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RESEARCH ARTICLE

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Influence of COVID-19 on the emergence of stone-tool use behavior in a population of common long-tailed macaques (*Macaca fascicularis fascicularis*) in Thailand

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Abstract

Stone tool use is a rare behavior across nonhuman primates. Here we report the first population of common long-tailed macaques (*Macaca fascicularis fascicularis*) who customarily used stone tools to open rock oysters (*Saccostrea forskali*) on a small island along the Thai Gulf in Koh Ped (KPE), eastern Thailand. We observed this population several times during the past 10 years, but no stone-tool use behavior was observed until our survey during the coronavirus disease 2019 (COVID-19) pandemic in July 2022. KPE is located in Pattaya City, a hotspot for tourism in Thailand. Tourists in this area frequently provided large amounts of food for the monkeys on KPE. During the COVID-19 curfew, however, tourists were not allowed to access the island, and monkeys began to face food scarcity. During this time, we observed stone-tool use behavior for the first time on KPE. Based on our observations, the first tool manipulation was similar to stone throwing (a known precursor of stone tool use). From our observations in March 2023, we found 17 subadult/adult animals performing the behavior, 15 of 17 were males and mostly solitary while performing the behavior. The *M. f. fascicularis* subspecies was confirmed by distribution, morphological characteristics, and mtDNA and *SRY* gene sequences. Taken together, we proposed that the stone tool use behavior in the KPE common long-tailed macaques emerged due to the COVID-19 food scarcity. Since

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Abbreviations: KPE, Koh Ped island; Mfa, *Macaca fascicularis aurea*; Mff, *M. fascicularis fascicularis*.

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traveling is no longer restricted many tourists have started coming back to the island, and there is a high risk for this stone tool-use behavior to disappear within this population of long-tailed macaques.

KEYWORDS

COVID-19, *Macaca fascicularis fascicularis*, oyster, stone throwing, stone tool use

1 | INTRODUCTION

Customary stone-tool use (McGrew, 1998) is not widespread throughout the animal kingdom. The use of percussive stone tools by nonhuman primates (NHPs) in natural settings has been widely studied and has garnered significant attention due to the close evolutionary relationship with technology-dependent humans (Haslam et al., 2009). To date, there are five wild NHPs, including West African chimpanzees (*Pan troglodytes* verus; Sugiyama & Koman, 1979), bearded capuchins (*Sapajus libidinosus*; Fragaszy et al., 2004), Burmese long-tailed macaques (*Macaca fascicularis aurea* (*Mfa*); Malaivijitnond et al., 2007), yellow-breasted capuchins (*S. xanthosternos*; Canale et al., 2009), and white-faced capuchins (*Cebus capucinus imitator*, Barrett et al., 2018) that have been reported to perform stone-tool use behaviors during foraging in their natural habitats. Some similarities between NHP stone-tool use and hominin tool evidence suggest similar evolutionary mechanisms behind the development of stone-tool use behaviors. Understanding the circumstances for the emergence of tool use within a population can help us better understand the cognitive and behavioral driving factors underlying technological and innovation development in our lineage.

Macaca fascicularis, commonly known as the long-tailed macaque, is a species of Old-World monkey found throughout Southeast Asia, including Myanmar, Thailand, Laos, Cambodia, Vietnam, Malaysia, Indonesia, and the Philippines (Fooden, 1995). They are the second most widely distributed macaque species, following the rhesus macaque (*M. mulatta*). The classification system based on geographic distribution and morphological characteristics divided them into 10 subspecies (Fooden, 1995). Until recently, *Mfa* has been the only subspecies associated with stone-tool use in the context of extractive foraging, using hammerstones and anvils to open hard-shelled foods such as nuts and oysters (Gumert et al., 2009, 2011, 2019; Malaivijitnond et al., 2007). *Mfa* originates in Myanmar and distributes southeastwardly along the Andaman Sea Coast through the Mergui Archipelago, where they live in close contact with common long-tailed macaques (*M. fascicularis fascicularis* (*Mff*)) in Southwestern Thailand (Bunlungsup et al., 2016; Fooden, 1995; Phadphon, Kanthaswamy, et al., 2022). Although the *Mff* subspecies have been observed to use tools for sexual activities (Cenni et al., 2022) and water acquisition (Cenni et al., 2023), they have never been reported to use stones to crack open the encased foods, neither in their natural habitats (Fooden, 1995; Malaivijitnond et al., 2011) nor in captivity upon training (Bandini & Tennie, 2018). Based on the mtDNA, Y chromosome (*SRY* and *TPSY*) genes, whole genome sequences, and autosomal SNPs analyses, it has been suggested that the two subspecies are genetically distinct (Bunlungsup et al., 2016; Matsudaira et al., 2018; Osada et al., 2021; Phadphon, Kanthaswamy, et al., 2022). Thus, it was hypothesized that genetic predisposition might play a critical role in the emergence and development of stone-tool use behaviors in wild long-tailed macaques (Gumert et al., 2019; Reeves et al., 2023).

In general, ecological factors could also affect the emergence and development of stone-tool use behaviors (Gumert et al., 2019). Environmental conditions may be crucial in driving the behavioral divergence observed between species or subspecies. Based on their distribution range, *Mfa* subspecies inhabited coastal and estuary habitats to a greater extent than the overall *Mff* populations. Marine resources such as oysters, snails, mollusks, and invertebrate animals were abundant in a coastal environment. Thus, the ecological conditions appeared to favor the emergence of stone-tool use behavior through natural selection. A similar occurrence was also observed in capuchin monkeys residing on islands where they developed the capacity to exploit marine resources (Barrett et al., 2018), which might be due to achieving a sustainable number of nutritional requirements in these habitats. The development of stone-tool use behavior could include exposure to learning opportunities (culture), such as role models among social partners as well as the way their activities shape the environment (Gumert et al., 2019; Reeves et al., 2021; Tan et al., 2018).

During the COVID-19 pandemic in July 2022, we surveyed the *Mff* population living on the island in the Gulf of Thailand, namely Koh Ped (KPE). The island is near Pattaya, a city known for tourism in Thailand. Several hundred macaques have reportedly lived on KPE for at least 60 years. Due to the scenic view of KPE, the tourists arrive on the island daily by boats and yachts. They provided the monkeys with diverse foods such as mangoes, cucumbers, nuts, and watermelons daily. As a result, the monkeys were well habituated to the presence of humans. Although we visited the KPE several times these past 10 years to observe the population, we had never seen stone-tool use behaviors in these monkeys.

