strikes against a different plane from which he is seated. (**c**) The arrow points to the indentation scarred into the face of this pounding hammer. Pen is for size reference and is 150 mm long. (**d**) The point of this axe hammer has been severely scarred from repeated use as indicated by the arrow. Knife is for size reference and is 83 mm long (photographs by M. Gumert).

Fig. 6. The grips used by macaques to hold axe hammers. (**a–c**) Different precision finger/passive palm pinch grips used to hold hand-sized axe hammers. The thumb appears to press the tool firmly into the fingers and the palm is a passive buttress of the tool. (**d**) A precision grip between the fingers and thumb used to hold small axe hammers where the tool is not buttressed by the palm (photographs by M. Gumert).

Fig. 7. The grips used by macaques to hold pounding hammers. (**a**) A power grip used in one-handed pound hammering where the fingers squeeze the tool into the base of the palm with support from the slightly outstretched thumb. (**b** and **c**) Power grips used in two-handed pounding with thumbs slightly out-stretched (b) and thumbs adducted into fingers (c). (**d**) A macaque manually presses both hands together onto each side of a pounding hammer exerting force from the fingers, palm, and thumbs (photographs by M. Gumert).

gripping between the fingers and palm with the thumb sometimes being used to stabilize. There seemed to be some gradation though, as the one-handed pounding tools were sometimes used with a similar pinching grip as with axe hammers, but observation showed the tool appeared less well controlled mainly owing to the large size of the tool relative to the hand (see supplemental video). The axe-hammering grip relied more on precision finger-to-thumb gripping, whereas pound hammering was more reliant on power finger-to-palm gripping. The axe-hammering grip was a form of precision pinching, although we observed no evidence of precision handling such as rotation or translation of the tool in the hand, and the tool moved in conjunction with movement of the entire hand.

Our video analysis showed further differences between pounding and axing. When macaques axed at oysters they struck the food item more rapidly than when using a pounding tool at an anvil (t-test: df $= 58$, $t = 6.887$, $P < 0.01$). The rate of axing was nearly three times faster than pounding. Macaques struck food items 29.4 times per minute when axing and only 10.62 times per minute when pounding. In addition, 47% of axing events were directed toward a different plane, whereas no pounding events (0%) were ever directed to other planes (df $= 58$, $t = 5.037$, $P < 0.01$). During axing, macaques often struck a different plane (Figs. 1 and 5b) and when pounding always struck at the same plane (Figs. 1 and 5a) in which they were seated. Macaques used axe hammers more rapidly and struck at targets across a wider spatial orientation relative to body position than they did with pounding hammers.

Shell Picks

In our last two observation periods, we began to observe that in at least one region of the island the macaques utilized auger shells (*Turritella attenuata*) to pick open oyster shells. These shells were conically shaped like a cork-screw, and when a macaque used an auger shell as a tool the shell was grasped by the wider end and the pointed end was used to strike oysters attached to boulders (Fig. 8a). Grips were harder to discern as we had no close-up photographs of these grips. It appeared gripping was sometimes a precision pinch with the tool passively buttressed by the palm, and sometimes a power finger/active palm grip with the fingers coiled around the tool with the thumb outstretched or opposed tip-to-tip with the middle finger. No empirical data was collected on the properties of these shells. They appear to be used in a similar manner to the stone axe hammers,

Fig. 8. (**a**) A young adult female macaque uses an auger shell pick to strike oysters attached to a large boulder. She is striking at a plane different from where she is standing. The female uses the shell pick in a manner similar to stone axe hammering, and is using the sharp point of the tool to pick at the oyster. (**b**) The arrow points to the worn tip of this auger shell that is the result of repeated striking on the tip of the tool, which before wear would have ended in a sharp pin-like point. The tool is grasped in the hand at the wide end and the point is used to chip oysters. The knife is for size reference and is 83 mm long (photographs by M. Gumert).

but were used more pick-like owing to the conical structure of the tool tapered into a sharp point (see Fig. 8b & supplemental video).

DISCUSSION

During our study, *M. f. aurea* clearly did not select tools randomly, and they used two distinct tool types. Therefore, it seemed that macaques selected stones with specific qualities to use as tools, and did not just randomly obtain stones from the enormous litter of stones available. Of greatest distinction was the difference between tools used for axing oysters and pounding loose food items on anvil stones. We labelled these two tool types as axe hammers and pounding hammers. Axe hammers were smaller, hand-sized stones, where the points of the stone were more frequently directed toward the oyster when used (Fig. 5b and d). In contrast, pounding hammers were larger and heavier, where the broader surfaces of the stone were more frequently oriented toward the food item (Fig. 5a and c). A third type of tool was the auger shell oyster picks that were used in nearly the same manner as axe hammers by utilizing the point of the shell to chip oysters (Fig. 8).

