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Stone-throwing by Japanese macaques: form and functional aspects of a group-specific behavioral tradition

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ABSTRACT

Throwing is a major behavioral component of hominid evolution. Comparison of this behavior across a broad range of non-human primate species is needed to elucidate the phylogenetic constraints on throwing behavior. In this study of stone-throwing in Japanese macaques, we present a systematic multi-group comparison of the frequency and prevalence of this behavior as well as detailed descriptions and quantitative data on the form, context, and possible social transmission of stone-throwing. Stone-throws were mainly underarm, performed from a tripedal posture, and often accompanied by repeated vertical leaps. We found marked individual hand preferences for throwing, but no consistent group-level handedness. Our results support the hypotheses relating body posture, throwing style, and handedness in throwing by primates. Based on the analysis of the contexts that may elicit the behavior, we postulate that unaimed stone-throwing in Japanese macaques may serve to augment the effect of agonistic displays, and accordingly, can be regarded as spontaneous tool-use. Our findings are consistent with the comparative data using modern non-human primate species to model the structural processes and functional aspects of throwing evolution in early hominids. This study supports the view that tool-use evolves from initially non-functional behaviors, such as stone handling, which is a form of object play. Stone-throwing by Japanese macaques meets several criteria of a behavioral tradition, including group-specificity. This first report of a stone-tool-use tradition in Japanese macaques is of direct relevance to the question of the evolution of stone technology in hominids.

Introduction

Throwing is considered a major behavioral component of human evolution. There is little doubt that the emergence of throwing behavior had important socio-ecological and neuro-cognitive effects during all stages of hominid evolution (Darlington, 1975). First, the ability to project objects with force, velocity, and accuracy probably provided our prehistoric primate ancestors with numerous advantages, such as greater hunting and offensive success, better defense against predators and rivals, and the possibility to cooperate through food-sharing by transferring food items thrown within and between social groups (Dennell, 1997; Westergaard et al., 1998; Watson, 2001). Second, throwing is predominantly a one-handed sequential-movement operation exposed to selection pressures in the natural environment of early hominids. Throwing constraints may have contributed to the pre-adaptation of their growing brain and changing body to a variety of traits, including handedness, bipedalism, and complex language processing (Calvin, 1983; Fifer, 1987; Hopkins et al., 1993; Churchill and Schmitt, 2002; Schmitt et al., 2003).

Due to their physical properties and ubiquity, stones are likely to have been the first effective and ready-to-use missile-weapons for our primate ancestors (Fifer, 1987; Isaac, 1987). Unfortunately, archeological evidence for the evolution of stone-throwing behavior in hominids is rare: fossil forelimb bones are rare and unlike most other stone-tools, thrown stones were presumably scattered away from body parts (Darlington, 1975; but see Leakey, 1948). Although the cognitive processes which underlay the throwing behavior in humans are more complex than those which underlay the throwing behavior in monkeys and apes, models of early hominid throwing behavior can be tested by a comparative approach using modern non-human primate species (Calvin, 1983; Westergaard and Suomi, 1995; Cleveland et al., 2003).

From the structural viewpoint, several hypotheses have been proposed to relate skeletal modifications, body posture, throwing style, and handedness in throwing (Calvin, 1983; Fifer, 1987; Knüsel, 1992; Hopkins et al., 2005). As opposed to monkeys that exhibit underarm throwing from a tripedal posture, the ability for chimpanzees, bonobos, and humans to perform overarm throws by

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maintaining a bipedal stance may be due to similar structures of hip and shoulder joints (Beck, 1980; Calvin, 1983; Savage-Rumbaugh et al., 2001). This distinction in throwing style and posture plays a crucial role in the explanation of the prevalence of right-handedness observed in human populations (Annett, 2002), whereas chimpanzees and capuchin monkeys did not show clear hand preference for throwing at the group level (Westergaard et al., 2000; McGrew and Marchant, 2001; but see Hopkins et al., 2005). Regarding functional aspects, Calvin (1993) hypothesized that predatory or defensive-aimed stone-throwing by early hominids (defined as the goal-directed projection of stones toward an identifiable target: Westergaard and Suomi, 1994) emerged from unaimed or non-directional throwing of objects, similar to that which has been observed in non-human primates as part of agonistic displays (Beck, 1980).

Therefore, research examining the form, context, and learning of stone-throwing in various non-human primate species, including throwing posture, handedness, direction, and distance, description of the thrown stones, and assessment of the situations that may elicit the performance and social transmission of throwing, can provide vital insight into the biological basis and evolution of stone-throwing in humans (Fifer, 1987; Westergaard et al., 2000; Hopkins et al., 2005). A variety of monkeys and apes living in natural and captive conditions, particularly capuchins (*Cebus* spp.), baboons (*Papio* spp.), macaques (*Macaca* spp.), and chimpanzees (*Pan* spp.), were reported to perform aimed and unaimed stone-throwing, either spontaneously or in problem-solving tasks (e.g., Goodall, 1964; Hamilton et al., 1975; Tokida et al., 1994; Westergaard et al., 2000).

However, with respect to spontaneous stone-throwing in non-human primates, we lack detailed descriptions and quantitative data on the form, context, and learning of the behavior, systematically collected and based on long-term observations of multiple social groups of various species across the primate order. There are at least four reasons for this lack of information: 1) most reports on this behavior are based on interviews of primate keepers in zoos or anecdotal accounts relayed from anonymous travelers encountering wild primates (Hall, 1963; Kortlandt and Kooij, 1963; Beck, 1980); 2) the performance of stone-throwing in non-human primates is uncommon (Torigoe, 1985); 3) throwing behavior is generally exhibited by one individual or at the most a few group members, depending on their age/sex class or social status, mostly dominant adult males, although this is more inferred from incomplete evidence than significant correlations (e.g., Schaller, 1963; Goodall, 1964; Struhsaker, 1975; Nishida et al., 1999); and 4) stone-throwing has been reported most frequently in primate species that use tools in other contexts, namely capuchins and chimpanzees (Beck, 1980; Torigoe, 1985).

The genus *Macaca* is the most widely distributed of non-human primates. Its 20 extant species feature a broad diversity of social relationships, and present a variety of morphological and behavioral adaptations to different environments that make this taxon of particular interest for research on evolutionary biology and ecology (Fa and Lindburg, 1996; Thierry et al., 2004). However, macaques are not frequent tool-users and are not considered frequent stone-throwers (Beck, 1980; Torigoe, 1985). More data are needed to provide a broader inter-species comparison and to elucidate the phylogenetic constraints on throwing behavior. Any further information on stone-throwing (or lack thereof) in macaques is of interest to the debate surrounding the evolution of this behavior in humans.