During our first survey of the KPE population after the COVID-19 travel restrictions were lifted, conducted between July 11 and 16, 2022, two adult males were observed for the first time using stones as tools to open oysters. The island's seashore is covered mainly with rock oysters (*Saccostrea forskali*; Krabuansang et al., 2020) attached to the rock outcrop. Stone pebbles suitable for stone tool use were widely abundant along the shore. The monkeys on KPE were assumed to have started using stone tools to access encased foods such as oysters during the COVID-19 pandemic; however, the exact time it first emerged remains unknown. Here, the genetic background of the KPE macaque population, *Mff* subspecies, was confirmed using mtDNA and *SRY* gene sequence, and the morphological characters were identified. The preliminary assessments of the demographic distribution (age and sex) of the new tool behavior on KPE macaques were presented.

2 | METHODS

2.1 | Ethical statement

The permit for research and sample collection in Thailand was approved by the National Research Council of Thailand and the Department of National Parks, Wildlife, and Plant Conservation of Thailand. The Institutional Animal Care and Use Committee of the National Primate Research Center of Thailand-Chulalongkorn University approved the experimental protocols of this study (Protocol Review no. 2075007). The research adhered to the American Society of Primatologists (ASP) Principles for the Ethical Treatment of Non-Human Primates.

2.2 | Study sites and monkey observation

KPE (GPS: 12°45′ N, 100°50′ E), also known as Koh Klet Kaew or Monkey Island, is situated on the eastern coast of Thailand, in the Gulf of Thailand (Figure 1). The small island has a shoreline of 2.78 km, covering an area of 0.24 km^2. The island is located only about 600 m away from the mainland, close to a tourist hotspot, Pattaya. Several hundreds of long-tailed macaques were living on KPE, which is under the authority of the Royal Thai Navy. The animals regularly interacted with humans, including climbing on people's shoulders or heads and fed human-provisioned food directly by hand.

The pre-pandemic data collection was occasionally done using the group-scan sampling method (approximately 30 min/time) when animals were exposed to the seashore while the navies visited the island for anthropogenic food or drinking water provisioning to animals. The researchers visited the island at least once a year for population monitoring and sometimes for feeding behaviors.

The KPE was revisited on the March 12–15, 2023, 0800–1800 h, in total 1030 min, and pictures and video footage were taken by S. Panjan using a Nikon COOLPIX W300 camera (Nikon). When the animals were not in sight, we walked along the seashore where the oyster beds were. We searched for evidence of stone-tool use, for example, a stone placed on top of a larger rock with pieces of oyster shell and evidence of use damage on a hammerstone or anvil. Once the monkeys were located, they were followed, and a minimum distance of at least 3 m was kept (Kumpai et al., 2022). Each stone-tool use behavior displayed by any individual was filmed, resulting in 31 min of video footage. Besides the rocky seashore, monkeys were also followed on the beach and on the forest fringe to observe the consumption of other foods and plants, which were collected and identified afterward. If more than two monkeys appeared on the seashore, the scan sampling method was used first. After the scan session was completed and animals were found using stone tools to extract foods, the animal sitting close to the observer was selected for focal sampling. After the focal animal completed his/her stone tool use, the next round of scan sampling and focal animal sampling (for another stone-tool user) was performed.

2.3 | Morphospecies identification and specimen collections

Based on the distribution range (Fooden, 1995), these macaques were identified as *Mff*. They were confirmed as a subspecies of *M. fascicularis* based on morphological characteristics, mainly their cheek hair pattern, vertex of head crest, and pelage color (Bunlungsup et al., 2016; Fooden, 1995; Phadphon, Kanthaswamy, et al., 2022*). Mff* has a brighter pelage color; the lateral facial crest hairs sweep upward from near the angle of the jaw to the lateral margin of the crown. The hairs of the temporal region are anteriorly directed, a so-called transzygomatic pattern. Head crests are either present or absent. Unlike *Mff*, *Mfa* has a darker dorsal pelage color and no head crest. Furthermore, they exhibit an infrazygomatic pattern of the lateral facial crest hairs: the crest occurs near but inferior to the mandibular region and terminated superiorly in a whorl shape on the cheek, and hairs of the temporal region are posteriorly directed from an eye to an ear (Bunlungsup et al., 2016; Fooden, 1995).

Thirty-one fecal samples were randomly and noninvasively collected from defecated excretions. The feces were swabbed using a cotton swab and stirred in 1.5 mL lysis solution (Hayaishi & Kawamoto, 2006; 0.5% (w/v) sodium dodecyl sulfate, 100 mM EDTA pH 8.0, 100 mM Tris-HCl pH 8.0 and 10 mM NaCl). The swab was done at the surface of the feces for gastrointestinal cell collection. To maximize several gastrointestinal cells harvested, these steps were repeated 3 times per sample before storing the solution at room temperature until DNA extraction.

2.4 | Polymerase chain reaction (PCR) amplification and sequencing of partial mtDNA and *SRY* gene

The gDNA was extracted from the fecal samples using the QIAamp DNA/Fast DNA Stool Mini kit (QIAGEN Inc.) following the manufacturer's protocol. The mtDNA was amplified using HVS-F (5′-CCGCCC ACTCAGCCAATTCCTGTTCT-3′) and HVS-R (5′-CCCGTGATCCATC GAGATGTCTT-3′) primers (Bunlungsup et al., 2016), of which the product size was 835 bp covering the hypervariable segment I (HVSI) of the D-loop region, tRNA proline, tRNA threonine, and cytochrome

