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Stone tool transport by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*)

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ABSTRACT

Archaeologists have used stone transport as a proxy to understand a variety of cognitive, logistical and social problems faced by human ancestors. In the same way, tool transport in our close relatives, non-human primates, has been seen as an important indicator of material selection proclivities, and as a contributing factor to the formation of activity sites as part of niche construction processes. Non-human primate transport behaviour also assists in framing evolutionary scenarios for the emergence of stone tool use in the hominin lineage. Here, we present the first study of directly observed stone tool transport in wild and unhabituated Burmese long-tailed macaques (*Macaca fascicularis aurea*) in Thailand. These macaques were observed during intertidal foraging activities, during which they pound open hard-shelled molluscs with stone tools. We recorded 2449 transport bouts, when a long-tailed macaque carried a stone tool from one prey target to the next, and found that on average the same tool was used to sequentially consume nine prey items in each foraging episode. The maximum number of prey items consumed in a single episode was 63. We found that tools used to open sessile oysters typically were used to consume more prey per episode than those employed on motile prey, and females transported tools further than males. Heavier tools (>200 g) were rarely transported more than a few metres, but the longest transport distance was over 87 m. Importantly for primate archaeological analysis of macaque tool use sites, we found that the median transport distance was 0.5 m, meaning that tools are very often used in the immediate vicinity of the place they were collected by a macaque.

1. Introduction

The tool use and construction behaviour of many animals, from birds to insects to cephalopods, involves transport of materials around the landscape (Hansell and Ruxton, 2008; Shumaker et al., 2011). Transport is also recognised from the earliest known archaeological record, produced by Pliocene hominins in East Africa (Plummer, 2004). Because of its ubiquity, material transport has been used as a proxy to give insights into a variety of related activities, including the cognitive and logistical implications of selecting suitable raw materials for tool manufacture or use (Chappell and Kacelnik, 2002; Finn et al., 2009), and investigating how tool users move around their world and interact with other groups (Braun, 2013; Brumm, 2010). Transport is also crucial for the creation of sites—locations of repeated tool use and discard—which are a fundamental unit of both tool behaviour and archaeological analyses.

Stone transport has been a frequent topic of study in wild stone-tool-using non-human primates, particularly the nut cracking behaviour of West African chimpanzees (*Pan troglodytes verus*) (Boesch and Boesch, 1984; Carvalho et al., 2012) and robust capuchins (*Sapajus* spp.) (Hanna et al., 2015; Massaro et al., 2012; Visalberghi et al., 2009). These studies show that a small number of primates from both the Old and New World have converged on a proclivity to transport stone tools to the location of either fruiting trees or suitable anvils. Such behaviour results in accumulations of stone tools, which are recoverable (Mercader et al., 2002, 2007) and identifiable (Visalberghi et al., 2013) through the application of analytical techniques derived from archaeological practice (e.g., Carvalho, 2011; Haslam, 2012, 2014; Haslam et al., 2009, 2014; Luncz et al., 2015). Aside from these instances of primate use of stones for foraging, Japanese macaques (*Macaca fuscata*) handle stones in playful, nonfunctional patterns (Leca et al., 2016). As part of this behaviour, they transport and accumulate stones in ways that mirror other primates' tool use sites (Huffman and Quiatt, 1986; Quiatt and Huffman, 1993). Similarly, some West African chimpanzees (*Pan troglodytes verus*) have been reported to throw and bang stones against trees, again resulting in an observable accumulation (Kühl et al., 2016).

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Here, we report on the natural stone tool transport behaviour of wild, island-dwelling, Burmese long-tailed macaques (*Macaca fascicularis aurea*), and discuss how transport patterns displayed by these primates may contribute to the formation of archaeologically-identifiable macaque tool-use sites. Burmese long-tailed macaques use stone tools to process molluscs, crustaceans and nuts in Thailand (Malaivijitnond et al., 2007) and Myanmar (Carpenter, 1887), and will carry stones they are using as tools. Studies have shown that they select stones based on hardness and mass, depending on the food source (Gumert et al., 2009; Gumert and Malaivijitnond, 2013). To date there have been no systematic observation studies that analyzed how long-tailed macaques transport naturally occurring materials, although we know that they leave accumulations of stone and shell debris around anvil sites (Gumert et al., 2009), in much the same manner as chimpanzees and capuchins. When researchers provided unhabituated *M. f. aurea* with stones, with only occasional direct observation of their subsequent use, the macaques moved tools on average 3.8 m from the provisioning site, with smaller oyster tools being moved the farthest, up to 99 m away from their original location (Gumert and Malaivijitnond, 2013).