Stone-throwing in Japanese macaques has recently been listed as one of the numerous behavioral patterns of the stone handling (SH) repertoire of this species (Leca et al., 2007a,b; Nahallage and Huffman, 2007a). Defined as seemingly-playful stone-directed manipulative actions, SH is considered a traditional behavior, socially transmitted between same-age partners, such as peer playmates and across generations from mother to offspring (Huffman, 1984, 1996; Huffman and Quiatt, 1986; Nahallage and Huffman, 2007b). We found major inter-group differences in the frequency of occurrence and the prevalence of SH patterns, with local variants being customary in some troops, and rare or even absent in others, performed by a majority of individuals in some troops, and only idiosyncratically in others (Leca et al., 2007a,b).

Although showing inter-group differences is not sufficient evidence for culture, the "group-contrast" method has often been used as a first step to identify candidates for cultural behaviors, particularly in primate stone-tool cultures (e.g., Whiten et al., 1999). However, data on the rate and form of stone-throwing behavior in different troops within the same monkey species have not been reported in the literature so far (but see Leca et al., 2007a for general data). From a functional viewpoint, the current SH patterns observed in Japanese macaques are regarded as a non-instrumental manipulation of stones with no obvious survival value (Huffman, 1984, but see Nahallage and Huffman, 2007a for a possible ultimate function of SH). However, Huffman (1996) suggested that if SH persists sufficiently in a given troop, direct material benefits may be acquired in the future, provided some modifications of the behavioral patterns or the direct integration of SH with foraging activities (e.g., stone-tool-use) or social interactions (e.g., agonistic display) (Huffman and Quiatt, 1986; Huffman and Hirata, 2003; Leca et al., 2008a). Since stone-throwing is considered tool-use according to Beck's (1980) definition, this particular SH pattern is a strong candidate for such transformations. From this perspective, Japanese macaques could be used as a non-human primate model for processes that contributed to the evolution of stone-throwing in early hominids.

In an effort to encourage the compilation of relevant data on stone-throwing in non-human primate species and stimulate general interest in the evolution of hominid throwing behavior, this paper will address the following questions: When Japanese macaques throw stones, do they perform an overarm action? Do they stand bipedally? Do they show hand preference? Do they throw from an elevated position? How far do they throw? Do they select particular stones? Do they aim or do they throw at random as part of a display sequence? Does stone-throwing occur in all troops or is it a group-specific behavioral practice? Is there evidence for social transmission of this behavior among group members? Can stone-throwing in Japanese macaques be referred to as a behavioral tradition?

In this study of stone-throwing in Japanese macaques, we aim to: 1) present a systematic multi-group comparison of the frequency and prevalence of this behavior; 2) provide further descriptive and quantitative data on the form of stone-throwing, including motor patterns, postures, handedness, throwing location, direction, and distance, as well as the number and size of stones thrown; 3) document the contexts of occurrence of stone-throwing events and propose functional explanations for this behavior; and 4) investigate the channels and modes of intra-group diffusion of stone-throwing with regards to age, sex, and dominance classes.

Materials and methods

Subjects and study conditions

We observed a total of 10 troops of Japanese macaques (*Macaca fuscata*) at six geographically isolated sites in Japan (Table 1). Captive troops were supplied with commercial primate pellets, vegetables, or fruits. Free-ranging troop members gathered regularly around feeding sites where they were artificially provisioned with cereal grains by the staff technicians of the Koshima Field Station, Kyoto University (Kosh.) or by the staff members and managers of monkey

Table 1
Ranging condition and location of the 10 study troops

Troop full name (abbreviated name)	Ranging condition[a]	Study site
Arashiyama A (Ara.A)	CP	Primate Research Institute, Inuyama, Aichi prefecture
Wakasa A (Wak.A)	CP	Primate Research Institute, Inuyama, Aichi prefecture
Takahama (Takh.)	CP	Primate Research Institute, Inuyama, Aichi prefecture
Japan Monkey Centre (JMC)	CP	Japan Monkey Centre Inuyama, Aichi prefecture
Koshima (Kosh.)	FR	Koshima Islet, Miyazaki prefecture
Arashiyama E (Ara.E)	FR	Iwatayama Monkey Park, Arashiyama, Kyoto prefecture
Shodoshima A (Sho.A)	FR	Wild Monkey Park, Shodoshima Island, Kagawa prefecture
Shodoshima B (Sho.B)	FR	Wild Monkey Park, Shodoshima Island, Kagawa prefecture
Takasakiyama B (Tak.B)	FR	Takasakiyama Natural Zoo, Takasakiyama, Oita prefecture
Takasakiyama C (Tak.C)	FR	Takasakiyama Natural Zoo, Takasakiyama, Oita prefecture

[a] CP: captive (large outdoor enclosure); FR: free-ranging.

parks (Ara.E, Sho.A, Sho.B, Tak.B, and Tak.C). The free-ranging troops living at the same site (Sho.A and Sho.B at Shodoshima, and Tak.B and Tak.C at Takasakiyama) had overlapping home ranges and came into occasional contact. Although stone availability was highly variable according to the study site, we found no significant correlation between site-specific stone availability and SH frequency (Leca et al., 2008b).

The daily observation period was between 7:00 am and 6:00 pm, divided into one-hour blocks, and observations were roughly equalized across the blocks. Visibility was excellent since captive troop members could be sampled from observation platforms overhanging the enclosures, with no major obstacles blocking the view, and free-ranging troop members could be approached and sampled within 3–5 m. This research was conducted in accordance with PRI's Rules and Guidelines for Animal Health and Welfare.

Data collection procedure

As Hopkins et al. (2005) pointed out, since throwing in animals is a rare and somewhat unpredictable behavior, the methods of data collection can be very flexible. Like most other surveys on throwing behavior in non-human primates (e.g., Goodall, 1964; Hamilton et al., 1975; Visalberghi, 1993; Nakamichi, 1998; Hopkins et al., 2005; Wittiger and Sunderland-Groves, 2007), this study of stone-throwing in Japanese macaques was based on opportunistic observations. In conjunction with focal and group scan sampling (cf. Leca et al., 2007a for further detail on these observational methods), the throwing events were also collected by all occurrence sampling (data set #1 collected by JBL and NG on the 10 troops from August 2003 through February 2005) and ad libitum sampling (data set #2 collected by CADN on the Takh. troop from May 2003 through December 2006; cf. Altmann, 1974). All occurrence sampling (also referred to as 'conspicuous behavior recording' by Martin and Bateson, 1993) was made possible because throwing behavior meets the three criteria set by Altmann (1974): 1) observation conditions are excellent, 2) throwing events are highly 'attention-attracting,' and 3) throwing events never occur too frequently to record.

A *throw* was considered to occur any time an individual picked up a stone from the ground, released it with an active swinging movement of the forelimb, and propelled it through the air in a ballistic motion. The movement of the forelimb differentiates this behavior from dropping, pushing, or kicking down a stone from an off-ground position. Subjects were never encouraged to throw for the purpose of this study, but instead observations were made on spontaneous stone-throwing behaviors.

