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RESEARCH ARTICLE

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Analysis of sea almond (*Terminalia catappa*) cracking sites used by wild Burmese long-tailed macaques (*Macaca fascicularis aurea*)

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Nut-cracking is shared by all non-human primate taxa that are known to habitually use percussive stone tools in the wild: robust capuchins (*Sapajus* spp.), western chimpanzees (*Pan troglodytes verus*), and Burmese long-tailed macaques (*Macaca fascicularis aurea*). Despite opportunistically processing nuts, Burmese long-tailed macaques predominantly use stone tools to process mollusks in coastal environments. Here, we present the first comprehensive survey of sea almond (*Terminalia catappa*) nut-cracking sites created by macaques. We mapped *T. catappa* trees and nut-cracking sites that we encountered along the intertidal zone and forest border on the coasts of Piak Nam Yai Island, Thailand. For each nut-cracking site, we measured the physical properties (i.e., size, weight, use-wear) of hammer stones and anvils. We found that *T. catappa* trees and nut-cracking sites primarily occurred on the western coast facing the open sea, and cracking sites clusters around the trees. We confirmed previous results that nut cracking tools are among the heaviest tools used by long-tailed macaques; however, we found our sample of *T. catappa* stone tools lighter than a previously collected sea almond sample that, unlike our sample, was collected immediately after use within the intertidal zone. The difference was likely the result of tidal influences on tool-use sites. We also found that tool accumulations above the intertidal region do not resemble those within them, possibly leading to incomplete assessments of macaque stone tools through archaeological techniques that would use these durable sites.

KEYWORDS
long-tailed macaque, nut-cracking, stone hammer, stone tool use

1 | INTRODUCTION

Stone tool-use is rare in non-human primates and only occurs in a few species. Across the known stone-tool-using taxa, nut-cracking is the only known stone-tool percussion shared by all (Haslam, 2012; Haslam et al., 2009). Despite this commonality, there is variation in how exclusively each stone-tool-using species crack nuts. For example, nut cracking accounts for all of the stone hammering behavior in West African chimpanzees (*Pan troglodytes verus*) (Boesch & Boesch, 1983) and most of robust capuchin monkeys (*Sapajus* spp.) (Ottoni & Izar, 2008; Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011). These species use stone tools in forested or dry scrub mainland environments, respectively, where nuts are present.

Burmese long-tailed macaques (*Macaca fascicularis aurea*) use stone tools in coastal environments on some islands along Thailand's Andaman Sea coast in Ranong (Gumert, Hoong, & Malaivijitnond, 2011; Gumert, Kluck, & Malaivijitnond, 2009; Malaivijitnond et al., 2007), and studies have concentrated on Piak Nam Yai Island (PNY), in Laem Son National Park. This island consists of mangroves, rocky shores, sandy beaches, and mountainous tropical forest (Gumert, Hamada, & Malaivijitnond, 2013). Here, rocks are very abundant along the rocky shores and in some parts of the mangroves. At PNY, macaques customarily use unmodified stones to pound open dozens of genera of mollusks, including sessile rock oysters (*Saccostrea cucculatta*) and motile gastropods such as nerites (*Nerita* spp.), drills (*Thais* spp. and *Morula* spp.), and trochids (*Monodonta labio*) (Gumert et al., 2009; Gumert & Malaivijitnond, 2012). Most of the marine prey processed by macaques is exposed in the intertidal zone during the low tides, during which macaques forage most extensively along the coasts. Aside from marine prey, the macaques also process a few plant fruits, including sea almonds (*Terminalia catappa*, Figure 1), coconuts (*Cocos nucifera*), and pandanus keys (*Pandanus tectorius*) along the coasts (Gumert & Malaivijitnond, 2012), including at sites above the intertidal zone.

Stones used by macaques as percussive tools at PNY range in mass from 16 to 5,166 g, and stone size varies across food sources, with oyster tools being the lighter tools ($\bar{x}$ = 81 g) and nut tools being the heaviest ($\bar{x}$ = 1,590.3 g) (Gumert & Malaivijitnond, 2013). Use-wear marks on the stones are strongly associated with the action with which the tools were used (Haslam, Gumert, Biro, Carvalho, & Malaivijitnond, 2013). Clear use-wear differences occur between tools used to open sessile oysters, and those used to open unattached mollusks, crustaceans, and nuts. Stones used to open sessile oysters showed use-wear mostly on the small points of the tools, while stones used to pound motile mollusks or nuts more often had use-wear of their broad faces (Gumert et al., 2009).