Pound hammering is comparable to the customary stone tool use reported in chimpanzees and capuchins because they also use a hard and heavy stone to smash a food item placed on an anvil [Boesch & Boesch, 1990; de A Moura & Lee, 2004; Fragaszy et al., 2004a; Mannu & Ottoni, 2009; Matsuzawa, 1994; McGrew, 1992; Ottoni & Mannu, 2001; Sugiyama & Koman, 1979; Visalberghi et al., 2007, 2009]. In contrast, axe hammering appears different from previously reported forms of tool use in other naturalistic studies of nonhuman primates. Unverified early reports suggest that capuchins might have been seen using stones to crack open oysters in Columbia (see Beck, 1980 for review). A more recent report documented that capuchins (*C. apella apella*) were observed cracking attached oysters at the base of trees in a Brazilian mangrove. This report indicated that the monkeys did not use stones, but rather used other oyster shells, and it was not reported if the behavior was customary or not [Fernandes, 1991]. Andaman long-tailed macaques also cracked oysters attached to mangrove trees, but on Piak Nam Yai they mainly used axe hammers for this task. We have not observed macaques using other oyster shells to crack oysters, only the auger shells mentioned previously.

Exploiting seafood along the rocky shores of Piak Nam Yai Island may represent a significant proportion of the diet of these macaques, and groups were observed to engage in tool use along the shores for hours at a time each day. Further work will be needed to determine exactly what proportion of tool-extracted food makes up the diet of these macaques. It seems likely though that shellfish obtained from the intertidal zones may be of high importance to the survival of long-tailed macaques on small island habitats. Consequently, the origin of this stone tool tradition or culture may have been a behavioral adjustment to the ecology of small, rocky island habitats where enormous amounts of shell food were available during low intertidal shifts. Possibly, shifts in seasonal fruiting pushed some populations of macaques to explore different niches on such an island environment, leading to the emergence of stone-use traditions to exploit hard-cased food sources in intertidal zones. Alternatively, the intertidal zones may have simply provided a more productive and stable food source that eventually attracted macaques away from their typical highly frugivorous feeding habits. Lastly, it is also plausible that some components of the tool-using behavior of *M. f. aurea* are the result of biological adaptations to living in intertidal habitats. Further study will be needed to investigate the origins of this behavior, as this will be important to understanding how animal traditions are formed.

Macaques as Tool Users

Macaques and other cercopithecines have not been observed to be particularly adept tool users [Panger, 2007], which has always been a bit of a conundrum because cercopithecines, especially macaques, have dextrous hands with a good precision gripping ability [Christel, 1994; Napier & Napier, 1985]. Precision gripping has been considered an important aspect to the evolution of tool use [see Marzke, 1997 for a discussion], and thus given the hand ability of macaques we would expect them to be good tool users. Our work on the macaques of the Andaman Sea region sheds light on this conundrum and demonstrates that indeed in the appropriate conditions, macaques can fully exploit their hand gripping ability to become skilled tool users and develop customary forms of tool use. The macaques of Piak Nam Yai Island use stone tools on a daily basis to extract food items in the intertidal zones of islands and coastal habitats, and they utilize this skill in other regions such as forests and streambeds. They appear to select tools based on the food being processed, indicating they could possibly have some understanding of the requirements for the food extraction process.

Macaque axe hammering appears to be a more coordinated form of tool use than pound hammering. This is because the axe hammers investigated were more frequently scarred on the smaller points of the tool, which suggests that axe hammering was done with greater precision and control than pound hammering in order to strike the tool repeatedly on these smaller surfaces. Moreover, when axe hammering, the macaques used precision pinching between the fingers and thumb to grip the stone, but in pound hammering typically used a form of power gripping between the fingers and palm. This difference could result in better control of axe hammers. By applying perpendicular force on the dermatoglyphic ridges there is greater friction produced than when sliding the ridges over the surface of an object [Buck & Bär, 1993]. The pinching between the fingers and thumb of a precision grip produces this kind of perpendicular force and therefore produces a firmer grip [Marzke, 1997]. Consequently, this grip provides a stronger hold and greater control over a tool than a power grip. When utilizing a power grip, the fingers press the object into the palm and this squeezing may exert some amount of parallel, or sliding, force by the object along the surface of the palm. This might cause the power grip to produce less friction on the dermatoglyphic ridges than the more perpendicular force applied in the precision pinching grip. As a result, the hand may have less control over the object in a power grip and will require more frequent repositioning of the tool (see supplementary video).