For each throwing event reported here, the three observers recorded the date, the identity of the thrower, and the throwing variant (throw, throw and jump, throw and sway, or throw and run: cf. Leca et al., 2007a). Regarding data set #1, JBL and NG also systematically recorded whether the individual threw the stone: 1) from a position located on or off the ground; 2) from a tripedal, bipedal, or sitting posture; 3) overhand or underarm; 4) with its left or right hand; 5) forward, backward, upward, or sideways; and 6) at a distance of less than 1 m, 1–3 m, 3–5 m, or greater than 5 m. They also recorded the number of stones thrown and an estimation of their sizes (highest dimension of a stone) according to four size categories: S1 (2–10 mm), S2 (11–50 mm), S3 (50–100 mm), and S4 (more than 100 mm; cf. Leca et al., 2008b). To evaluate the contexts or situations that may elicit the throwing behavior, JBL and NG recorded the activity of the thrower 15 seconds before throwing as well as the occurrence and location of major intra-group and external disturbances (e.g., aggressive interactions, and loud noise, respectively).

In a good proportion of cases (71 out of 83 throwing events, i.e., 85% of the cases), all these data were dictated as verbal comments on video-recorded focal samples, even when the thrower was not the focal subject (cf. Martin and Bateson, 1993). In the remaining cases (12 out 83 throwing events, i.e., 15% of the cases), these data were collected by pen and paper (cf. Leca et al., 2007a for a detailed description of the observation procedure used in the study of SH behaviors). In Table 2, we present information on data set #1 collected in each troop. Regarding data set #2, CADN did not systematically collect the above mentioned data on how the individual threw the stone. Depending on the type of analyses, these data were pooled with data set #1 or not (see below).

Data analysis

We defined the total troop observation time as the total time in hours spent observing each troop, including focal time, scan time, and time spent collecting all occurrence samples and ad libitum data. When multiple observers were present (i.e., during focal and ad libitum sessions), two types of observation time were distinguished and summed. First, observation time during focal sessions was subject-based and calculated by adding up the focal hours the subjects were observed. Second, observation time during ad libitum sessions was observer-based and calculated by adding up the times each observer viewed the subjects. We verified inter-observer reliability using the kappa coefficient of Cohen (1960). Based on individual identities, activities, and interactions, we found $k = 0.92$.

For only some of the study troops (Ara.A, Wak.A, Takh., Kosh., and Ara.E) were all members identifiable. In the troops where individual identities of all members were not known during the observation (JMC, Sho.A, Sho.B, Tak.B, and Tak.C), only subjects that could be reliably recognized, based on obvious morphological criteria retrieved from video records (e.g., scars, broken finger), were used in the analyses requiring individually sampled subjects (Leca et al., 2008a). For the purpose of analyses, we distinguished three age classes, namely "young" (1–3 years), "growing" (4–10 years), and "grown-up" (11 years and greater; Leca et al., 2007b). In each troop, there were individuals belonging to all age and sex classes, with the exception of Ara.A, where the age class labeled as "growing" was missing (Leca et al., 2007b).

Individuals over one year of age were ranked in a dominance hierarchy according to the direction of agonistic interactions. We carried out hierarchical rank order analysis with the aid of Matman, Noldus, a software program that calculates Landau's linearity index

Table 2
Data set #1 collected in the 10 studied troops[a]

Troop	Study period	Troop size	No. subjects sampled in group scans[c]	No. subjects individually sampled[d]	Total troop observation time (hr)	No. SH records	Percentage of individuals observed throwing	Observed frequency of throwing	Expected frequency of throwing
Ara.A	Sep–Dec 2003	18	18 ± 0	18	179.9	43	0	0	1.9
Wak.A	Aug–Nov 2003	19	18 ± 1	19	224.6	345	5	2	2.4
Takh.	Sep–Dec 2003[b]	46	45 ± 1	46	449.2	1,536	24	83	11.9
JMC	Aug 2003–Apr 2004	102	95 ± 6	76	99.1	212	2	2	5.6
Kosh.	Jan–Feb 2004	88	47 ± 13	61	339.7	30	0	0	9.4
Ara.E	May–Aug 2004	141	77 ± 22	132	431.3	1,031	0	0	19.6
Sho.A	Feb 2005	450	227 ± 48	55	77.6	167	0	0	10.4
Sho.B	Feb 2005	350	156 ± 22	54	51.5	97	0	0	4.7
Tak.B	Dec 2003–Jan 2004	438	299 ± 31	74	22.8	134	0	0	4.0
Tak.C	Dec 2003–Jan 2004	676	394 ± 51	172	73.8	573	0	0	17.1
TOTAL		2,328	1,376 ± 195	707	1,949.5	4,168	n/a	87	87.0

[a] Frequency is defined as the total number of occurrences. Expected values are derived from a total of 87 throw events recorded in the 10 troops and weighted by the mean number of scan sampled subjects and the total troop observation time. n/a = not applicable.
[b] Data set #1 only.
[c] Mean values ± SD.
[d] In focal, all occurrence, and ad libitum samples.

(h'), which is corrected for ties and unknown relationships (de Vries et al., 1993). We verified the linearity of the dominance hierarchy for 46 individuals belonging to the Takh. troop (h' = 0.52, directional consistency index = 0.97, $p < 0.001$; cf. de Vries, 1995). We distinguished three classes of individuals according to their dominance rank: high-ranking, middle-ranking, and low-ranking individuals ($n = 15$, 16, and 15, respectively). Based on 354 hours of subject-focal samples collected in the Takh. troop, we calculated the affiliation scores within each of the 1,035 possible dyads by adding up the duration of body contact and the time spent within one meter proximity. According to the affiliation score, we distinguished three types of dyads ($n = 345$ dyads for each type): weakly affiliated dyads (affiliation score: mean ± SD = 0.3 ± 0.4 min), moderately affiliated dyads (3.3 ± 1.5 min), and strongly affiliated dyads (26.0 ± 41.9 min).

Stone handling activity was defined as the manipulation of stones by performing at least one of the 36 behavioral patterns listed in Table 3 (Leca et al., 2007b). We defined five classes of prevalence of SH patterns, namely widespread (when the pattern was observed in more than 50% of individually-sampled troop members), common (between 20 and 50%), scarce (between 5 and 20%), idiosyncratic (between 0 and 5%), and absent (0%). A SH episode collected by focal or ad libitum sampling was referred to as a SH record. Individuals that were observed to throw a stone at least once were categorized as throwers, and those that were never observed to throw a stone were categorized as non-throwers. The activities of the thrower 15 seconds before throwing were ascribed to five categories (after Kortlandt and Kooij, 1963): 1) inactive (resting and grooming), 2) locomotion, 3) stone handling, 4) social or locomotor play, and 5) disturbance-related vigilance.