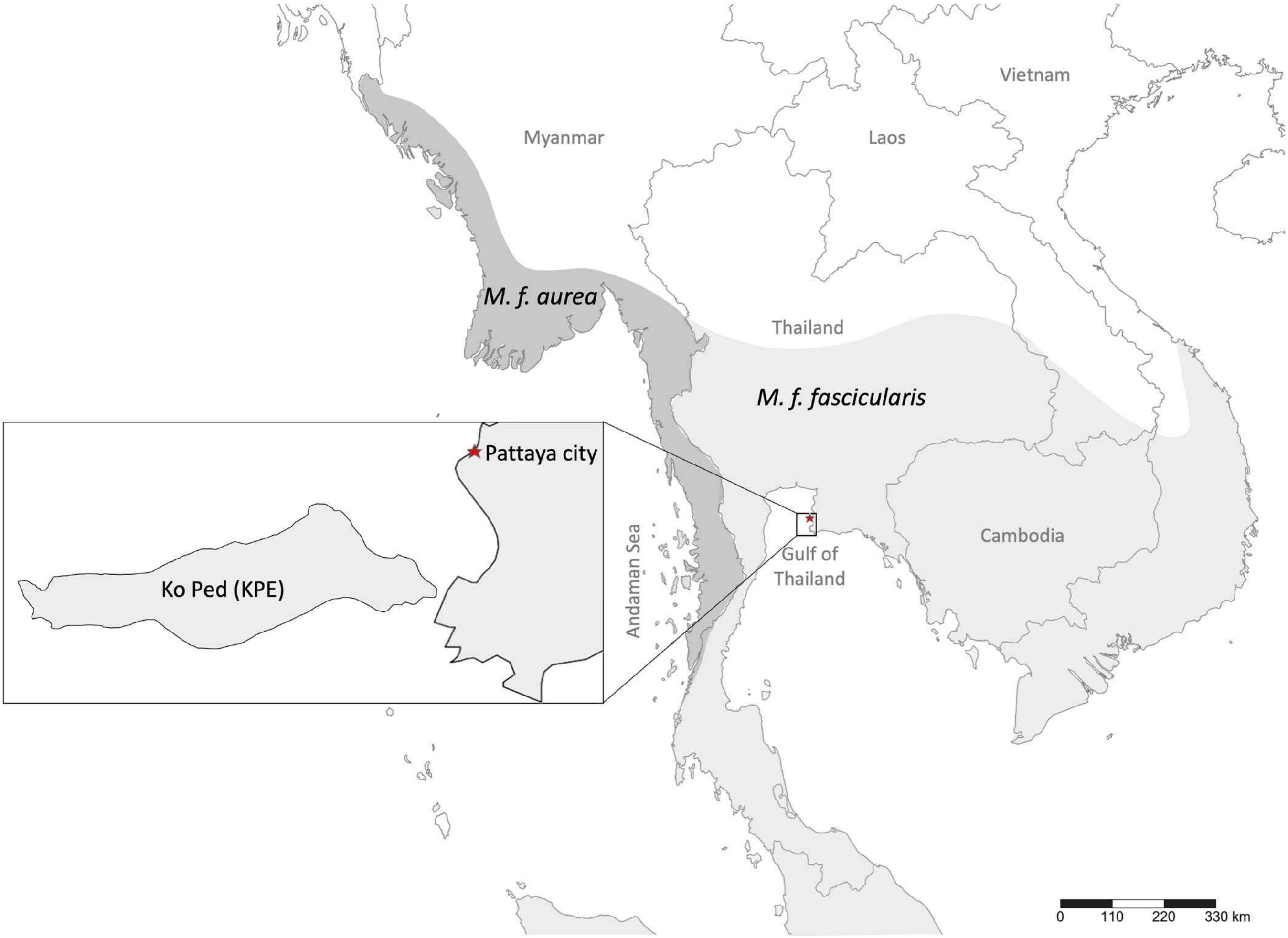

FIGURE 1 The geographic distribution range of *Macaca fascicularis aurea* (dark grey) and *M. f. fascicularis* (light grey) and the location of Koh Ped and Pattaya city in Thailand.

b. The amplification was carried out at 94°C for 1 min, followed by 35 cycles of 94°C for 30 s, 60°C for 30 s, and 72°C for 1 min, and ended up with 72°C for 5 min for final elongation.

The partial *SRY* gene was amplified using *SRY*-FN (5′-TCGCAGCCTCCTTGTTTTTGA-3′) and *SRY*-RN (5′-TCATGGGTCGCTTCACTTTATCC-3′) primers (Phadphon, 2022). The amplification was carried out at 94°C for 1 min, 40 cycles of 94°C for 30 s, 62°C for 30 s, and 72°C for 1 min, followed by 72°C for 5 min. Within the 216 bp *SRY* fragments, two polymorphic sites (nos. 42 and 132 of *SRY* Refseq of *M. mulatta* (NM 001032836.1)) were acquired and used to identify *Mfa* (T&C), *Mff* (A&T) and *M. mulatta* (T&T), respectively. PCR mixtures of mtDNA and *SRY* amplification contained 0.5 U ExTaq DNA Polymerase (Takara Bio Inc.), 0.3 mM of each primer, and 50–100 ng DNA template in the manufacturer's buffer.

The PCR products were run on 2% (w/v) SYBR Safe stained agarose gel-TAE electrophoresis and visualized under the Nucleic acid Bioimaging Instrument (NαBI) blue illuminator (Neo Science Co., Ltd.). The PCR amplicons were cleaned up using ExoSAP-IT™ (Thermo Fisher Scientific) and purified using BigDye XTerminator™ (SAM solution, BigDye XTerminator™ bead solution) following the manufacturer's protocol before submitting to Macrogen, Inc. for sequencing with the same primer sets.

2.5 | Phylogenetic tree analysis of mtDNA sequences

The mtDNA sequences were trimmed and aligned using BioEdit 7.2 (Hall, 1999), and the phylogenetic trees were constructed with the Maximum Likelihood (ML) and Bayesian Inference methods. Thirty-one sequences of mtDNA at 573-bp size were analyzed. The GenBank-retrieved Chinese *M. mulatta* sequence (LC093173) and *M. sylvanus* sequence (NC002764) were included in the analysis as outgroups, while the other sequences were retrieved from Bunlungsup et al. (2016, 2017). The best substitution model was selected based on the Bayesian information criterion (BIC) using MEGA X (Kumar et al., 2018). The ML tree was constructed under HKY + G + I model with 1000 bootstraps in MEGA X (Kumar et al., 2018). The Bayesian tree was constructed under the same model using MrBayes 3.1.2 (Huelsenbeck & Ronquist, 2001). The analysis was run for 1,000,000 generations, and parameters were sampled every 500 generations. The convergence of the MCMC runs was checked in Tracer 1.5 (Rambaut & Drummond, 2009) with the trace plot and over 200 effective sample size (ESS) values for all parameters. The first 25% of data were discarded as burn-in, the remaining data were combined, and a 50% majority-rule consensus tree with posterior probability on each branch was summarized. The tree was visualized in FigTree 1.3.1. (Rambaut, 2010).

3 | RESULTS

3.1 | Phenotype and genotype identification

By morphospecies identification, all monkeys on KPE had transzygomatic cheek-hair patterns and a head crest (Figure 2a,b) as seen in *Mff* (Bunlungsup et al., 2016; Fooden, 1995). Their pelage color was light, as seen in Indochinese *Mff* (Figure 2c; Hamada et al., 2008).