The unhabituated macaque group discussed in this study lives on the small island of Piak Nam Yai (PNY), off the west coast of Thailand, and they habitually use stone tools to exploit a wide range of shellfish and other intertidal taxa (Gumert et al., 2009; Gumert and Malaivijitnond, 2012; Malaivijitnond et al., 2007; Tan et al., 2015) (Fig. 1). Our aim was to document both the ways that macaques transport stones and prey items from one place of use to the next, and how they chain isolated *bouts* of tool use into *episodes* (see definitions in Methods) that involved repeated use of the same tool. Based on the assumption that individuals will act to minimise energetic cost during stone transport (Massaro et al., 2012), our hypotheses were that: (i) stone tool transport from one bout to the next would involve primarily short moves; (ii) smaller tools would be carried longer distances than larger tools; and (iii) smaller tools would be used for longer (more bouts per episode) than larger tools.

2. Methods

The study site was on the northeastern shore of Piak Nam Yai Island (N 9° 35′, E 98° 28′) in the Andaman Sea and part of Laem Son National Park (LSNP), Ranong District, Thailand. PNY is approximately 1.7 km^2 with 5.4 km of coastline, and in 2011 was home to about 200 wild Burmese long-tailed macaques living in nine main groups (Gumert et al., 2013; Tan et al., 2015). The coastline consists of rocky shore, mangrove, and sandy beach. The western, seaward shore is primarily rocky, with a few small sandy beaches, while the eastern, bayward side also has a mangrove forest.

During our study we investigated one group of unhabituated macaques inhabiting the mangrove region of PNY, the Mangrove (MN) group, which contained about 30 individuals and inhabited a 1.35 km coastal range (Gumert et al., 2013). The MN group home range included patches of shoreline with dense concentrations of stones, as well as mangrove areas with fewer stones available. It also contains few large boulders, such that transport is almost entirely horizontal rather than up and down rocky outcrops. MH and APG collected video data on tool transport from 16 November to 19 December 2012, by taking video recordings (Sony HDRCX130EB Camcorder) from a long-tail boat that was anchored offshore from the island, approximately 20 m from the subjects. Binoculars were used to assist in cases where it was not clear whether a macaque was holding a tool, or prey item. The PNY macaques were unhabituated and unidentified to the researchers collecting data and coding the video. Each subjects' sex was recorded when apparent to permit assessment of whether one sex was transporting tools further than the other.

To facilitate judgment of transport distances, we temporarily placed flags every 2 m along the coastline, in the intertidal zone, within the MN group's range on the northeast of PNY (Fig. 2). The flags were removed at the end of the observation season, and the macaques did not interact in any way with the flags. The macaques typically foraged along the intertidal zone at low tide, moving either northwards or southwards as a loose group, so our flags were positioned to follow their expected travel path. The flags covered a total distance of 400 m, with the southern end of the flag line at N 9° 34′ 45.6″, E 98° 28′ 16.4″, covering both more and less dense areas of stone coverage. This strategy enabled us to conservatively estimate transport of tools parallel to the flag line to the nearest 0.5 m from our videos, as 1 m intervals were readily interpolated from the flag placement. We also recorded an estimate of prey item transport distances, where a prey item was visibly transported in a macaque's hand and subsequently processed with a stone tool, to the nearest 0.5 m. We did not record transport of prey in macaque cheek pouches, which means that our data on this topic should be considered to be a subset of likely total prey transport.

We defined a tool use *bout* as the use of a stone tool to pound open a prey item, commencing when the macaque began to strike the item and concluding when the macaque either consumed the prey or moved on to a different item, having failed to break open the prey. We defined a tool use *episode* as a sequence of two or more consecutive bouts by the same macaque using the same tool on different prey items, usually with transport of the tool between bouts (definitions were modified following Masataka et al., 2009). An episode began when a macaque first picked up a stone that was subsequently used as a pounding tool, and

Fig. 1. Macaque stone tool transport and use for oyster pounding by two individuals inhabiting the mangrove region of Piak Nam Yai. The male macaque on the left is transporting a stone hammer in his left hand in (a), and uses it in (b). The female macaque on the right pounds open oysters attached to a rock in (a), and has transported the same tool to a new pounding site in (b).