We also found that axe hammering was done more rapidly than pound hammering, and was used to strike targets over a wider range of motion. This shows that the macaques were striking rapidly on the small point surfaces of the tool, and were therefore exerting force repeatedly onto a smaller surface area during a shorter time frame than during pound hammering. Moreover, this rapid striking using the point of a tool was observed to occur toward targets across a wide spatial orientation from the body. In contrast, smashing downward was the only motion of striking observed during pound hammering.

It seems probable that rapidly striking toward a differing plane (e.g. over one's head) requires a firm grip with good control of the tool. In contrast, the minimum requirements of pound hammering only need to be a controlled drop onto the target. Therefore, pound hammering may not require as firm a grip as axe hammering in order to be effective. Moreover, if the grip is lost during a pound-hammering series, it can be re-established after each strike because the tool can be supported on the plane the macaque is positioned on after each strike (see supplemental video for an example of this re-grasping of the tool). In contrast, during axe hammering, there is less opportunity for re-establishing a grip once the rapid hammering begins because striking involves the quick recoiling of the hammer back into strike position. This is especially important when hammering to a different plane because a poor grip or need to re-establish a grip could more easily lead to dropping the tool or ineffectively striking. Future work should test hypotheses on the degree of control that macaques actually have over axe hammers, and whether factors such as greater friction produced by the pinching finger-to-thumb/passive palm grip contribute to any greater control or coordination the macaque might have.

Precision, Tool Scarring, and Hand Grip

Napier [1980] distinguished two basic types of hand grips, the precision grip and the power grip. Precision gripping was argued to be used for fine manipulations and the power grip was employed when force was the primary requirement. Furthermore, precision gripping involved pad-to-pad thumb–index finger gripping, and power gripping involved finger–palm grasps. The hand grips we observed in long-tailed macaques using axe hammers do not fall neatly into this dichotomous classification, and better fit into Marzke and Wullstein's [1996] more detailed categorization used in a comparison of chimpanzees and humans. In these categories, precision and power are integrated together by expanding the definition of precision grip to include grips between fingers and thumb that produce a pinching force on the object being controlled. Long-tailed macaques grip axe hammers in ways that fit into this classification scheme. They used a precision pinch buttressed into their palm. This likely represents the fact that the task requires both precision and power, and the macaques are adjusting their hand grip to accommodate this bimodal need. Hand-grip is also likely related to the physical demands owing to the size of the object [Pouydebat et al., 2009], with smaller objects being more precisely held and larger objects having to be gripped with more strength from the palm to support the size and weight.

The precision used in axe hammering is evident after investigating the scar patterns on the tools. Tools used to hammer oysters showed significantly more scarring on the points when compared with tools for other food sources. Oyster tools also tended to be smaller than other tools, and thus we considered them a distinct tool, which we termed axe hammers. Given that the tool was smaller and involved more use of the small points, it can be concluded that the tool was used more precisely. The macaque used a small tool and used a smaller element of the tool than they did when they used pound hammers, which were larger and used a broader surface. To make clear the basis for the distinction, we could compare this to a human using a chisel to break off small parts of a stone compared with a sledge-hammer to smash the stone. The former is a more precise tool than the latter, and would produce finer scarring patterns. Based on the usage pattern and hand-grip style observed in macaques, we conclude that the axe hammer is a higher precision tool than the pounding hammer. Further research is needed, though, to determine if this degree of precision is necessary to open oysters and to better understand why macaques use this more precise method for opening oysters.