All 573-bp mtDNA sequences analyzed showed 100% homology, thus, only three KPE mtDNA sequences were included in the phylogenetic analysis. The ML and Bayesian phylogenetic trees of mtDNA showed a similar topology; therefore, only the Bayesian tree was used in this study (Figure 3). The tree indicated the divergence of the *Mfa* clade from the *M. mulatta*/*Mff* clade before the divergence of the *M. mulatta* and *Mff* clades. As for the *Mff* clade, there were two subclades separated by the Isthmus of Kra (10° 15′N, 99° 30′E); the northern Indochinese and the southern Sundaic subclade. KPE monkeys belonged to the Indochinese *Mff* subclade.

By analyzing the 216 bp of the *SRY* gene, 12 of 31 samples could be amplified and sequenced. Two variable sites in all 12 animals were T and T, which indicated the *M. mulatta* haplotype, and this was named as *M. mulatta*/Indochinese *Mff* clade in Bunlungsup et al. (2016, 2017).

Taken together for the mtDNA and *SRY* gene analysis, KPE monkeys were identified as *Mff* subspecies of the Indochinese form.

3.2 | Stone-tool use behavior

During our (re)visit in March 2023, after the restrictions of COVID-19 were lifted, and tourists occasionally visited KPE island, the evidence of stone-tool use, that is, pieces of oyster shells and stones with evidence of percussive use-damage on the oyster bed or rock anvils was searched. The key personnel of the Royal Thai Navy and the boat drivers were also interviewed. They reported that monkeys had never used stones to crack open foods. Monkeys roamed freely and were observed to forage for foods categorized as natural or human-provisioned foods. Natural foods included invertebrate animals, that is, crabs, rock oysters (*Saccostrea forskali*), venus clam, commercial bivalves (*Gafrarium tumidum*), and plants, that is, catappa nut (*Terminalia catappa*), mangrove pods (*Rhizophora sp.*), young buds of Bantigue (*Pemphis acidula*) and young fruit of *Chaetocarpus castanocarpus*. Human-provisioned foods included sea fish, banana, cucumber, carrot, purple cabbage, pineapple, watermelon, spring onion, and ripe mango.

Seventeen animals were identified using percussive stones to crack open the rock oysters attached to the rock anvil by S. Panjan (Figure 4, Table 1, and Supporting Information: Video clip S1). All were subadults and adults, and 15 out of 17 were males. One adult male monkey was seen performing the behavior twice, on March 12 and 13, 2023. Compared to other stone tools using macaque populations (Gumert et al., 2009; Gumert, Hoong, et al., 2011; Tan et al., 2018), these animals did not manipulate the stone well; mostly, they held the large stones (weighing >1 kg) with two hands while they were sitting, raised the hands up not higher than their shoulder, and threw stone onto the oyster bed. We named this stone manipulation as "pound-hammering-like." Once the shell cracked, monkeys used their hand(s) or teeth to open the oysters (or gnaw manipulation in Bandini & Tennie, 2018) to consume the meat. Some monkeys threw the stone more randomly (see Supporting Information: Video clip S1), not directly targeting the oysters. Mostly adult males performed the behavior while they were foraging in solitary.

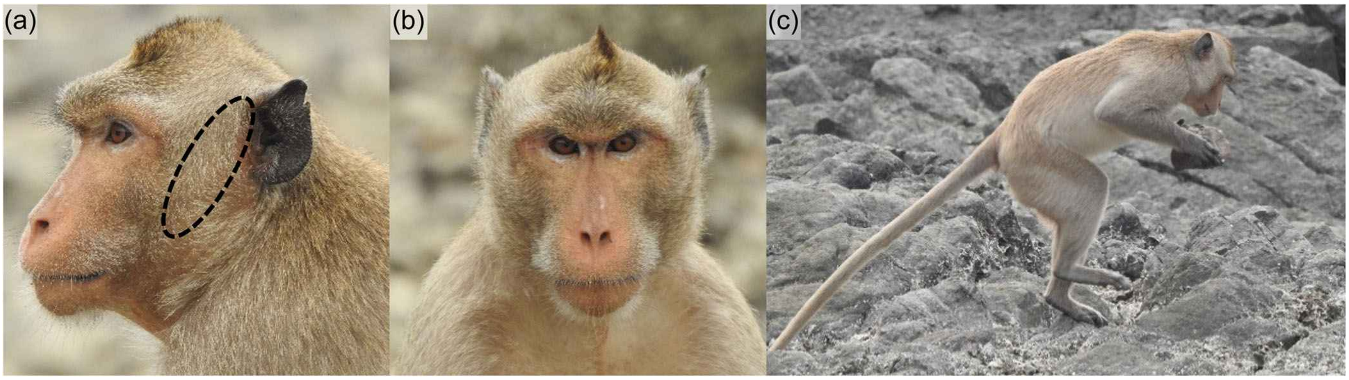

FIGURE 2 Adult male with transzygomatic cheek hair pattern (a; dashed circle), head crest (b), and light pelage color (c).