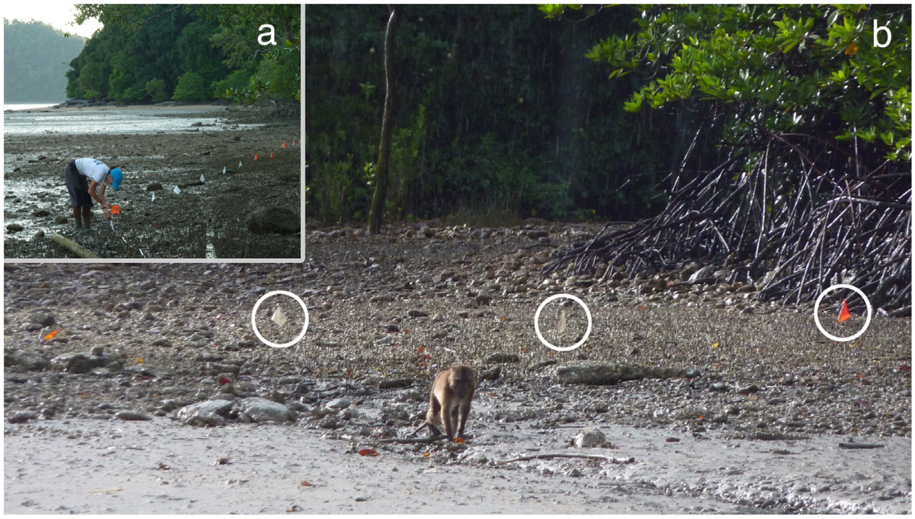

Fig. 2. Flag placement, northeast Piak Nam Yai. (a) APG placing flags. (b) A macaque transporting a stone tool; flags spaced every 2 m are circled.

ended with the abandonment of the tool, with no time limit set between bouts.

In our study we only observed macaques using tools on molluscs. We distinguished between pounding of oysters that were attached to a rocky substrate, and pounding of motile prey, which were gastropods that were picked up and placed on a stone anvil prior to pounding. Prey transport only applied to the latter category. We did not code any transport episodes for which we were uncertain whether the macaque was holding either a tool or prey item.

We assessed the number of strikes per bout, and the rate of strikes per minute, as proxies for the likelihood of use-wear developing on the tools (Haslam et al., 2013). We do not have precise data on the correlation between wear formation and the number of strikes for which a tool has been used, but we note that higher rates of striking, and macaque retention of a tool through multiple bouts with high numbers of strikes per bout, likely increases the chances that damage to the tool's surface will be recognisable during future surveys or excavations. We therefore recorded these variables as part of our interest in the formation of archaeologically-recognisable animal tool-use sites.

To complement our video data, we collected a sample of tools following their observed use by the macaques, whenever we could precisely identify the initial pick-up and final discard points for a tool. These tools were collected from the MN group range over a longer period than the video data recording, in November and December of both 2012 and 2013, and included tools from the complete intertidal range of the MN group. This process involved waiting for the macaques to move away following tool discard, then landing the boat onshore and recording the total distance of tool movement using a tape measure. For these tools we recorded both the total transport distance and the stone weight, which was not possible from the videos.

Two-tailed Mann-Whitney *U* tests were used to compare the number of bouts per episode for sessile and unattached prey items, and to compare tool transport distances by sex, with alpha set to 0.05.

3. Results

We recorded a total of 2449 individual tool-use bouts, from just over 11 h of video recordings. These bouts involved 248 separate episodes of stone tool use. On average, each episode included nine bouts (that is, nine separate prey items were consumed in a row with the same tool; range 1–63) (Fig. 3). The macaques used the smaller tools for significantly more bouts per episode than the larger stones (Mann-Whitney: $n_1 = 196$, $n_2 = 52$ $U = 3105.5$; $p < 0.0001$).

We were able to assess the tool transport distance for 2446 bouts, ranging from 0 m (the macaque did not move position when starting to process a new prey item) to a maximum of 11 m (Fig. 4). The median transport distance was 0.5 m, and in 27.4% of bouts ($n = 671$) the macaque moved <0.5 m. We found that 88% ($n = 2153$) of all tool use bouts involved the macaque transporting the tool a metre or less.