To characterize hand preference in throwing, we did not use the handedness index (HI) because of its total insensitivity to sample size (cf. McGrew and Marchant, 1997; but see Hopkins et al., 1993, considering that a single observation of throwing per subject is sufficient to evaluate individual hand preferences). Instead, we used binomial tests (two-tailed) at the individual and population levels with a minimum of six data-points—that is, at least six throws per subject to allow subjects to be tested for lateralization, and at least six lateralized subjects to allow populations to be tested for lateralization (cf. McGrew and Marchant, 1997). After such testing, subjects reaching statistical significance were categorized as left- or right-handed, depending on the direction of the difference, and those failing to reach statistical significance were categorized as ambilateral. Subjects with less than six throws were classified as unknown.

We used data set #1 to: conduct inter-troop comparisons; provide quantitative data on throwing postures, directions, and distances; estimate the size of stones thrown; and assess the context of throwing events. We used data sets #1 and 2 to: report the identity of throwers; provide quantitative data on throwing variants, the number of stones thrown, and handedness; and assess throwing dissemination in the Takh. troop. With the exception of a few iterative throws, most throws were not consecutive events, but instead were separated by long periods of time on the order of hours or even days. On temporal grounds, we believe that the occurrence of a throwing event was not likely to bias the chances of the occurrence of another equivalent throwing event. Thus, throwing events could be considered independent data-points, allowing statistical tests based on pooled data to be conducted.

To evaluate the influence of different contexts on the number of throws observed, we conducted a Friedman test followed by multiple paired comparisons based on mean ranks (cf. Siegel and Castellan, 1988). To test the effect of sex and dominance or age on throwing rate, we used Mann-Whitney and Kruskal-Wallis tests, respectively. To test the difference between the observed and expected distributions of throwing frequencies in the study troops, we used a chi-square goodness-of-fit test. We used chi-square tests of independence from contingency tables to test the associations between: 1) throwing distance and throwing direction, posture, or variant; 2) the size of the stones thrown and the size of the stones used in other SH patterns; 3) throwing direction and the location of the disturbance source; and 4) age, sex, and dominance classes and the distribution of throwers and non-throwers. For post-hoc examination of chi-square tests, we calculated the adjusted standardized residuals and considered statistically significant those z-scores that were $\geq |1.96|$. The Yates' correction for continuity was incorporated into chi-square tests. Statistical analyses were performed using the SPSS 12.0 analytical program. Significance levels were set at $\alpha = 0.05$.

Results

Stone-throwing as a troop-specific behavior

When considering data set #1, we found striking inter-troop differences in the frequency of stone-throwing. Throwing events were recorded 83 times in the Takh. troop, whereas the behavior was recorded only twice in the Wak.A troop and twice in the JMC troop. Stone-throwing was never recorded in the other troops. After weighting the data by the number of sampled subjects and

Table 3
Inter-troop differences in the prevalence of the 36 major SH patterns categorized according to general activity patternsn (after Leca et al., 2007b)

Category name	Troop									
	Ara.A	Wak.A	Takh.	JMC	Kosh.	Ara.E	Sho.A	Sho.B	Tak.B	Tak.C
Investigative activities										
Bite	S	W	W	S	S	S	S	I	S	S
Hold/pick	C	W	C	S	S	C	C	S	S	S
Lick	S	W	W	I	I	S	A	A	S	S
Put in mouth	S	W	W	I	A	S	S	S	S	I
Move inside mouth	A	C	C	I	A	I	A	A	I	I
Sniff	S	W	W	S	S	C	I	I	C	C
Locomotion activities										
Carry	A	S	C	S	S	C	C	S	C	C
Carry in mouth	A	C	C	I	A	I	I	I	I	I
Grasp walk	S	C	W	S	I	W	C	S	C	C
Move and push/pull	A	S	C	S	I	S	I	S	I	S
Toss walk	S	S	W	S	A	S	A	A	I	I
Collection (gathering) activities										
Cuddle	C	W	W	S	S	W	C	C	C	C
Gather	S	C	W	I	I	W	C	C	C	C
Grasp with hands	S	W	W	S	S	W	C	C	W	C
Pick up	C	C	W	I	I	W	S	S	C	C
Pick and drop	A	A	C	A	A	I	I	A	S	S
Pike up small stones	A	A	S	A	A	S	A	A	I	S
Complex manipulative activities										
Clack	S	S	C	S	A	A	I	I	S	I
Combine with object	A	C	C	I	A	S	A	I	A	I
Flint	A	C	C	S	A	S	I	S	S	C
Flint/rub/tap in mouth	A	S	S	A	A	A	A	A	A	I
Flip	A	S	C	A	A	I	A	A	I	A
Pound on surface	A	S	C	S	A	I	I	A	A	S
Roll in hands	S	C	W	S	I	C	C	S	C	C
Rub/roll on surface	C	W	W	C	I	C	C	C	C	C
Rub stones together	A	C	C	I	A	W	S	C	C	C
Rub with hands	S	C	W	S	S	C	S	I	S	S
Rub with mouth	A	S	I	A	A	A	A	A	A	A
Scatter	S	C	W	S	I	W	C	C	C	C
Shake in hands	A	A	I	I	A	I	A	I	I	I
Slap	A	A	S	I	A	A	A	A	A	A
Spin	A	A	I	A	A	A	A	A	A	A
Stone groom, put on fur	A	C	S	I	A	I	I	I	A	A
Swipe	A	S	I	A	A	I	A	A	I	S
Throw (all variants)	A	I	C	I	A	A	A	A	A	A
Wash/put in water	A	A	S	I	A	S	A	A	A	A

W = Widespread (pattern observed in more than 50% of individually-sampled troop members); C = Common (20<–≤ 50%); S = Scarce (5<–≤ 20%); I = Idiosyncratic (0<–≤ 5%); A = Absent (0%).

the total observation time in each troop to obtain expected throwing frequencies, we found a statistically significant difference between the observed and expected distributions of throwing frequencies in the 10 study troops (chi-square goodness-of-fit test, $df = 9$, $\chi^2 = 493.7$, $p < 0.001$; cf. Table 2). In the Takh. troop, the observed frequency of throwing was considerably greater than the expected frequency, whereas the reverse was found in the other troops, and particularly in large and/or long-observed troops (Ara.E, Sho.A, and Tak.C).

Interestingly, the Takh. troop also presented the largest number of SH records. It could be argued that the observed frequency of throwing may simply reflect the number of SH records collected in a given troop. Although we could not statistically test this correlation (due to the large number of zero values in the former data set), we found no sign for such a tendency. For example, there was no stone-throwing event in the 1,031 SH records of the Ara.E troop and in the 573 SH records of the Tak.C troop.