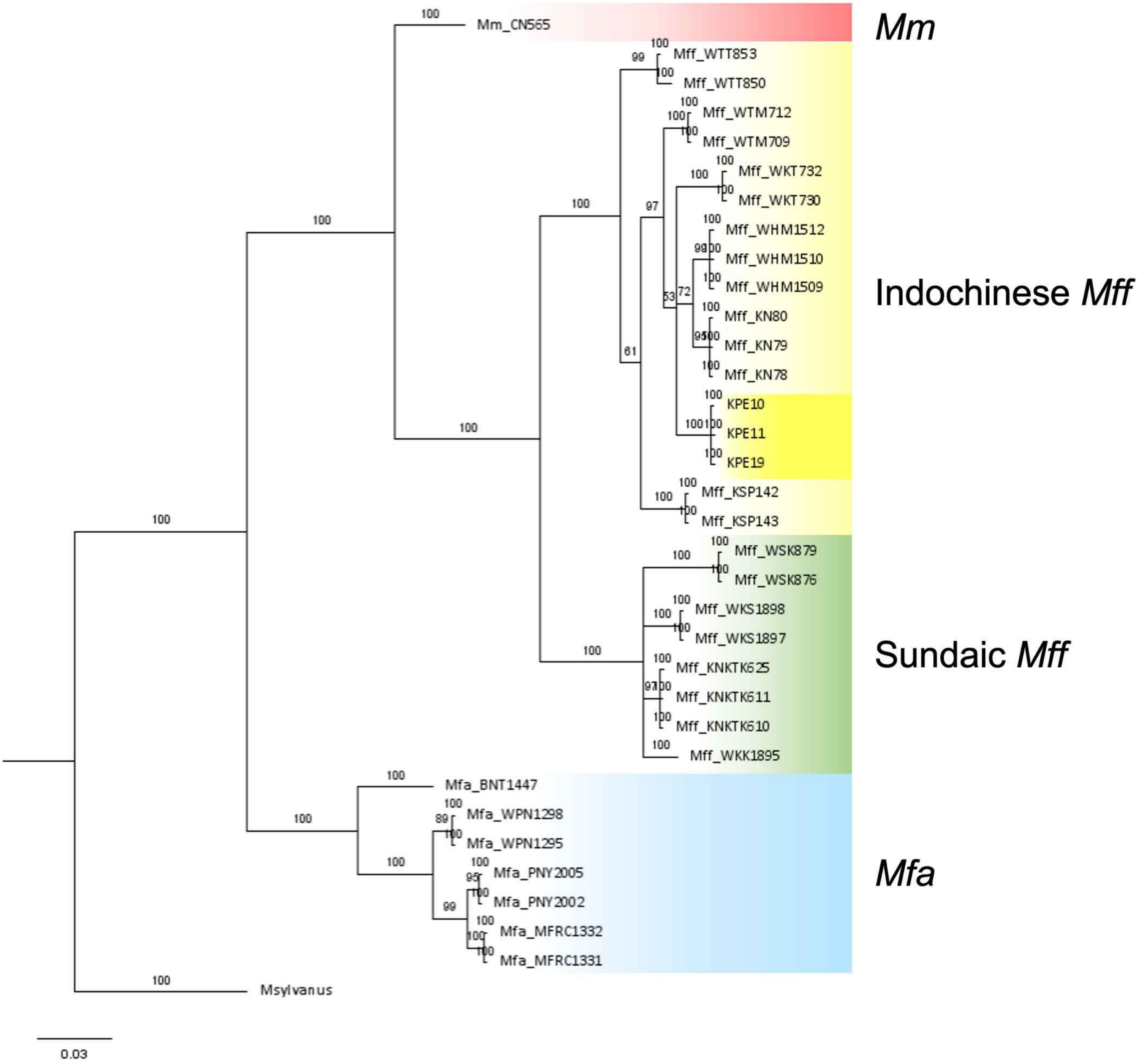

FIGURE 3 Bayesian phylogenetic tree based on 573 bp of the mtDNA gene. The tree's three-letter codes correspond to those of Bunlungsup et al. (2017). The dark yellow color indicates the Koh Ped (KPE) samples that were analyzed in this study. The numbers on each branch refer to the posterior probability/bootstrap values.

4 | DISCUSSION

This is the first report of the stone-tool use in the context of extractive foraging in *Mff*, marking them as the sixth wild NHP species observed to perform this behavior. They were identified as *Mff* subspecies based on distribution, morphological, and genetic (mtDNA and *SRY* gene) characteristics. Bunlungsup et al. (2017) revealed the past introgression of *M. mulatta* males to the Indochinese *Mff* population (Bunlungsup et al., 2017), where the introgression was terminated at the vicinity of the Isthmus of Kra, and the Indochinese *Mff* harbored the *M. mulatta* Y-chromosome gene, thus in this study, the two *SRY* gene SNPs (T and T) analyzed confirmed that the KPE monkeys belonged to the Indochinese form of *Mff* subspecies. In the past, only *Mfa* (Malaivijitnond et al., 2007) and hybrids between *Mff* × *Mfa* (Luncz et al., 2017; Tan et al., 2018) were reported to perform stone-tool use behavior to access encased foods. Even though it was a training program, captive *Mff* were unable to develop the behavior (Bandini & Tennie, 2018). It was therefore concluded that the genetic predispositions of *Mfa* played a crucial role in the emergence and development of this behavior in long-tailed macaques (Bandini & Tennie, 2018; Gumert et al., 2019). Although the KPE macaques were identified as *Mff*, genetic

FIGURE 4 A series of rock oysters-cracking by an adult male. The rock oysters (red arrow) were attached to the rock anvil, and an animal used percussive stone-tool to open the oysters.

TABLE 1 Sex and age class of stone-tool use macaques observed on Koh Ped Island.

Sex	Male		Female	
Age-class	Adult	Sub Adult	Adult	Sub Adult
March 12, 2023	2	-	-	-
March 13, 2023	5 (+1*)	1	1	-
March 14, 2023	7	-	1	-
All	14 (+1*)	1	2	-

*This adult male was observed to perform stone-tool use behavior on March 12 and 13, 2023, he was not repeatedly counted on March 13, 2023.

contributions from *Mfa* into this population cannot be ruled out. The use of mtDNA and *SRY* genes has some disadvantages as it could not predict the level of autosomal genetic introgression from *Mfa* (Bunlungsup et al., 2016). For example, two populations of *Mff* living in the northern region of Thailand (GPS: 15°56′ N and 13°02′ N;) were identified carrying 11% and 14% of *Mfa* genetic ancestry analyzed by 868-autosomal SNPs. Thus, the level of genetic admixture of *Mfa* ancestry in the KPE population should be assessed by autosomal SNP marker in the near future (Phadphon, Kanthaswamy, et al., 2022).

The composition of the animal's habitat, such as the availability of suitable stone materials (i.e., potential hammerstones and anvils), the presence of encased foods (i.e., oysters in KPE), and free time associated with food provisioning (i.e., the “opportunity hypothesis”) (Cenni et al., 2022, 2023), enabled the emergence of the stone-tool use behavior. Based on the discovery of stone-tool use behavior in the KPE-*Mff* during the COVID-19 episode, indicated that even though optimal environmental conditions for tool use have existed for several decades, without the pressure of food scarcity, this specific behavior would likely not have developed (Bandini & Tennie, 2018). This finding supports “the necessity hypothesis” proposed by Fox et al. (1999) for tool use among orangutan populations where sustenance-needs require maintenance of tool use during resource scarcity (Fox et al., 1999). For the KPE *Mff* population, human-provisioned foods are the most efficient option for sufficient caloric intake. Similarly, food scarcity and starvation risk were also proposed as key factors in the emergence of nut-cracking behavior in yellow-breasted capuchins living in dry forests and thorn scrub in the Caatinga biome, Brazil (Canale et al., 2009; de A. Moura & Lee, 2004). Similarly, chimpanzees used stone tools to exploit *Coula* nuts more frequently in the dry season, during which their primary food sources were scarce (Boesch & Boesch, 1984). It was found that the seasonality of stone-aided nutcracking behavior in Savannah bearded capuchin monkeys (*Sapajus libidinosus*) was explained by “the opportunity hypothesis” rather than “the necessity hypothesis” (Spagnoletti et al., 2012). As the oyster-cracking behavior of this KPE population was discovered during the time of the COVID-19 lockdown, the food scarcity over 3 years should pressure the animals to adapt to their marine environment. Thus, this sheds light on the positive magnitude of COVID-19 in wildlife.