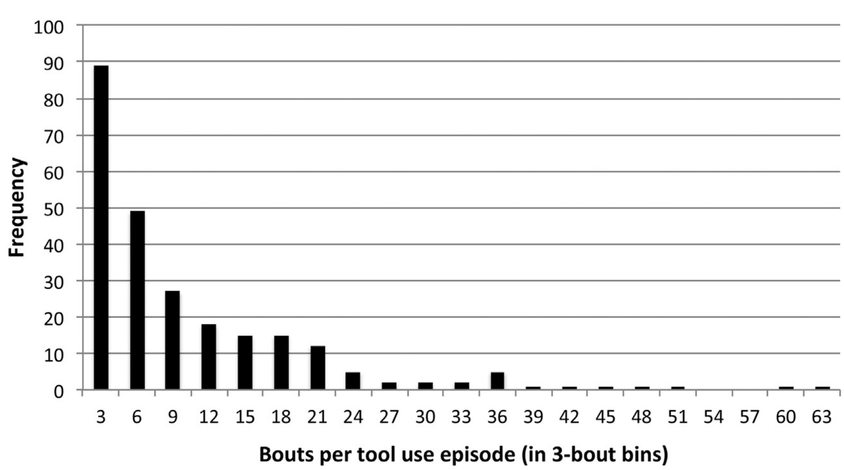

Fig. 3. Frequency of macaque stone tool use bouts per episode of observed tool use at Piak Nam Yai, collected into bins of 3 bouts.

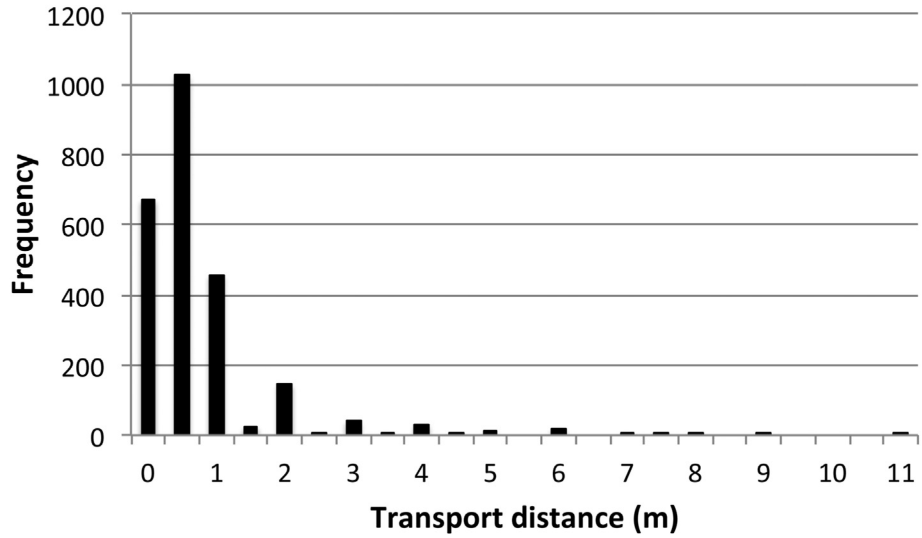

Fig. 4. Macaque stone tool transport distances between bouts, Piak Nam Yai.

We measured 49 episodes of tool transport in which we could identify and collect the used tool, covering distances from 0.19 m to 87.61 m. The collected tools ranged in size from 18.7 g to 4078 g (Fig. 5). No tools over 200 g were transported more than 5 m in a complete episode, and 21 of the 49 tools (43%) were discarded within 2 m of the spot from which they were originally picked up, even when multiple prey items were processed in the interim.

We observed 365 instances of transport of unattached prey items. Prey was moved a maximum of 4 m to a suitable anvil from where it was collected, although 327 (89.6%) of prey transport events were at or below our conservative measurement threshold of 0.5 m. We were able to assess the number of strikes required to successfully open each prey item for 2286 tool-use bouts. The number of strikes per bout ranged from 1 to 86 strikes when opening oysters attached to the rocky substrate ($n = 1996$; median $= 7$), and 1 to 60 strikes when opening gastropods and other items that were not attached to the substrate and were placed on a stone anvil prior to pounding ($n = 290$; median $= 3$) (Fig. 6). Macaques struck the target prey during tool bouts an average of 1.67 strikes/s for oyster pounding, and 0.4 strikes/s for unattached molluscs. Observing a higher rate for oyster processing replicates results previously recorded on PNY (Gumert et al., 2009, 2011; Tan et al., 2015), however, our observed rates were lower than those recorded in other detailed studies of tool striking (Gumert et al., 2011; Tan et al., 2015).