We also found major inter-troop differences in the prevalence of stone-throwing in comparison with the other 35 SH patterns reported in Japanese macaques (Table 3). "Throw" is the only SH pattern that is common in one troop (i.e., observed in about a fourth of sampled individuals [Takh.: 11 throwers out of 46 individuals, or 24% of troop members in data set #1, and 14 throwers out of 46 individuals, or 30% of troop members in data sets #1 and 2]), whereas it was idiosyncratic in two other troops (JMC: two throwers out of 102 individuals, or 2% of troop members, and Wak.A: one thrower out of 19 individuals, or 5% of troop members), and absent in most other troops (0% in Ara.A, Kosh., Ara.E, Sho.A, Sho.B, Tak.B, and Tak.C).

By contrast, most other SH patterns were either widespread and/or common in two or more troops (e.g., "sniff": bring a stone near to one's nose and sniff it; "grasp walk": walk with one or more stones in the palm of one or both hands; "cuddle": grab or cradle a stone against the chest; and "roll in hands": roll a stone in one's hands), or scarce and/or idiosyncratic in some troops but absent in the others (e.g., "pick up small stones": pick up small stones and hold them between fingertips; "flint in mouth": strike a stone against another held in mouth; "shake in hands": take stone(s) in one's open palm hand and shake the stone(s) with the hand moving back and forth; and "wash": put a stone in water or pick up a stone from water and rub it with hands). Finally, a few other SH patterns were widespread or common in one troop, and scarce or idiosyncratic in several others (e.g., move and push, clack, pound on surface, and stone groom). These first analyses show that stone-throwing as a common behavioral practice is specific to the Tahk. troop.

Form of the stone-throwing behavior

Throwing styles and postures. With the exception of two throws, all throwing events recorded in the Takh. troop from data set #1 consisted of a stone being picked up from the ground and released with an underarmed shoveling movement of one forelimb. Of 83 throws, only two overhand throwing actions (2.4%) were observed. There was no obvious preparation phase before throwing, defined as the movement of the forelimb up and away from the next throwing direction (cf. Wood et al., 2007).

Despite individual differences, Table 4 shows that most throws were performed from a tripedal posture (75.9%), as opposed to bipedal (21.7%) and sitting postures (2.4%). Only two individuals, a young female and a growing male, maintained a bipedal posture almost as often as a tripedal posture while throwing. The only two overhand throws were performed from a sitting posture. Most throwing events occurred from a position located on the ground (77 out 83 throws, i.e., 92.8%) where the subjects spent about three quarters of their time (72.7% for the Takh. troop: see Leca et al., 2008b).

Four throwing variants. In their comprehensive list of the 45 SH patterns performed by Japanese macaques, Leca et al. (2007a) distinguished four throwing variants. Here, we provide a more detailed description of each of these variants: 1) *throw and jump*: the stone-throwing behavior is accompanied (preceded and/or followed) by repeated vertical leaps performed from a tripedal stance; 2) *throw and sway*: the stone-throwing behavior is accompanied (preceded and/or followed) by a rapid and exaggerated swaying (i.e., standing and shifting body weight from side to side) or tossing (i.e., rocking head and upper torso back and forth in the vertical plane while the hindlimbs remain stationary); 3) *throw and run*: the stone-throwing behavior is accompanied (preceded and/or followed) by a rapid backward running while scattering about other stones or pieces of food present on the ground; and 4) *throw*: throw a stone without jumping, swaying, or running.

The four throwing variants were observed several times in the Takh. troop (Table 4), with a large majority of 'throw and jump' (64.7%

Table 4
Distribution of stone-throwing events and quantification of throwing form in throwers from the Takh. troop according to age, sex, dominance class, and ranked in chronological order of their first observed throwing behavior (date in month/day/year)[a]

Individual	Age (yr)/ sex	Dom. class	First obs.[b]	No. throws[b]	Throwing variant[b]				Throwing posture[c]			Throwing direction[c]				Throwing distance[c] (m)				Handedness[b]		
					TH	TJ	TS	TR	Tp	Bp	Sit	Fw	Bw	Uw	Sw	<1	1–3	3–5	>5	L	R	HP (p)
Sora	16/F	LR	08/04/03	2	0	2	0	0	1	0	0	0	1	0	0	0	0	1	0	0	2	unk
Tsuyu[d]	19/F	HR	09/01/03	9	5	2	0	2	8	0	0	0	6	0	2	0	1	1	6	9	0	LH (.004)
Haiiro	5/M	HR	09/04/03	7	0	4	2	1	5	1	0	1	3	1	1	0	4	1	1	0	6	RH (.031)
Kakoo	3/F	MR	09/10/03	30	14	15	1	0	9	12	0	0	4	11	6	7	10	4	0	3	21	RH (< .001)
Take[d]	15/F	HR	09/10/03	30	1	29	0	0	20	0	0	0	20	0	0	0	0	1	19	0	22	RH (< .001)
Peke	6/M	MR	10/12/03	12	1	9	2	0	7	5	0	2	0	4	6	2	10	0	0	12	0	LH (< .001)
Yama	12/F	HR	10/19/03	1	0	1	0	0	–	–	–	–	–	–	–	–	–	–	–	–	–	unk
Sakura	2/F	MR	10/26/03	9	0	9	0	0	2	0	0	0	0	2	0	1	1	0	0	0	2	unk
Kaede	2/F	LR	10/28/03	2	2	0	0	0	2	0	0	0	0	1	1	2	0	0	0	2	0	unk
Ao[d]	22/M	HR	11/13/03	6	0	6	0	0	5	0	0	0	0	5	0	0	0	5	0	5	0	unk
Mizu	1/M	LR	11/14/03	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	1	0	unk
Taiyo	3/M	MR	12/11/03	2	2	0	0	0	1	0	1	1	0	1	0	1	1	0	0	1	1	unk
Oka	2/M	MR	06/14/04	3	1	0	0	2	–	–	–	–	–	–	–	–	–	–	–	–	1	unk
Kiro	8/M	HR	08/05/04	2	0	0	2	0	–	–	–	–	–	–	–	–	–	–	–	2	0	unk
Uncertain	–	–	–	3	3	0	0	0	3	0	0	0	0	3	0	2	0	1	0	–	–	unk
Total				119	30	77	7	5	63	18	2	4	34	28	17	16	27	14	26	35	55	

[a] TH: throw, TJ: throw and jump, TS: throw and sway, TR: throw and run; Tp: tripedal, Bp: bipedal, Sit: sitting; Fw: forward, Bw: backward, Uw: upward, Sw: sideways; L: number of left-handed throws, R: number of right-handed throws, HP (p): hand preference (and p-value obtained with binomial tests), LH: left-handed, RH: right-handed, unk: unknown.Uncertain: regarding the thrower identity, there was an uncertainty between two individuals but some elements of the throwing behavior could be recorded.
[b] Data sets #1 and 2.
[c] Data set #1 only.
[d] Individual who was observed throwing before but the exact date is not available.

of the 119 throwing events collected in data sets #1 and 2), and to a lesser extent, 'throw' (25.2%). The variants 'throw and sway' and 'throw and run' were notably less frequent at 5.9% and 4.2%, respectively. Six members of the Takh. troop performed at least two different throwing variants, and among them, four individuals displayed three different throwing variants. In contrast, only the simple 'throw' variant was performed in the two throwing events recorded in the Wak.A troop. Out of the two throwing events recorded in JMC, one 'throw' and one 'throw and run' were displayed.