A Three-Species Model for NHP Stone Tool Use

Macaque hand grips have typically been considered to have more hand precision ability than other nonhuman primates and have been noted for the ability to finely manipulate small objects [Christel, 1994; Christel & Billard, 2002; Christel & Fragaszy, 2000; Fragaszy et al., 2004b; Fragaszy, 1998; Matsuzawa, 2001; Napier & Napier, 1985; Susman, 1998; Tanaka, 1995]. The hand grip we observed for axe hammering by these macaques is similar to the grip typically used by the chimpanzees of the Taï Forest, which use stone tools to crack open Coula and Panda nuts [Boesch & Boesch, 1993]. Although Boesch and Boesch [1993] referred to it as simply a power grip, Marzke and Wullstein [1996] labelled and categorized the Taï Forest chimpanzee grip as a form of precision grip called the cup grip because it involved precision pinching of the fingers and thumb. They further explained though that the chimpanzees had a weaker grip than humans and that humans use a cradle grip, which uses the thumb to press the object firmly into the fingers. Moreover, in the chimpanzee cup grip the tool is kept static with no precision handling such as in humans, which are capable of rotating and translating the object with their fingers. Rather, in chimpanzees, the tool moves in conjunction with the entire hand. In our macaques, the tool was also kept static relative to the whole hand, but we suspect that the finger-to-thumb grip may be stronger than that of chimpanzees and more comparable to the human cradle grip. We suggest this because our observations show the fingers and thumb pinching the tool (Fig. 6) and because macaques are known to have greater pad-to-pad precision gripping preference and ability than chimpanzees [Christel, 1994; Napier & Napier, 1985; Pouydebat et al., 2009].

Descriptions of how capuchins hold stone tools are also similar to the macaques we studied. Westergaard and Suomi [1997] stated that capuchins held a stone with a finger-to-thumb pinch with support of a down-turned palm, but they did not label it a cup grip. Rather, they labelled it a power grip, which contrasts with Marzke and Wullstein's [1996] assessment of this similarly described grip in chimpanzees. It is unclear whether the capuchin grip of stone tools is truly different, but better comparison between macaques, capuchins, and chimpanzees will be needed to clarify this issue. Pound-hammering style in macaques also appeared similar to capuchins. Macaques pick up a large, heavy stone with two hands and grasp the stone between their fingers and palm and strike down. Alternatively, they sometimes grasp the rock between two open hands and pound down. Some even stood up and then put their full weight into the strike, similar to the style observed in wild bearded capuchins [Fragaszy et al., 2004a]. Macaques presumably have more hand control than capuchins because they have greater volar opposability, have better individual digit control, and have a saddle joints in their thumb [Christel & Fragaszy, 2000; Fragaszy, 1998] and therefore we might expect macaques to be able to exert more control and force in a precision grip than capuchins. Despite this difference, capuchins are highly manipulative, have an exceptional degree of innervation between the spine and fingers [Fragaszy, 1998], and have greater thumb robusticity than macaques [Westergaard & Kuhn, 2001]. These factors can account for the convergence we see in the hand dexterity of macaques and capuchins, despite their differences in hand anatomy.

The above comparisons show the utility of comparing the three nonhuman primates that customarily use stone tools in wild settings. Adding in macaques and capuchins as models to help place human tool use into a comparative perspective will prove to be a new and interesting approach compared with the traditional model that compared mainly chimpanzee stone tool use to human beings and extinct hominids. For example, both capuchins and macaques are reported to use precision grips more frequently (70–80%) to pick up small items (i.e. 4% the size of the hand) than great apes (~30%), and in similar proportions to humans. Moreover, capuchins use thumb–distal grips more often to grasp items that are 40% the length of their hand (~80%), which is similar to adult humans, whereas macaques are more like apes and use power grips (~60%) for such tasks. Human children on the other hand, use thumb–distal grips and power grips equally (40%) to pick up items of such size [Pouydebat et al., 2009]. Overall, capuchins provide a good model for understanding the convergence of traits associated with stone tool use, whereas macaques and chimpanzees provide a good model for potential homologous traits associated with stone tool use.

We expect that further investigation into the stone tool use of *M. f. aurea* will be an important addition to our understanding of material culture, the emergence of primitive technology, and the traits associated with stone tool using abilities. We can compare the stone tools of macaques to the tools of chimpanzees and capuchins, and question why macaques use axe hammering on oysters. Is axe hammering a unique skill of long-tailed macaques, or is it just the result of inhabiting a rock-rich environment where shelled food items are attached to substrates, that chimpanzees and capuchins could just as easily do? Moreover, macaque axe hammering could provide us with a better understanding of the anatomy and neurobiology necessary for tool use requiring high levels of control and hand dexterity. This is because the demands to produce the precision scar patterns found on axe hammers appeared to require greater hand control than in pound hammering. Lastly, as macaques have a finer precision gripping ability than other nonhuman primates we can ask what features of the macaque hand are related to their ability to use axe hammers, and whether these relate to any features shared with humans. Further research using the tripartite nonhuman model of chimpanzees, capuchins, and macaques to understand stone tool use will provide a platform to investigate these questions. Moreover, comparing humans to this tripartite model will help us better place human tool use into a clearer comparative perspective among the anthropoid primates.

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