We were able to identify the subject's sex for 1655 bouts, including 1018 female bouts and 637 male bouts. We found that although there is overlap in the distances involved, females transported tools significantly further than males (averaging 0.76 ± 1.15 m for females and 0.58 ± 1.08 m for males) (Mann-Whitney $U = 273.930$; $p < 0.0001$).

4. Discussion

Long-tailed macaques in our study routinely transported and reused stone tools to process various shellfish prey in intertidal mangrove environments at PNY. Supporting our hypothesis, transport distances between bouts were typically short (less than a metre), with larger tools being much less likely to be transported more than a few metres in an entire tool-use episode. Fewer than ten prey items were typically consumed per episode, but in one exceptional case a macaque consecutively consumed 63 prey items in a single episode, re-using and transporting the same tool. Furthermore, smaller tools (which are most often used for oyster processing) were used for more consecutive bouts than larger tools, supporting our third hypothesis. We also replicated the previous finding that the macaques employed a faster strike

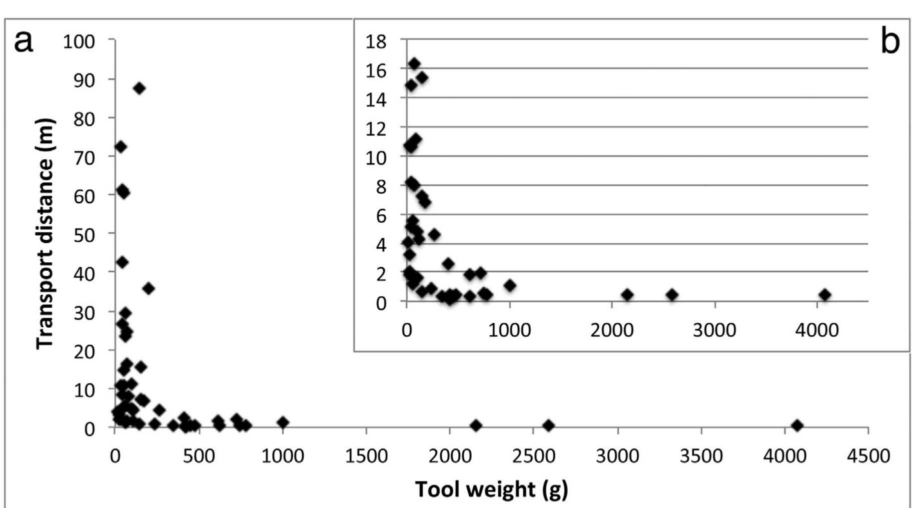

Fig. 5. Macaque stone tool transport distances per episode and tool weight, Piak Nam Yai. (a) Full dataset ($n = 49$). (b) Tools transported <20 m ($n = 39$). The axis labels apply to both plots.