A dichotomous categorization of stone tools has been used to distinguish those referred to as axe-hammers for sessile oysters, and pound hammers for unattached encased foods, including nuts (Gumert et al., 2009). This broad categorization is useful in identifying how macaque stone tools were used in the past (Haslam et al., 2013, 2016a). Recently, Tan, Tan, Vyas, Malaivijitnond, and Gumert (2015) showed that macaque stone tools contains greater variation than previous indirect reports. These authors classified the stone tools used by macaques into three hammering classes based on the surface of the stone use: face, edge, or point. Variation in macaque tool use relates to the food sources being opened, as well as individual variation.

The most common nuts that macaques open with stones at PNY are the fruits of the sea almond tree (*T. catappa*, Figures 1 and 2) (Gumert & Malaivijitnond, 2012). *T. catappa* is a coastal tree that when mature is 25–40 m in height. It is originally from the subtropical and tropical zones of Indian and Pacific Oceans, although today the tree is spread all across the tropics (Orwa, Mutua, Kindt, Jamnadass, & Anthony, 2009; Thomson & Evans, 2006). Fruiting seasons are variable and sporadic across the species' range and individual trees. The green, fibrous fruit (Figure 2B) encases two entwined cotyledons (Thomson & Evans, 2006). The tree is coastally adapted, thus their fruits have a cork-like structure allowing them to float and disperse across the sea. These trees are mainly situated along the upper border of the intertidal zone, and they drop fruit along this zone. Unlike the continual availability of mollusks along the coasts (Gumert & Malaivijitnond, 2013; Tan et al., 2015), both in time and space, sea almonds are only available at their trees and during their fruit production. As a result, the availability of sea almonds to macaques is more limited than marine prey, and, therefore, less predictable.

Geographical spatial surveys of nut-cracking sites have been conducted in bearded capuchins (*Sapajus libidinosus*) in Fazenda Boa Vista (Visalberghi, Haslam, Spagnoletti, & Fragaszy, 2013) and Goiás state (Mendes et al., 2015), Brazil. Cracking-sites were found to cluster together by groups of anvils that were in the vicinity of each other, and appear to be repeatedly used over time, based on the presence of tool-use remains. These clusters are places where capuchins are most likely to use and gather tools (Visalberghi et al., 2013; Haslam et al., 2016b).

FIGURE 1 An adult Burmese long-tailed macaque (*M. fascicularis aurea*) processing sea almonds (*Terminalia catappa*) with a stone hammer tool on Piak Nam Yai, Laem Son National Park, Thailand, in 2011 (Photo by Michael D. Gumert)

FIGURE 2 (A) A sea almond cracking site on Piak Nam Yai, with basalt hammer and anvil, and old sea almond debris accumulated both on and off the anvil. This anvil has not been affected by tides. The scale is 10 cm. (B) Fresh sea almond fruit. (C) Basalt hammer with dark sea almond residue in the center of the tool face (Photos by Michael Haslam)

This accumulation of tools and leftover on specific location provide sites where potential archaeological remains are most likely to be recovered (Haslam et al., 2016b). Chimpanzees (*P. t. verus*) also reuse nut-cracking sites (Boesch & Boesch, 1983; Sakura & Matsuzawa, 1991), and archaeological examination have uncovered chimpanzee tools up to 4,300 years old (Mercader et al., 2007; Mercader, Panger, & Boesch, 2002). Similar spatial assessments can be done for macaque nut-cracking sites, allowing us to determine repeatedly used nut-cracking areas within macaque home ranges, and to identify zones where nut-cracking is most likely to produce archaeological assemblages.