Generally, it might not be common for other NHPs to exploit marine food sources. *Mff*, however, is familiar with aquatic ecosystems; they are good swimmers (Fooden, 1995). Additionally, KPE-*Mff* were customarily fed by tourists, focusing their attention on the forest to the seashore. The animals could have learned about marine food sources through increased exposure to the shore. The observed stone manipulation pattern was named “pound-hammering-like” because the monkeys did not handle the stone throughout the usual cracking processes. They dealt with the stone with two hands, raised their hands to their chests, and threw the stone into the oyster beds. Object (tree-branch) throwing was previously observed in a population of wild chimpanzees intending to attack the unfamiliar person approaching (Sugiyama & Koman, 1979). Most chimpanzees that displayed this behavior were also adult males, similar to the observed stone-throwing in KPE-*Mff*. It might be that, in some situations, an adult male *Mff* threw a stone into an oyster bed, accidentally cracked open the oyster shells, saw the broken shell, and accessed oyster meat afterward.

Based on the actions of stone-throwing described in the literature, we proposed that the “pound-hammering-like” behavior in the KPE population originated from uncoordinated stone-throwing (the first step before stone-tool use) and modified it over time to percussive stone-tool use. Stone-throwing was also described in West African chimpanzee (*Pan troglodytes verus*, Kühl et al., 2016), Japanese macaque (*M. fuscata*; Leca et al., 2008), and chacma baboon (*Papio ursinus*; Hamilton et al., 1975). Stone-throwing has been reported most frequently in NHP species that used tools in other contexts, i.e., capuchin monkeys and chimpanzees. Stone-throwing in Japanese macaque has been listed as one of the numerous behavioral patterns of the stone-handling repertoire of this species (Leca et al., 2008). Compared to Japanese macaques, the closest living NHP species to *Mff*, stone-throwing styles in Japanese macaques were generally "underarm throwing," which is different from what was observed in KPE-*Mff*. The stone-throwing of Japanese macaques was performed from a tripedal posture (one-handed sequential-movement operation) and often accompanied by repeated jumps (Leca et al., 2008), while the stone-handling in KPE-*Mff* was performed with two hands while sitting, which looked similar to "pound-hammering" which is more advanced than the stone-throwing. The directions of stone material thrown by Japanese macaques were backward, upward, sideways, or forward (Leca et al., 2008), while KPE-*Mff* threw stones vertically and directed downwards. Throwing of stones in KPE-*Mff* at the end of pound-hammering-like processes might be a result of the stone being very heavy (> 1 kg) compared to their body weight (adult males, ranging 5–8 kg; Hamada et al., 2008) which was far beyond their capacity to hold it for a long while they were sitting. However, throwing causes a loss of accuracy. From a functional viewpoint, the stone-throwing observed in Japanese macaques evolved from nonfunctional behaviors, such as stone handling in the form of object play (Leca et al., 2008). At the same time, the pound-hammering-like in KPE-*Mff* was a targeted (oyster) foraging activity. Because this stone-tool use behavior only recently emerged in the KPE population, it is interesting to investigate whether it evolved from nonfunctional stone-throwing into functional stone-tool use. It will be necessary to observe the macaques of KPE further to investigate if the animals will modify the stone manipulation style and select smaller and lighter stones for oyster cracking, as seen in the pureblood *Mfa* living at Piak Nam Yai island, southwestern Thailand (Gumert et al., 2009, 2011). The heavy stone use might also explain why the oyster-cracking behavior was observed only in KPE-*Mff* adults/subadults, and 88% were males.

How the behavior spread throughout the KPE group is still unknown. However, since many KPE males were observed to perform this behavior while solitary, it might have been difficult for other animals to observe and learn. Tan et al. (2018) reported that young long-tailed macaques preferred to learn to use stone tools from closer, older, and better tool users. Previously, Bandini and Tennie (2018) experimentally tested captive *Mff* by motivating them with provided ecological materials necessary for pound-hammering, that is, hammering stones, shelled nuts, and stone anvils. However, the captive *Mff* did not perform the pound-hammering behavior, even not after repeated demonstrations. The researchers concluded that the *Mff* could not learn pound-hammering and that the levels of individual learning abilities and motivation to attend to socially mediated information of *Mff* differed from those of *Mfa*. However, our study shows that wild *Mff* can develop stone pound-hammering-like behavior if the motivation is strong enough to encourage the acquisition. In this case, at least 2 years (2020–2022) of exposure to severe food scarcity due to the COVID-19 pandemic is the cause. Besides, it suggests that the emergence of stone tool behavior is not related to a critical period of learning, at around 3 years of age, as seen in wild juvenile *Mfa* × *Mff* hybrids (Tan et al., 2018) because, in the KPE population, only subadults/adults were observed performing the behavior.

As seen in the stone-tool use in *Mfa* at Piak Nam Yai Island, southwestern Thailand (Gumert, Hoong, et al., 2011) and *Mfa* × *Mff* hybrids at Koram Island, southern Thailand (Luncz et al., 2017; Tan et al., 2018), and the stone-throwing in Japanese macaques, stone-manipulating behaviors were suggested to transmit from one generation to the next generation via maternal kinship and social proximity (Leca et al., 2008). "Pound-hammering-like" behavior observed in KPE females was rare (only 2 out of 17 stone tool users). The newly emerged tool behavior might quickly disappear after tourism has returned to the island and people start provisioning the animals again. It might be a tragedy for science because many research questions await investigation. For example, how many populations on the island can use stone-tools? How does the new stone-tool behavior spread amongst and between group members? What is the feeding range between stone-tool users and non-stone-tool users? Do they use stones to crack other food types, and what is the manipulation style? What is the size, shape, and weight changes of selected stone-tools? What does the efficiency of stone-tool use in KPE-*Mff* compared to the pureblood *Mfa* and the *Mff* × *Mfa* hybrids? (Gumert et al., 2009, 2011, 2019), and, if no human disturbance occurs, can this behavior develop to the level seen in *Mfa* monkeys?