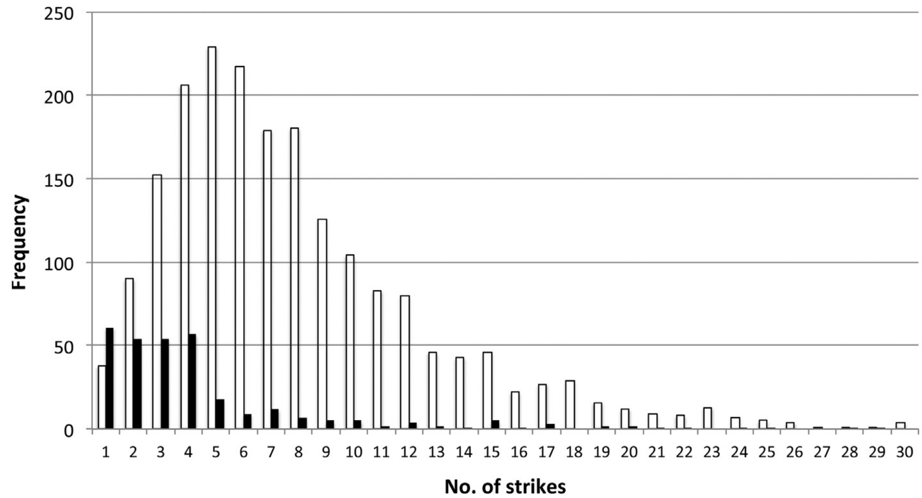

Fig. 6. Frequency of macaque strikes used to open sessile (open bars) and motile prey (black), Piak Nam Yai. For clarity, the x-axis excludes the small number of bouts (n = 18) that exceeded 30 strikes for a single prey item.

rate when processing oysters rather than unattached (motile) prey items.

We found that females routinely carried tools between bouts further than males did, although in both cases the average transport distance was similar at between 0.5 m and 1 m. One plausible explanation for this finding is that females open sessile oysters more often than males (Gumert et al., 2011), and sessile foods are typically processed with smaller tools (Gumert et al., 2009). Given our finding that the macaques move smaller tools further during a tool use episode, greater female transport distances may therefore simply be a result of their tendency to use more oyster-processing tools than males.

Our study clearly demonstrates that macaques are moving both stones and prey around the coasts on which they forage. While we found that macaques can transport a single stone tool over 87 m in a single foraging episode, similar to transport behaviour reported in previous work (Gumert and Malaivijitnond, 2013), in general we found that most tools were not moved very far between bouts. Macaque stone tool transport for at least 0.5 m between prey items was very common, occurring almost three-quarters of the time. On the other hand, when motile prey items were transported, it was most often for very short distances, of 0.5 m or less. These data demonstrate a strong tendency in these animals to hold on to a tool, transport it and re-use it several times while foraging on different prey. We also found that when tools were abandoned, it was most often within a few metres of both the spot from which the tool was originally picked up, and very close to the last location of tool use. This pattern suggests that accumulation of used tools close to anvils and oyster-bearing substrates should be common, acting as a helpful guide to future archaeological investigation of macaque activity areas.

We observed that tool size affects the average distance that tools were moved, building on previous inferences from experimental work at PNY (Gumert and Malaivijitnond, 2013). In particular, heavier tools were transported very short distances, and thus larger hammers used to pound motile prey items were deposited very close to, or on top of, anvil stones. After abandonment, incoming tides typically caused such stones to slide down to rest beside the anvil, beginning the process of accumulation. Small stones can be moved further by the tides, however most are deposited near an oyster bed or anvil, and so will also accumulate at such sites. The accumulation of stones around pounding sites establishes a strong co-location of used stone hammers with both anvils and oyster-bearing substrates, increasing the likelihood of tool re-use. In turn, re-use contributes to the development of wear patterns, as previously reported (Gumert et al., 2009; Haslam et al., 2013), which enhances our ability to recognise and interpret the past use of macaque tools. As a case in point, both tool accumulation and use-wear data assisted in the recent archaeological recovery and identification of macaque tools at PNY (Haslam et al., 2016).

Our study contributes a first look at how macaques move materials around their environment while processing encased coastal resources, contributing to the formation of a patterned tool-use landscape. Worn tools, as well as crushed food remains, collect around anvils and oyster beds, which should over time alter how stones and shells accumulate along the shores on which macaques forage. These predictable environmental changes caused by macaques form a clear target for archaeological excavation, aided by the deposition of sediment by tidal forces. In broader perspective, we expect that future analysis of the stone accumulations themselves will provide comparative data for other primates that regularly engage in stone transport, including humans, West African chimpanzees, bearded capuchins and Japanese macaques.