In this study, we aimed to collect the first information toward assessing the spatial arrangement of macaque nut-cracking tools. We charted the distribution of *T. catappa* trees on PNY and identified, mapped, and measured all observable anvils and hammers used for sea almond processing. We used these data to examined the spatial relationship between tool sites and sea almond trees, identifying clusters of nut-cracking sites. We also assessed the weight and use-wear on nut-cracking tools to compare with previous reports. A more detailed description of the nut-cracking sites of Burmese long-tailed macaques will offer new data for intra and inter species comparison, that is, to examine how nut cracking might differ from opening marine prey by macaques as well as to compare macaques nut cracking with capuchins and chimpanzees.

2 | METHODS

2.1 | Study Site

The study was conducted from 19 to 22 January 2015 on PNY (9° 34.876′N; 98° 28.105′E). We list site features here according to Gumert et al. (2013). PNY is located approximately 750 m from the mainland and has an area of 1.7 km^2. There is 5.5 km of shoreline, of which 66% is rocky shore, 29% is mangrove and 5% is sandy beach. During low tide many mud flats are exposed in the mangrove regions, in which macaques are observed to forage. We conducted our studies along the island's coast, and traversed all coastal environment types. The interior of the island contains freshwater streambeds and mountainous tropical forest. As of 2011, the island contained approximately 200 Burmese long-tailed macaques (*M. f. aurea*), living in nine groups, with sizes varying from 8 to 35 individuals. Tool-use is exhibited by at least 88% of the mature macaques on the island (Gumert et al., 2013).

2.2 | Survey Procedures

Three researchers (TF, NS, and MH) walked the island shore (from intertidal zone to tree line), during the low tides, looking for sea almond trees and nut-cracking sites (Figure 2). We considered intertidal zone as an area that is affected by daily tidal fluctuations, being completely submersed in water during the highest tidal periods, and completely exposed during the lowest. When a *T. catappa* tree more than 2 m in height was located, we used a GPS Unit (Garmin Oregon 450) to record the location of the tree. Trees under that size were difficult to spot, and appears to be immature, so we choose to concentrate our efforts on the bigger trees. All sea almond nut-cracking sites (Figure 3) encountered were also marked using GPS. Adapted from Visalberghi et al. (2013), a used sea almond cracking site was defined by the presence of (i) a flat surface that could serve as an anvil; (ii) a hammer stone with clear use marks and/or sea almond residue, either on or within 2 m of the putative anvil; and (iii) cracked sea almond remains on the anvil (Figure 2).

2.3 | Measurements of Sea Almond Cracking Sites

At each nut-cracking site, we measured, to the nearest cm, the longest length and the width (at half the length and perpendicular to it) of the horizontal surface of the anvil and distance to the nearest *T. catappa* tree. We also scored the presence of use-wear marks on the anvil. We estimated the number of fruits cracked open with stone tools by counting the remnant part of the husks and categorized their age as either fresh (i.e., green and moist husks) or old (i.e., brown and dry husks) (Figure 3). For each stone tool, following the method from Falótico and Ottoni (2016), we measured, with tape measure, the length, width and thickness to the nearest mm. We weighed the stone, using a luggage scale, to the nearest tenth of a kg. Lastly, we visually identified the lithic material.

We assessed the use-wear patterns on all stone tools observed during this study. We identified the presence of use-wear in the flat faces, edge, or point of the stone. We classified the stones as “axe hammer” if the damage was concentrated in the point and edges and as “pound hammer” if the damage was on the flat faces.

2.4 | Analysis of Sea Almond Cracking Tools

We compared our stone tools to previously collected stone tools used to crack open sea almonds and marine preys. Using Kruskall–Wallis test and Dunn–Bonferroni corrected pair-wise post hoc, we compared the weights of stone tools found in our sample (n = 102) to the weight of stone tools (n = 371) collected in 2011 (Gumert & Malaivijitnond, 2013), used to crack open marine prey and sea almonds, and to the weight of stone tools collected in 2008 (n = 20), used to crack open sea almonds (Gumert et al., 2009). The 2008 set was collected in the same manner as the current data set. The 2011 methods of collection were similar to the current study, except that many tools were directly observed while in use, including the 65 sea almond hammer tools, and measured immediately after use in the intertidal zone. We did not directly observe any tool used in this study, and thus all tools in our study were used in the past. To compare the differences in nut tool samples collected at different times, in differing conditions, we compare how our sample related to previous tool samples regarding the food sources, and if there might be any differences in nut tool samples collected. Statistical analyses were run with alpha set to 0.05, two-tailed. All statistical tests were performed on IBM SPSS 23.