AUTHOR CONTRIBUTIONS

Raza Muhammad: Formal analysis (equal); methodology (supporting); writing—original draft (equal). **Titiporn Kaikaew**: Investigation (supporting). **Suchada Panjan**: Investigation (supporting). **Suthirote Meesawat**: Investigation (supporting). **Wipaporn Thabthimthong**: Investigation (supporting); methodology (supporting). **Sunchai Payungporn**: Methodology (supporting); writing—review & editing (equal). **Jirawat Apipattarachaiwong**: Resources (equal). **Sreetharan Kanthaswamy**: Conceptualization (equal); writing—review & editing (equal). **Yuzuru Hamada**: Investigation (equal); methodology (equal); writing—review & editing (equal). **Lydia V. Luncz**: Conceptualization (equal); writing—review & editing (equal). **Suchinda Malaivijitnond**: Conceptualization (equal); funding acquisition (equal); methodology (equal); project administration (equal); resources (equal); supervision (equal); writing—original draft (equal).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data on stone-tool use behaviors are available in the supplementary material of this article.

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REFERENCES

de A. Moura, A. C., & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science*, *306*(5703):1909. https://doi.org/10.1126/science.1102558

Bandini, E., & Tennie, C. (2018). Naive, captive long-tailed macaques (*Macaca fascicularis fascicularis*) fail to individually and socially learn pound-hammering, a tool-use behaviour. *Royal Society Open Science*, *5*(5), 171826. https://doi.org/10.1098/rsos.171826

Barrett, B. J., Monteza-Moreno, C. M., Dogandžić, T., Zwyns, N., Ibáñez, A., & Crofoot, M. C. (2018). Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus capucinus*. *Royal Society Open Science*, *5*(8), 181002. https://doi.org/10.1098/rsos.181002

Boesch, C., & Boesch, H. (1984). Possible causes of sex differences in the use of natural hammers by wild chimpanzees. *Journal of Human Evolution*, *13*(5), 415–440. https://doi.org/10.1016/S0047-2484(84)80055-X

Bunlungsup, S., Imai, H., Hamada, Y., Gumert, M. D., San, A. M., & Malaivijitnond, S. (2016). Morphological characteristics and genetic diversity of Burmese long-tailed Macaques (*Macaca fascicularis aurea*). *American Journal of Primatology*, *78*(4), 441–455. https://doi.org/10.1002/ajp.22512

Bunlungsup, S., Imai, H., Hamada, Y., Matsudaira, K., & Malaivijitnond, S. (2017). Mitochondrial DNA and two Y-chromosome genes of common long-tailed macaques (*Macaca fascicularis fascicularis*) throughout Thailand and vicinity. *American Journal of Primatology*, *79*(2), e22596. https://doi.org/10.1002/ajp.22596.

Canale, G. R., Guidorizzi, C. E., Kierulff, M. C. M., & Gatto, C. A. F. R. (2009). First record of tool use by wild populations of the yellow-breasted capuchin monkey (*Cebus xanthosternos*) and new records for the bearded capuchin (*Cebus libidinosus*). *American Journal of Primatology*, *71*(5), 366–372. https://doi.org/10.1002/ajp.20648

Cenni, C., Christie, J. B. A., Van der Pant, Y., Gunst, N., Vasey, P. L., Wandia, I. N., & Leca, J. B. (2022). Do monkeys use sex toys? Evidence of stone tool-assisted masturbation in free-ranging long-tailed macaques. *Ethology*, *128*(9), 632–646.

Cenni, C., Thierry, B., Wandia, I. N., & Leca, J.-B. (2023). Tool-assisted water scooping in Balinese long-tailed macaques. *Behaviour*, *160*(8–9), 817–836.

Fooden, J. (1995). Systematic review of southeast Asian longtail macaques, *Macaca fascicularis* (Raffles, [1821]). *Fieldiana Zoology*, *81*, 1–206. https://doi.org/10.5962/bhl.title.3456

Fox, E. A., Sitompul, A. F., & Van Schaik, C. P. (1999). Intelligent tool use in wild Sumatran orangutans. In S. T. Parker, R. W. Mitchell, & H. L. Miles (Eds.), *The mentality of gorillas and orangutans* (Vol. 480, pp. 99–116). Cambridge University Press.

Fragaszy, D., Izar, P., Visalberghi, E., Ottoni, E. B., & De Oliveira, M. G. (2004). Wild capuchin monkeys (*Cebus libidinosus*) use anvils and stone pounding tools. *American Journal of Primatology*, *64*(4), 359–366. https://doi.org/10.1002/ajp.20085

Gumert, M. D., Hoong, L. K., & Malaivijitnond, S. (2011). Sex differences in the stone tool-use behavior of a wild population of Burmese long-tailed macaques (*Macaca fascicularis aurea*). *American Journal of Primatology*, *73*(12), 1239–1249. https://doi.org/10.1002/ajp.20996

Gumert, M. D., Kluck, M., & Malaivijitnond, S. (2009). The physical characteristics and usage patterns of stone axe and pounding hammers used by long-tailed macaques in the Andaman sea region of Thailand. *American Journal of Primatology*, *71*(7), 594–608. https://doi.org/10.1002/ajp.20694

Gumert, M. D., Tan, A. W. Y., Luncz, L. V., Chua, C. T., Kulik, L., Switzer, A. D., Haslam, M., Iriki, A., & Malaivijitnond, S. (2019). Prevalence of tool behaviour is associated with pelage phenotype in intraspecific hybrid long-tailed macaques (*Macaca fascicularis aurea* × *M. f. fascicularis*). *Behaviour*, *156*(11), 1083–1125. https://doi.org/10.1163/1568539X-00003557

Hall, T. A. (1999). BioEdit: A user-friendly biological sequence alignment editor and analysis program for windows 95/98/NT. Nucleic acids symposium series.