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References

Boesch, C., Boesch, H., 1984. Mental map in wild chimpanzees: an analysis of hammer transports for nut cracking. Primates 25, 160–170.
Braun, D., 2013. The behavior of Plio-Pleistocene hominins: archaeological perspectives. In: Sponheimer, M., Lee-Thorpe, J., Reed, K., Ungar, P. (Eds.), Early Hominin Paeoecology. University Press of Colorado, Boulder, Colorado, pp. 325–351.
Brumm, A., 2010. 'The falling sky': symbolic and cosmological associations of the Mt William greenstone axe quarry, Central Victoria, Australia. Camb. Archaeol. J. 20, 179–196.
Carpenter, A., 1887. Monkeys opening oysters. Nature 36, 53.
Carvalho, S., 2011. Extensive surveys of chimpanzee stone tools: from the telescope to the magnifying glass. In: Matsuzawa, T., Humle, T., Sugiyama, Y. (Eds.), The Chimpanzees of Bossou and Nimba. Springer, Dordrecht, pp. 145–155.
Carvalho, S., Biro, D., Cunha, E., Hockings, K., McGrew, W.C., Richmond, B.G., Matsuzawa, T., 2012. Chimpanzee carrying behaviour and the origins of human bipedality. Curr. Biol. 22, R180–R181.
Chappell, J., Kacelnik, A., 2002. Tool selectivity in a non-primate, the New Caledonian crow (*Corvus moneduloides*). Anim. Cogn. 5, 71–78.

Finn, J., Tregenza, T., Norman, M., 2009. Defensive tool use in a coconut-carrying octopus. Curr. Biol. 19, R1069–R1070.

Gumert, M., Malaivijitnond, S., 2012. Marine prey processed with stone tools by Burmese long-tailed macaques (*Macaca fascicularis aurea*) in intertidal habitats. Am. J. Phys. Anthropol. 149, 447–457.

Gumert, M., Malaivijitnond, S., 2013. Long-tailed macaques select mass of stone tools according to food type. Philos. Trans. R. Soc. B 368. http://dx.doi.org/10.1098/rstb.2012.0413.

Gumert, M., Hamada, Y., Malaivijitnond, S., 2013. Human activity negatively affects wild stone tool-using Burmese long-tailed macaques *Macaca fascicularis aurea* in Laem Son National Park, Thailand. Oryx 47, 535–543.

Gumert, M., Hoong, L.K., Malaivijitnond, S., 2011. Sex differences in the stone tool-use behavior of a wild population of Burmese long-tailed macaques (*Macaca fascicularis aurea*). Am. J. Primatol. 73, 1–11.

Gumert, M., Kluck, M., Malaivijitnond, S., 2009. The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman Sea region of Thailand. Am. J. Primatol. 71, 594–608.

Hanna, J.B., Schmitt, D., Wright, K., Eshchar, Y., Visalberghi, E., Fragaszy, D., 2015. Kinetics of bipedal locomotion during load carrying in capuchin monkeys. J. Hum. Evol. 85, 149–156.

Hansell, M., Ruxton, G., 2008. Setting tool use within the context of animal construction behaviour. Trends Ecol. Evol. 23, 73–78.

Haslam, M., 2012. Towards a prehistory of primates. Antiquity 86, 299–315.

Haslam, M., 2014. Primate archaeobotany: the potential for revealing nonhuman primate plant-use in the African archaeological record. In: Nixon, S., Murray, M.A., Fuller, D. (Eds.), The Archaeology of African Plant Use. Left Coast Press, Walnut Creek, CA, pp. 25–35.

Haslam, M., Cardoso, R.M., Visalberghi, E., Fragaszy, D., 2014. Stone anvil damage by wild bearded capuchins (*Sapajus libidinosus*) during pounding tool use: a field experiment. PLoS One 9, e111273.

Haslam, M., Gumert, M., Biro, D., Carvalho, S., Malaivijitnond, S., 2013. Use-wear patterns on wild macaque stone tools reveal their behavioural history. PLoS One 8, e72872.

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., Du, A., Hardy, B.L., Harris, J., Marchant, L., Matsuzawa, T., McGrew, W., Mercader, J., Mora, R., Petraglia, M., Roche, H., Visalberghi, E., Warren, R., 2009. Primate archaeology. Nature 460, 339–344.

Haslam, M., Luncz, L., Pascual-Garrido, A., Falotico, T., Malaivijitnond, S., Gumert, M., 2016. Archaeological excavation of wild macaque stone tools. J. Hum. Evol. http://dx.doi.org/10.1016/j.jhevol.2016.05.002.

Huffman, M.A., Quiatt, D., 1986. Stone handling by Japanese macaques (*Macaca fuscata*): implications for tool use of stone. Primates 27, 413–423.