2.5 | Spatial Analysis on Nut-Cracking Sites

We plotted the GPS points of trees and cracking sites on maps using Google Earth Pro 7.1 (Supplemental File S1). From this spatial data,

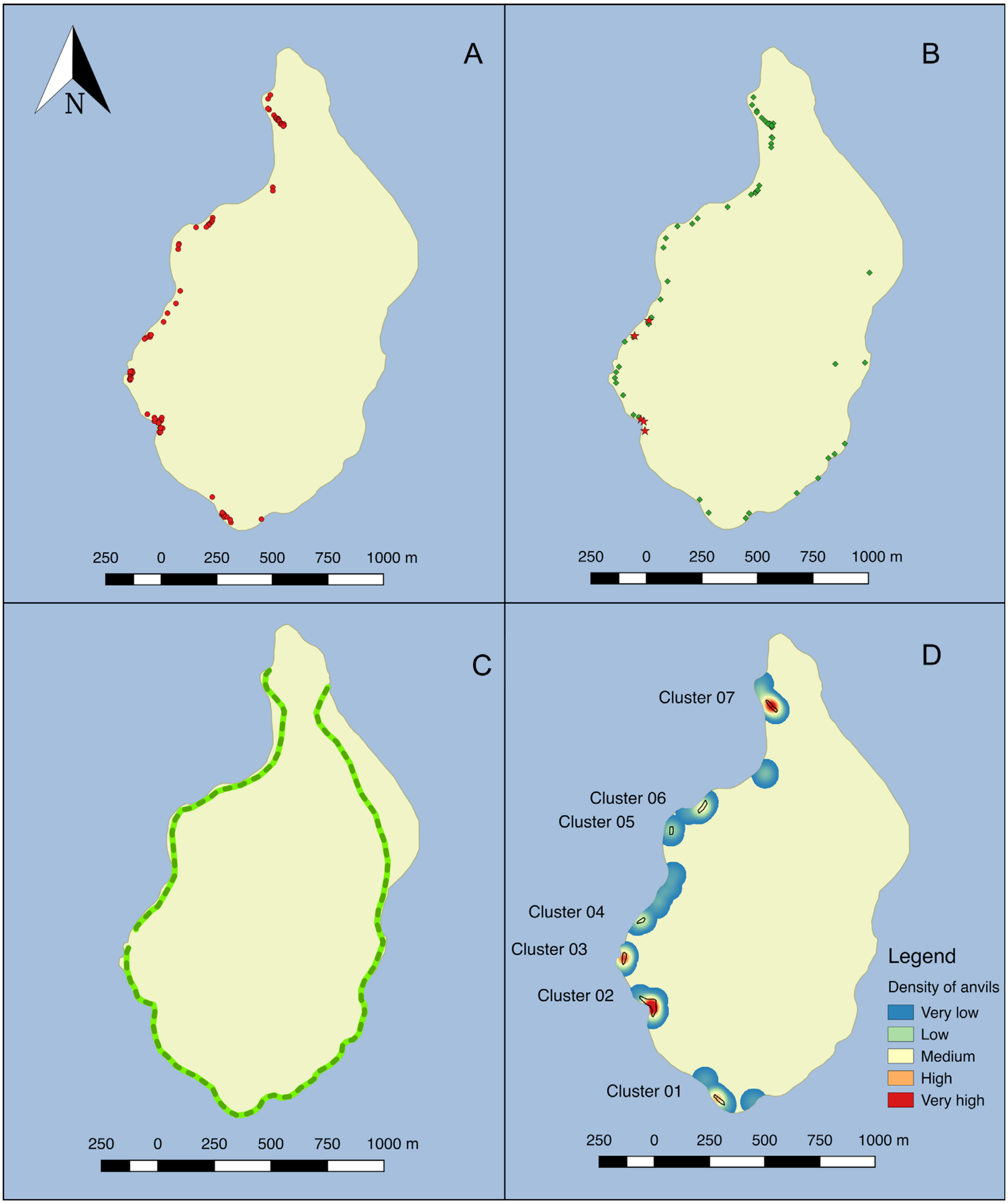

FIGURE 3 Map of Piak Nam Yai island showing the (A) location of the anvils sites (red); (B) *T. catappa* trees (green), with red star icons showing the fruiting trees; (C) the survey trail; and (D) a density map of anvils, with the seven clusters outlined in black and labeled