Ballistic motion and stones thrown. The stones thrown were propelled through the air according to four different directions: forward, backward, upward, or sideways (Table 4). A stone thrown forward or backward was released more or less horizontally or followed a slightly curved trajectory. A stone thrown upward was released more or less vertically (i.e., at about a 45 degree angle or greater), whereas a stone thrown sideways was released at about a 45 degree angle or less. Three quarters of throws were directed backward (41.0% of the 83 throwing events collected in data set #1) or upward (33.7%), whereas only one quarter of throws were displayed sideways (20.5%) or forward (4.8%). When a stone was thrown backward, it seemed to be propelled with greater velocity and force than when thrown forward, upward, or sideways.

Throwing distances ranged from about half a meter ($n = 16$ throws) to approximately 15 meters ($n = 12$). To test whether throwing distance was related to throwing direction, posture, or variant, we conducted chi-square tests of independence based on contingency tables representing the frequency of throws at distances of less than 1 m, 1–3 m, 3–5 m, or greater than 5 m among 1) backward throws versus throws in other directions; 2) throws performed from a tripedal posture versus throws performed from bipedal and sitting postures; and 3) throws accompanied by jumps, swaying, and running versus simple throws. We found a significant association between throwing direction and throwing distance ($n = 83$ throws, $\chi^2 = 60.9$, $df = 3$, $p < 0.001$). As suggested above, post-hoc examination of adjusted standardized residuals showed that backward throws were associated with significantly longer distance projections (more than 5 m) than throws performed in other directions.

We also found a significant association between throwing posture and throwing distance ($\chi^2 = 25.8$, $df = 3$, $p < 0.001$), with longer throws performed from a tripedal posture than from bipedal and sitting postures. Finally, throwing variant and throwing distance were significantly linked ($\chi^2 = 10.2$, $df = 3$, $p = 0.017$), with throws accompanied by jumps, swaying, and running associated with longer distance projections than simple throws.

Out of the 119 throwing events collected in data sets #1 and 2, one stone was thrown in 113 throws (95.0%) and two stones were thrown in 6 throws (5.0%). In the latter, the two stones were thrown iteratively during two successive throwing events. We compared the size of the stones thrown with the size of the stones used in some of the most representative SH patterns in the Takh. troop (cf. Leca et al., 2008b) and drawn from a same-sized data subset. The stones thrown were significantly bigger than the stones used to perform the following SH patterns: "cuddle" ($n = 83$ throws, $\chi^2 = 35.6$, $df = 3$, $p < 0.001$); "grasp with hands" ($\chi^2 = 41.2$, $df = 3$, $p < 0.001$); "roll in hands" ($\chi^2 = 44.5$, $df = 3$, $p < 0.001$); "rub/roll on surface" ($\chi^2 = 49.9$, $df = 3$, $p < 0.001$); and "sniff" ($\chi^2 = 29.3$, $df = 3$, $p < 0.001$). Post-hoc examination of adjusted standardized residuals showed that S3 stones were more often thrown than used during these SH patterns, whereas S2 stones were more often used in these SH patterns than thrown.

Handedness. In all throwing events, only one hand was used. No two-handed throws were observed. Among the five throwers for which hand preferences could be statistically evaluated, two individuals were categorized as left-handed (moreover, both were always left-handed, i.e., they used their left hand for 100% of throws) and three individuals were categorized as right-handed (among which two were always right-handed). There were no ambilateral subjects (Table 4). With only five lateralized subjects the troop could not be statistically tested for lateralization. However, an overall comparison of the distributions of left-handed versus right-handed throws was not consistent with a clear group-level handedness. When throwing from a bipedal posture, right-handed throws were twice as many as left-handed throws (12 versus 6 throws, respectively), but this difference was not statistically significant (binomial test, $p = 0.238$, two-tailed).

Stone-throwing as a display behavior

Context of throwing. We found a statistically significant effect of the context on the throwing frequency (Friedman test, $n = 12$, $df = 4$, $\chi^2 = 12.9$, $p = 0.012$). Multiple paired comparisons based on mean ranks showed that an individual was significantly more likely to throw a stone immediately after being engaged in disturbance-related vigilance activity than after being engaged in resting/grooming, locomoting, and stone handling activities ($p < 0.05$). Figure 1 shows that throwing was also more frequent under vigilance circumstances than in playing contexts, although the latter difference did not reach statistical significance ($p > 0.05$).

Despite individual behavioral differences, stone-throwing was seemingly performed as part of a response to various sources of disturbance, including loud noise produced by Japanese military aircrafts flying very low over the Primate Research Institute in practice maneuvers, and intra-group aggressive interactions. Under such circumstances, the thrower showed obvious signs of excitement. However, stone-throwing was never accompanied by vocalizations and never recorded in individuals directly involved in an aggressive interaction (i.e., the initiator or the recipient of an aggression).

Unaimed throwing. Several elements drawn from the observations support the view that stone-throwing in the Takh. troop was unaimed in the sense that stones were not thrown directionally: 1) the stone was generally not propelled in the direction of what may be perceived to be a potential danger: there was no significant association between throwing direction (upward versus roughly horizontal [i.e., forward, backward, and sideways]) and the general location of the disturbance source (above the ground [i.e., aircrafts] versus on the ground [i.e., aggressive interactions]) ($n = 39$ throws associated with external disturbances, $\chi^2 = 0.2$, $df = 1$, $p = 0.863$); 2) the percentage of forward throws was small (4.8%); 3) the thrower generally threw a stone from the spot where the stone was picked up, and was not often observed carrying a stone from one place to another before using it for throwing; 4) there was no apparent preparation phase and the thrower seldom looked up or back at a possible target before or after throwing (Leca, pers. observ.); and 5) no thrown stones ever hit a monkey.