Kühl, H.S., Kalan, A.K., Arandjelovic, M., Aubert, F., D'Auvergne, L., Goedmakers, A., Jones, S., Kehoe, L., Regnaut, S., Tickle, A., Ton, E., van Schijndel, J., Abwe, E.E., Angedakin, S., Agbor, A., Ayimisin, E.A., Bailey, E., Bessone, M., Bonnet, M., Brazolla, G., Buh, V.E., Chancellor, R., Cipoletta, C., Cohen, H., Corogenes, K., Coupland, C., Curran, B., Deschner, T., Dierks, K., Dieguez, P., Dilambaka, E., Diotoh, O., Dowd, D., Dunn, A., Eshuis, H., Fernandez, R., Ginath, Y., Hart, J., Hedwig, D., Ter Heegde, M., Hicks, T.C., Imong, I., Jeffery, K.J., Junker, J., Kadam, P., Kambi, M., Kienast, I., Kujirakwinja, D., Langergraber, K., Lapeyre, V., Lapuente, J., Lee, K., Leinert, V., Meier, A., Maretti, G., Marrocoli, S., Mbi, T.J., Mihindou, V., Moebius, Y., Morgan, D., Morgan, B., Mulindahabi, F., Murai, M., Niyigabae, P., Normand, E., Ntare, N., Ormsby, L.J., Piel, A., Pruetz, J., Rundus, A., Sanz, C., Sommer, V., Stewart, F., Tagg, N., Vanleeuwe, H., Vergnes, V., Willie, J., Wittig, R.M., Zuberbuehler, K., Boesch, C., 2016. Chimpanzee accumulative stone throwing. Sci. Rep. 6. http://dx.doi.org/10.1038/srep22219.

Leca, J.-B., Gunst, N., Pelletier, A.N., Vasey, P.L., Nahallage, C.A., Watanabe, K., Huffman, M.A., 2016. A multidisciplinary view on cultural primatology: behavioral innovations and traditions in Japanese macaques. Primates 1–6.

Luncz, L., Wittig, R., Boesch, C., 2015. Primate archaeology reveals cultural transmission in wild chimpanzees (*Pan troglodytes verus*). Philos. Trans. R. Soc. B 370. http://dx.doi.org/10.1098/rstb.2014.0348.

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., Hamada, Y., 2007. Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). Am. J. Primatol. 69, 227–233.

Masataka, N., Koda, H., Urasopon, N., Watanabe, K., 2009. Free-ranging macaque mothers exaggerate tool-using behavior when observed by offspring. PLoS One 4, e4768.

Massaro, L., Liu, Q., Visalberghi, E., Fragaszy, D., 2012. Wild bearded capuchin (*Sapajus libidinosus*) select hammer tools on the basis of both stone mass and distance from the anvil. Anim. Cogn. 15, 1065–1074.

Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R.T., Boesch, C., 2007. 4,300-year-old chimpanzee sites and the origins of percussive stone technology. Proc. Natl. Acad. Sci. U. S. A. 104, 3043–3048.

Mercader, J., Panger, M., Boesch, C., 2002. Excavation of a chimpanzee stone tool site in the African rainforest. Science 296, 1452–1455.

Plummer, T., 2004. Flaked stones and old bones: biological and cultural evolution at the dawn of technology. Yearb. Phys. Anthropol. 47, 118–164.

Quiatt, D., Huffman, M.A., 1993. On home bases, nesting sites, activity centers, and new analytic perspectives. Curr. Anthropol. 34, 68–70.

Shumaker, R., Walkup, K., Beck, B., 2011. Animal Tool Behavior: The Use and Manufacture of Tools by Animals. John Hopkins University Press, Baltimore.

Tan, A., Tan, S.H., Vyas, D., Malaivijitnond, S., Gumert, M., 2015. There is more than one way to crack an oyster: identifying variation in Burmese long-tailed macaque (*Macaca fascicularis aurea*) stone-tool use. PLoS One 10, e0124733.

Visalberghi, E., Haslam, M., Spagnoletti, N., Fragaszy, D., 2013. Use of stone hammer tools and anvils by bearded capuchin monkeys over time and space: construction of an archeological record of tool use. J. Archaeol. Sci. 40, 3222–3232.

Visalberghi, E., Spagnoletti, N., Ramos da Silva, E., de Andrade, F., Ottoni, E., Izar, P., Fragaszy, D., 2009. Distribution of potential suitable hammers and transport of hammer tools and nuts by wild capuchin monkeys. Primates 50, 95–104.