Hamada, Y., Suryobroto, B., Goto, S., & Malaivijitnond, S. (2008). Morphological and body color variation in Thai *Macaca fascicularis fascicularis* north and south of the Isthmus of Kra. *International Journal of Primatology*, *29*(5), 1271–1294. https://doi.org/10.1007/s10764-008-9289-y

Hamilton, W. J., Buskirk, R. E., & Buskirk, W. H. (1975). Defensive stoning by baboons. *Nature*, *256*(5517), 488–489. https://doi.org/10.1038/256488a0

Haslam, M., Hernandez-Aguilar, A., Ling, V., Carvalho, S., de la Torre, I., DeStefano, A., Du, A., Hardy, B., 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*(7253), 339–344. https://doi.org/10.1038/nature08188

Hayaishi, S., & Kawamoto, Y. (2006). Low genetic diversity and biased distribution of mitochondrial DNA haplotypes in the Japanese macaque (*Macaca fuscata yakui*) on Yakushima Island. *Primates*, *47*, 158–164. https://doi.org/10.1007/s10329-005-0169-1

Huelsenbeck, J. P., & Ronquist, F. (2001). MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics*, *17*(8), 754–755.

Krabuansang, K., Swatdipong, A., Samipak, S., & Beckles, D. M. (2020). Genetic diversity of *Saccostrea forskali* rock oyster in the Gulf of Thailand. *Applied Science and Engineering Progress*, *13*(2), 158–165.

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., … Boesch, C. (2016). Chimpanzee accumulative stone throwing. *Scientific Reports*, *6*(1), 22219. https://doi.org/10.1038/srep22219

Kumar, S., Stecher, G., Li, M., Knyaz, C., & Tamura, K. (2018). MEGA X: Molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution*, *35*(6), 1547–1549. https://doi.org/10.1093/molbev/msy096

Kumpai, P., Hamada, Y., Kanthaswamy, S., & Malaivijitnond, S. (2022). Gene flow from rhesus (*Macaca mulatta*) to cynomolgus macaques (*M. fascicularis*) and effects of introgressive hybridization on reproduction in two biomedically relevant non-human primate species. *Journal of Medical Primatology*, *51*(2), 108–118. https://doi.org/10.1111/jmp.12570

Leca, J.-B., Nahallage, C. A. D., Gunst, N., & Huffman, M. A. (2008). Stone-throwing by Japanese macaques: Form and functional aspects of a group-specific behavioral tradition. *Journal of Human Evolution*, *55*(6), 989–998. https://doi.org/10.1016/j.jhevol.2008.06.004

Luncz, L. V., Tan, A., Haslam, M., Kulik, L., Proffitt, T., Malaivijitnond, S., & Gumert, M. (2017). Resource depletion through primate stone technology. *eLife*, *6*, 1–16. https://doi.org/10.7554/eLife.23647.001

Malaivijitnond, S., Lekprayoon, C., Tandavanittj, N., Panha, S., Cheewatham, C., & Hamada, Y. (2007). Stone-tool usage by Thai long-tailed macaques (*Macaca fascicularis*). *American Journal of Primatology*, *69*, 227–233. https://doi.org/10.1002/ajp.20342

Malaivijitnond, S., Vazquez, Y., & Hamada, Y. (2011). Human impact on long-tailed macaques in Thailand. In M. D. Gumert & L. Jones-Engel, (Eds.), *Monkeys on the edge: Ecology and management of long-tailed Macaques and their interface with humans* (pp. 118–158). Cambridge University Press.

Matsudaira, K., Hamada, Y., Bunlungsup, S., Ishida, T., San, A. M., & Malaivijitnond, S. (2018). Whole mitochondrial genomic and Y-chromosomal phylogenies of Burmese long-tailed macaque (*Macaca fascicularis aurea*) suggest ancient hybridization between fascicularis and sinica species groups. *Journal of Heredity*, *109*(4), 360–371. https://doi.org/10.1093/jhered/esx108

McGrew, W. C. (1998). Culture in nonhuman primates? *Annual Review of Anthropology*, *27*(1), 301–328. https://doi.org/10.1146/annurev.anthro.27.1.301

Osada, N., Matsudaira, K., Hamada, Y., & Malaivijitnond, S. (2021). Testing sex-biased admixture origin of macaque species using autosomal and X-chromosomal genomic sequences. *Genome Biology and Evolution*, *13*(1), 1–14. https://doi.org/10.1093/gbe/evaa209

Phadphon, P. (2022). *Degree of genetic admixture in hybrid populations between Macaca fascicularis fascicularis and M. f. aurea in association with stone-tool-use behavior*. Chulalongkorn University, Thailand.

Phadphon, P., Kanthaswamy, S., Oldt, R. F., Hamada, Y., & Malaivijitnond, S. (2022). Population structure of *Macaca fascicularis aurea*, and their genetic relationships with *M. f. fascicularis* and *M. mulatta* determined by 868 RADseq-derived autosomal SNPs–A consideration for biomedical research. *Journal of Medical Primatology*, *51*(1), 33–44. https://doi.org/10.1111/jmp.12554

Rambaut, A. (2010). *FigTree v1.3.1*. Institute of Evolutionary Biology, University of Edinburgh, Edinburgh. http://tree.bio.ed.ac.uk/software/figtree/

Rambaut, A., & Drummond, A. (2009). *Tracer v1.5*. http://tree.bio.ed.ac.uk/software/tracer/

Reeves, J. S., Proffitt, T., & Luncz, L. V. (2021). Modeling a primate technological niche. *Scientific Reports*, *11*(23139), 109. https://doi.org/10.1038/s41598-021-01849-4

Reeves, J. S., Tan, A., Malaivijitnond, S., & Luncz, L. V. (2023). Simulation and social network analysis provide insight into the acquisition of tool behaviour in hybrid macaques. *Proceedings of the Royal Society B*, *290*(1995), 1–12. https://doi.org/10.1098/rspb.2022.2276

Spagnoletti, N., Visalberghi, E., Verderane, M. P., Ottoni, E., Izar, P., & Fragaszy, D. (2012). Stone tool use in wild bearded capuchin monkeys, *Cebus libidinosus*. Is it a strategy to overcome food scarcity? *Animal Behaviour*, *83*(5), 1285–1294.

Sugiyama, Y., & Koman, J. (1979). Tool-using and-making behavior in wild chimpanzees at Bossou, Guinea. *Primates*, *20*(4), 513–524. https://doi.org/10.1007/BF02373433

Tan, A. W. Y., Hemelrijk, C. K., Malaivijitnond, S., & Gumert, M. D. (2018). Young macaques (*Macaca fascicularis*) preferentially bias attention towards closer, older, and better tool users. *Animal Cognition*, *21*(4), 551–563. https://doi.org/10.1007/s10071-018-1188-9

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