Intra-group diffusion of the stone-throwing tradition

Age, sex, and social status of the throwers. There was no significant effect of age, sex, and dominance classes on the distribution of throwers and non-throwers in the Takh. troop (N = 46 individuals, age: $\chi^2 = 1.2$, $df = 2$, $p = 0.551$; sex: $\chi^2 = 1.5$, $df = 1$, $p = 0.379$; dominance: $\chi^2 = 1.4$, $df = 2$, $p = 0.490$). Although the number of throwing events observed per subject ranged from 1 to 30, the 14 throwers recorded in the Takh. troop belonged to all classes, males or females, low-, middle- or high-ranks, and were from one to 22 years of age (Table 4). Therefore, stone-throwing was not limited to particular individuals based on these life history features or social status.

Despite striking individual differences in the frequency of throwing events, this frequency was not significantly affected by the age and sex of throwers (age: Kruskal-Wallis test, $\chi^2 = 0.3$, $df = 2$, $p = 0.861$; sex: Mann-Whitney test, $z = -0.778$, $p = 0.456$). Although throwing frequencies in middle- and high-ranking individuals (mean ± SD = 11.2 ± 11.3 and 9.2 ± 10.6, respectively) were higher than in low-ranking individuals (1.7 ± 0.6), this difference did not reach statistical significance (Kruskal-Wallis test, $\chi^2 = 4.0$, $df = 2$, $p = 0.133$).

Propagation over time of the throwing behavior. The exact date and circumstances of appearance of the stone-throwing behavior in the Takh. troop are unknown. Based on 492 hours of data collected in this troop during another study conducted from July 2002 through July 2003, throwing events were very rare and only observed in very few older-aged individuals: Take (13–15 years), Tsuyu (17–19 years), and Ao (20–22 years; Rizaldi, pers. comm.). According to the 137 hours of observation done by CADN between May and July 2003, stone-throwing was not observed in the other troop members before August 4th, 2003. Table 4 shows the extent and chronology of observed propagation of the throwing behavior from this date.

Within a 12-month period, stone-throwing had been acquired by 11 more troop members in other age classes. Even if we do not consider the three individuals who were observed throwing before August 2003, the acquisition of the behavior seemed to occur within strongly affiliated dyads, and in fits and starts (i.e., at least two new stone-throwers could be recorded during short periods of time punctuated with longer periods during which no new thrower was recorded). For instance, Haiiro and Kakoo, as well as Peke and Yama, who had relatively high affiliation scores (36.4 and 23.6 min, respectively), were first observed throwing during the same week, respectively. Sakura and Kaede, who were peer playmates (affiliation score = 36.9 min), were first observed throwing within a two-day period. Moreover, the performance of the rare 'throw and run' variant by a mother (Tsuyu) and her offspring (Oka, affiliation score = 35.7 min) is suggestive of vertical transmission. Finally, stone-throwing appears to be a long-enduring SH variant that was still maintained in the Takh. troop in 2007 (Nahallage, pers. observ.).

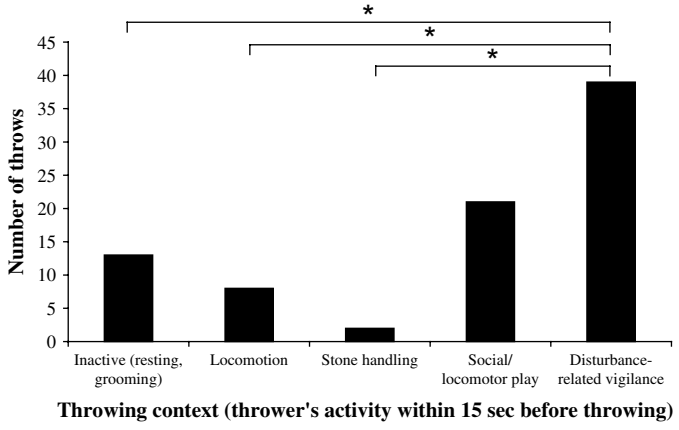

Fig. 1. Effect of the context on the number of stone-throwing events recorded in Takh. (*: $p < 0.05$).

Discussion

Our descriptive and quantitative data on the form and contexts of stone-throwing in Japanese macaques show that throws were mainly underarm, performed on the ground from a tripedal posture, and often accompanied by repeated vertical leaps. Generally, one relatively big (50–100 mm) stone was thrown at a time, and preferentially projected backward or upward and to heights of 15 meters. We found marked individual hand preferences for throwing, but no consistent handedness at the group level. Although there was no evidence for aimed throwing, stone-throwing events were more likely to occur during periods of disturbance than in other contexts, and throws were probably performed as part of a display sequence.

Even though a larger sample size would allow further analyses at the individual level, our data suggest that stone-throwing in Japanese macaques meets several criteria which represent evidence for a behavioral tradition (cf. Perry and Manson, 2003): 1) based on the

lack of previous reports on spontaneous stone-throwing in a social group of Japanese macaques and according to the present comparative evidence, we consider this behavior to be specific to the captive Takahama troop housed at the Kyoto University Primate Research Institute, although it is ecologically possible at other sites (cf. Leca et al., 2008b); 2) there were individual preferences in some of the four stone-throwing variants (i.e., similar behaviors with minor alterations in their form; 3) stone-throwing is conspicuous and attention getting, and naïve individuals are likely to have intently observed others performing the behavior before first exhibiting it themselves; 4) the behavior was observed to spread within the group from one age class to another (here vertically from older to young); 5) the transmission of the behavior seems to be socially-mediated since its dissemination happened in accordance with links via maternal kinship and social proximity; and 6) stone-throwing behavior has been maintained in the Takahama troop over a number of years and has even passed from one generation to the next. It should be noted that evidence for the last three criteria were based on case studies of few individuals rather than systematic analysis.

With regards to the form of stone-throwing, our results support the hypotheses relating body posture, throwing style, and handedness in throwing (Calvin, 1983; Fifer, 1987; Knüsel, 1992; Hopkins et al., 2005). Like most non-human primates reported to throw objects, and particularly other terrestrial cercopithecines, such as chacma baboons (*Papio ursinus*: Hamilton et al., 1975), Japanese macaques mainly exhibited underarm throwing from a tripedal posture. When a tripedal monkey performs stone-throwing, the hand is placed on the stone palm down and the stone can be tossed in different directions (mainly backward in our case). From a structural point of view, such underarm scooping is an action very close to "normal locomotion," being only a minor change from the usual swing of the limb in walking (Washburn and Jay, 1967). During the throwing action, there is little movement at the shoulder, the propulsive force being generated mainly by the hand, wrist, and forelimb. According to Washburn and Jay (1967), overhand throwing is impossible for most primates because they maintain a tripedal rather than a bipedal posture. Interestingly, we found that occasional overhand throws from an erect stance can occur in Japanese macaques. Likewise, in chimpanzees, body posture was related to throwing style, with most subjects standing bipedally while throwing overhand, whereas most underarm throws occurred from a tripedal stance (Hopkins et al., 2005).