following the method described by Mendes et al. (2015), we produced symmetrical matrixes containing linear distances between all anvils, and between all trees and anvils, using Lizardtech's DIVA-GIS 7.5 (Hijmans, Guarino, Cruz, & Rojas, 2001). We then used Google Earth Pro 7.1 and the matrix (Supplemental Table S2) to determine the maximum distance between any pair of anvils and the number of clusters of sea almond cracking sites. We manually assigned clusters of sea almond cracking sites by determining all groups of cracking sites not separated by more than 20 m and containing at least three cracking sites (the minimum number of points needed to define a geometric plane). For each cracking site cluster, we calculated its total area, measured the maximum distance between the farthest-apart anvil pair, counted total number of trees (fruiting and otherwise), anvils, and hammers, and calculated the density of trees, anvils, and hammers within the cluster. Clusters and their relative density were mapped using GIS (QGIS Development Team, 2016) to identify any areas of concentrated sea almond cracking sites.

These results adhere to the American Society of Primatologists principles for the ethical treatment of primates. NTU's IACUC approved our methods of collecting animal-used material in ARF SBS/NIE-A0210.

3 | RESULTS

We surveyed 4,818 m (88%) of PNY's shoreline, 12% of the shore being either too steep for us to access (western shore) or covered in tide when we tried to access it (northern shore) (Figure 3C). Along the survey route, we recorded 67 *T. catappa* trees, 90 sea almond cracking sites (Figure 3A and B), and 102 stone tools used to crack open sea almond nuts (Supplemental Table S3). Five *T. catappa* trees (7.5%) were fruiting during the surveys (Figure 3B).

We detected seven clusters of sea almond tool use activity (Figure 3C, Table 1). The clusters varied in size between 78 and 1,510 m^2, and the total number of anvils found in all clusters was 76 with between 3 and 20 anvils per cluster. The number of trees in all clusters was 17 and varied between 1 and 5 per cluster (Table 1). We found that clusters varied between 1.31 and 3.87 anvils per 100 m^2, 0.15 to 2.88 trees per 100 m^2, and 1.31 and 3.87 hammers per 100 m^2. Not all sites clustered. About 13 of the 67 sea almond trees were isolated by more than 20 m from any cluster, as well were 14 anvils and 14 hammers. The distance of the nearest *T. catappa* tree to each anvil-like surface ranged from 0.5 to 50 m ($\bar{x}$ = 9.7 m, SD = 8.5 m).

We found that 85% (n = 57) of the *T. catappa* trees were found on the western coast, and all but one anvil (n = 89) was also recorded on the western coast. Most trees (71%, n = 48) had an anvil within 20 m, and 95% of anvils were within 20 m of a *T. catappa* tree (n = 85). The furthest anvil was 50 m from a tree. All anvils were basalt boulders, immovable because of being too heavy or embedded in the ground. Anvils varied in length ($\bar{x}$ = 137.7 cm, SD = 52.9 cm, range: 46–293 cm) and width ($\bar{x}$ = 81.5 cm, SD = 38.4 cm, range: 17–220 cm). About 38 of the 90 anvils (42%) had observable use-wear on their surface. Eighty-one of the anvils (90%) had one hammer, while six (6.5%) had two hammers, and three (3.5%) had three hammers.

We examined the hammer stone tools and food debris at each tool site (Supplemental Table S3). Most of the sea almond cracking sites contained old sea almond husks (88%; N = 79) that were already dried and brown. Seven cracking sites (8%) contained only fresh husks, and four cracking sites (4%) contained both old and fresh husks. The hammer stones varied in weight ($\bar{x}$ = 922.9 g, SD = 690 g, range = 160–3,070 g), length ($\bar{x}$ = 15.8 cm, SD = 4.7 cm, range = 7–30 cm), width ($\bar{x}$ = 9.9 mm, SD = 3.3 mm, range = 5–26 mm) and thickness ($\bar{x}$ = 3.6 mm, SD = 1.4 mm, range = 1–8 mm). Most of the hammer stones were basalt (75%, N = 77) and the remainder were siltstone (12%, N = 12) or sandstone (13%, N = 13). The results from our use wear analysis showed that the most likely form of use for all of the sea almond hammers was the use of the flat faces for pounding (Supplemental Table S3).

When we compared the weight of this study stone tools with all the stone tools collected in 2011 and in 2008 (Figure 4), we found the groups to be significantly different, with stone tools used to crack open nuts or fruits being among the larger tools used by macaques (Kruskall–Wallis: N = 440, df = 6, H = 258.260, P < 0.001). Using Dunn–Bonferroni corrected pair-wise post hoc, we found that stone tools weight from the current sample differ from all groups except loose-bivalves (Z = −2.856, P = 0.090), drill and conches (Z = 0.965, P = 1.000), and sea almonds from 2008 (Z = 2.041, P = 0.867). Our

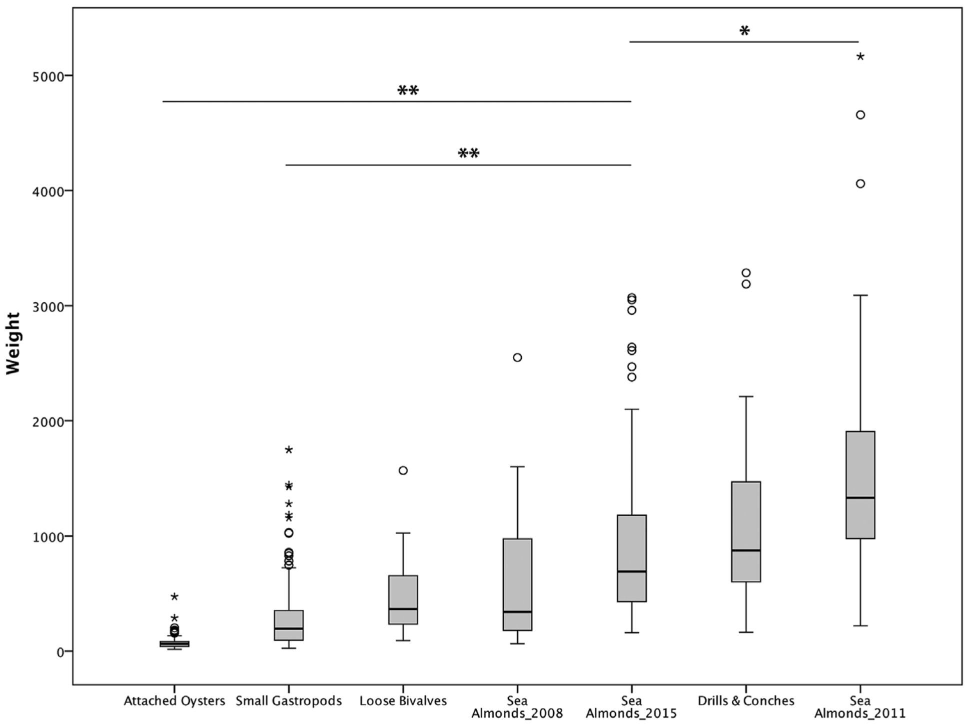

FIGURE 4 Comparison of hammer-weights across food resources cracked-open. The groups were significantly different. Our 2015 sample was lighter than the 2011 sample, which was completely collected on fresh nut-cracking site low in the littoral, but did not different from the 2008 sample which was collected from old site higher in the littoral, similar to most of our 2015 sample. Our sample was heavier than oyster and small gastropod tools. Dunn–Bonferroni corrected pair-wise post hoc tests were used to determine statistical significance; *P < 0.05, **P < 0.001

TABLE 1 Characteristics of sea almond-cracking site clusters

Cluster	*N* anvils	*N* hammers	*N T. catappa* trees	Fruiting trees in the cluster	Max. anvil distance within cluster (m)	Area of cluster (m^2)	Anvil density (anvil/ 100 m^2)	Hammer density (hammer/ 100 m^2)	Tree density (tree/ 100 m^2)
1	10	11	1	0	57.8	661	1.51	1.66	0.15
2	20	27	4	3	72.3	1510	1.32	1.79	0.20
3	12	15	2	0	41.8	392	3.06	3.83	1.02
4	5	5	2	1	34.6	312	1.60	1.60	0.64
5	3	3	1	0	24.8	77.6	3.87	3.87	1.29
6	7	7	2	0	51.0	534	1.31	1.31	0.37
7	19	20	5	0	64.7	520	3.65	3.85	2.88
Total/Average	76	88	17	4	49.57	572.37	2.33	2.56	0.94

sample tool size was significantly heavier than tools used on attached oysters ($H = -233.721$, $Z = -10.921$, $P < 0.001$) and small gastropods ($H = -138.110$, $Z = -8.331$, $P < 0.001$). Finally, the 2011 sample of nut-cracking tools was significantly heavier than the current sample ($Z = 3.547$, $P = 0.008$).

4 | DISCUSSION

We were able to identify discrete sea almond cracking sites, primarily around *T. catappa* trees. Most *T. catappa* trees were on the western coast of PNY, facing the Andaman Sea, which is the result of this plant dispersing through hydrochory (i.e., seed floating). We found all anvil clusters on the western coast as well, which we suggest is the result of two non-exclusive factors: (i) the abundance of *T. catappa* trees on that coast and (ii) the presence of intertidal mangrove along the east coast that can reduce surface accumulation of cracking debris there. Sea almond cracking sites were mostly clustered within 20 m of *T. catappa* trees, suggesting that the macaques are typically processing the nuts near the trees. The greatest distance an anvil was found from a tree was 50 m. Sea almond anvils appear to be repeatedly re-used, resulting in the accumulation of old food debris, stone hammers, and in some cases a combination of both roughened and smoothed sections on the upper surface of anvil boulders. A similar build-up of stone and nut shell debris has been noted, for example, at wild capuchin monkey nut cracking sites in Brazil (Mendes et al., 2015; Visalberghi et al., 2013).

The formation of long-tailed macaque sea almond cracking sites shows similarities with the nut-cracking sites of wild bearded capuchin monkeys and chimpanzees. Both macaques and capuchins create and reuse stone tool sites that are clustered around source trees, including *T. catappa* in this study, and palms (*Acrocomia aculeate*, *Astrocaryum campestre*, *Attalea* sp., *Hymenaea* sp., *Orbignya* sp., *Syagrus* sp.) or cashew trees (*Anacardium* sp.) for capuchin monkeys (Falótico & Ottoni, 2016; Haslam et al., 2016b; Mendes et al., 2015; Visalberghi et al., 2013, 2016). The clustering, however, appears to be affected by different variables depending on the environment. In the capuchin study site of Fazenda Boa Vista, the availability of lithic material limits the accumulation of capuchin tool debris, which clusters in areas with higher availability of lithic material than in the surrounding landscape that do not present good lithic material to process some of the local high resistant nuts (Visalberghi et al., 2007, 2009). In a survey on capuchin cracking sites on Cerrado areas in Brazil, 91% of the anvils were rocks of different sizes and material, and the authors suggests that even in places with low availability of dense lithic material, capuchins turn to alternative sources, such as less dense minerals and plant material to use as anvils and hammers, but still forming identifiable cracking sites clusters (Mendes et al., 2015). In the PNY macaques and the capuchins of Serra da Capivara National Park (Falótico & Ottoni, 2016), variation in stone availability does not seem to be a main factor in predicting the location of site formation, with resource trees being the primary predictor of where cracking sites are found. Scarcity of stone hammers was also found to affect site formation in West African Taï chimpanzees processing hard *Panda oleosa* nuts (Boesch & Boesch, 1983) and Bossou chimpanzees dealing with *Elaeis guinensis* nuts (Sakura & Matsuzawa, 1991; Sugiyama & Koman, 1979). Chimpanzees can accommodate for this by sometimes transporting stone tools for great distances (>500 m) to cracking sites near *Panda* trees (Boesch & Boesch, 1983). Such long-distance transport has not been observed to date at capuchin or macaque nut cracking sites.

A difference between capuchin and chimpanzee nut cracking sites and those of macaques is that the latter appears to be more transient. We have observed that *T. catappa* in the area of our research site have an atypical fruiting pattern (Supplemental Table S3), with trees fruiting individually at varying times making sea almond cracking a more opportunistic behavior in macaques. Capuchins are reported to also eat palm nuts opportunistically, but they have more species of nuts, fruits and seeds to exploit with stone tools (Mannu & Ottoni, 2009; Mendes et al., 2015; Spagnoletti et al., 2012). Another factor that could affect macaque sea almond-cracking is that the accumulation of sea almonds in the intertidal zone is minimal, as fruits, being buoyant and evolved for hydrochory, float away to sea by the tides, while most capuchins groups reported to use stone tools are in land environments (Ottoni & Izar, 2008). By washing away light stone tools as well as food debris present on the anvils, the tidal forces may affect macaque tool use behavior and tool site formation, making it more complex to compare to chimpanzee and capuchin nut-cracking sites and behavior.

We confirmed previous findings that stone hammers used to open sea almond nuts were among the heaviest tools used by macaques

(Gumert et al., 2009; Gumert & Malaivijitnond, 2013). However, our sample was significantly lighter in weight than a previous sea almond tool sample collected in 2011, but not from a sample collected in 2008. The 2008 and 2015 samples were collected using the same protocol, with most of the tools collected higher in the intertidal zone, and the remains were dried out older nut (2008: 100%, 2015: 89% old). In contrast, the 2011 sea almond data set was collected immediately after macaques were observed processing sea almonds in the lower intertidal zone, the remains being all fresh and green (0% old).

Past studies have shown macaques generally select the largest stone available for cracking nuts (Gumert & Malaivijitnond, 2013), and they may be doing the same when selecting stones to crack nuts in the highly rock-abundant shores, but the sites may not be preserved long enough to be registered. As an example, 4 days before starting the 2015 survey, the research team came across eight cracking sites low in the intertidal zone (Figure 5), but all eight tools and their debris were washed away a day later. Consequently, durable sea almond sites above the intertidal region, which represent much of our sample in this study, may not fully represent the range of macaque nut-cracking tools. Future archaeological comparison will need to be made between intertidal and forest nut-cracking sites. Studies are also needed to determine how well washed away material can be retrieved and have far it is moved.

The use-wear analysis of the stone tools demonstrated conclusively that macaque sea almond nut processing tools predominantly showed used wear on their broad faces, as past work has shown (Gumert et al., 2009). Nuts and motile shellfish are generally cracked on an anvil surface by striking down on the target with the face of the stone, which differs from axe hammers used to strike sessile oysters (Gumert et al., 2009; Haslam et al., 2013; Tan et al., 2015). These findings give indication of how the stones were used at the sites we collected from, and are consistent with how we expected them to be used. Such consistency of use-wear is useful for archaeological reconstruction of behavior in the absence of macaque observation (e.g., in unhabituated groups or archaeological settings).

FIGURE 5 A cluster of eight fresh sea almond cracking sites on Piak Nam Yai, lower in the intertidal zone (white arrows), 4 days before the survey started and similar to the conditions of the 2011 nut-cracking tool sample. One site shows sea almond debris on the anvil (black arrow), without the presence of the hammer. All tools and debris from the cluster were no longer present during the survey, the hammers and nuts having been washed away by tides shortly after formation (Photo by Michael Haslam)

We have presented here how long-tailed macaques form enduring nut-cracking sites and how they form around sea almond trees. Our results show large pounding stones and nut debris accumulate around anvils. The persistence of nut-cracking sites allows historical assessment of macaque tool use and also comparison to other durable nut-cracking sites in chimpanzees and capuchins. The sites we studied were above intertidal zone along the forest border, above the influences of tidal action, and thus do not represent all nut cracking sites of macaques on PNY. Future research will be needed to better assess macaque nut-cracking sites in the intertidal regions and compare them to the enduring macaque sites above the intertidal zone and with other species.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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SUPPORTING INFORMATION

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