The marked individual hand preferences for unaimed throwing found in this study are consistent with those reported in three Japanese macaques trained to throw stones directionally into a pipe to obtain food as part of an instrumental conditioning experiment (Tanaka et al., 2001). Strong individual hand preferences for aimed stone-throwing were also found in capuchins (Westergaard and Suomi, 1994, 1995), chimpanzees (Hopkins et al., 1993), and humans (Calvin, 1983). Our results on the lack of clear group-level handedness in Japanese macaques are in agreement with those obtained in capuchins and chimpanzees (Westergaard et al., 2000; McGrew and Marchant, 2001). In contrast, the strong right-hand bias found in human populations is often explained by the specialization of the left brain for the sequential-movement skills needed to finely control facial and hand muscles used in language and throwing, respectively (Calvin, 1983; Annett, 2002; Hopkins et al., 2005).

Regarding the functional aspects of the behavior, throwing objects randomly as part of an agonistic display is considered the most common tool-use in non-human primates according to Beck's (1980) definition. As predicted by Huffman (1996), and unlike most other SH patterns performed by Japanese macaques, unaimed stone-throwing observed in the Takahama troop during periods of disturbance and in conjunction with agonistic signals typical of this species (e.g., bouncing or swaying; cf. Modahl and Eaton, 1977) can be regarded as a spontaneous tool-using behavior. Although it is difficult to quantify the outcome of stone-throwing performances during agonistic displays (in terms of intimidation effectiveness or dominance assertion), we consider two direct benefits. First, due to the sight of a stone propelled through the air and the sound generated by a stone hitting against the concrete surfaces of the enclosure walls and floor, the stone thrown can be characterized as a "technological amplifier" (cf. Guilmet, 1977) or bimodal (visual and auditory) extension of the non-vocal display. As suggested for capuchins and chimpanzees (Nishida et al., 1999; Moura, 2007), the incorporation of stones into agonistic display is likely to be an effective means of capturing the attention of an otherwise inattentive social audience and augmenting the effect of the behavior. Second, since stone-throwing is often part of display sequences, there is little doubt that this behavior is "emotionally loaded" (Boesch and Boesch, 1981) and an expression of general excitement that may serve as a mechanism of tension reduction linked to disturbances.

There are at least two other possible explanations for this behavior. First, as observed in young chimpanzees (Goodall, 1986), our data suggest that stone-throwing by young members of the Takahama troop may serve to initiate social play by attracting the attention of peer playmates (but see Shimada, 2006). Second, when no obvious context (i.e., resting or grooming) could be reliably related to stone-throwing, we cannot rule out the possibility that the monkeys may simply enjoy performing this behavior and the sound associated with it. The idea of throwing as a pleasurable activity in animals and humans has often been discussed (Darlington, 1975; Calvin, 1983). Although pleasure is difficult to isolate and measure, the possible emotional process involved in throwing behavior may have physiological, hormonal, or neurological correlates that can reasonably be considered reinforcing components of the behavior. We currently have no additional data that would further support the latter interpretations. Nevertheless, all these explanations of stone-throwing are not mutually exclusive. As suggested by the cross-site observations of the leaf-clipping behavior in chimpanzees, the same behavior can have different functions depending on the context in which it is performed in different groups (Nishida, 1980; Boesch, 1995, 1996).

Although we did not find obvious behavioral patterns of stone-selection before throwing, the apparent preference for relatively large stones for throwing (as opposed to other typical SH patterns) is congruent with the tendency of stone-tool selectivity previously suggested in Japanese macaques (Weinberg and Candland, 1981; Tanaka et al., 2001). The preferential use of large stones for throwing or banging has also been observed in brown capuchins, chacma baboons, and chimpanzees (Hamilton et al., 1975; Nishida et al., 1999; Moura, 2007). The ability to categorize stone-tools according to their physical characteristics and functional properties has been attributed to several non-human primate species (Boesch and Boesch, 1983; Cleveland et al., 2003; Evans and Westergaard, 2004). Whether the stones used are modified or not (like in percussive or throwing behaviors, respectively), stone-selectivity is widespread among animals, and may be regarded as the first evolutionary steps to primate tool-making in general, and hominid stone-technology in particular (cf. Kortlandt and Kooij, 1963; Isaac, 1987; McGrew, 1992; Mercader et al., 2007).

Although throwing behavior is a component of the Japanese macaque repertoire (Torigoe, 1987), spontaneous throwing is generally not reported, even in studies focusing on object manipulation and social play in this species (e.g., Menzel, 1966; Shimada, 2006). In the rare reports of throwing in Japanese macaques, this behavior was either idiosyncratic or its performance was restricted to a very few group members. In another semi-free ranging Oregon troop, a male incorporated unaimed throwing of stones into his courtship displays, but stone-throwing never spread to other individuals (Eaton, 1972). Despite the invention by a female

Japanese macaque of the stone-throwing technique as a food-getting solution in an instrumental task, the behavior spread to only four group members during the following years (Tanaka et al., 2001). In contrast, stone-throwing in the Takahama troop was largely distributed among group members of all classes rather than exclusively restricted to a particular subset of the group (e.g., dominant adult males or juveniles).

How can we explain the specificity of stone-throwing prevalence in the Takahama troop, as opposed to the absence—or idiosyncratic presence—of this behavior in other troops of Japanese macaques? Among environmental factors, stone availability and food provisioning are not likely to account for such a difference (cf. Leca et al., 2008a,b). Instead, the existence of a group-specific stone-throwing tradition may reflect possible inter-troop variation in 1) the likelihood of behavioral innovations, 2) the social constraints on the early dissemination and long-term maintenance of such inventions, and 3) appropriate social and/or environmental reinforcement for continued practice and spread of an innovation (cf. Huffman and Hirata, 2003).

First, it is acknowledged that captive conditions may provide the monkeys with more free time than free-ranging conditions. More time available could lead to more opportunities for the exploration of stone by individuals, which in turn may result in a greater diversity in SH patterns, some potentially implanted in tool-use (Huffman and Quiatt, 1986). This interpretation is supported by the present results showing that the three troops in which stone-throwing was observed at least once were housed in captive settings, and previous findings showing that the troop with the highest rates of stone-throwing, namely the Takahama troop, was also the troop exhibiting the most diverse SH repertoire (Leca et al., 2007a). The performance of bouncing, swaying, or tossing patterns as behavioral responses to external disturbances was observed in several captive troops of Japanese and rhesus macaques (Modahl and Eaton, 1977; Nahallage, pers. observ.). Such forms of display seem to be common traits to these two macaque species. However, our results suggest that, although stones are available in all of these troops, they seem only to be incorporated into agonistic displays by troops in which SH is already an established behavioral tradition.

Second, chance may account for a good number of behavioral innovations (Reader and Laland, 2003). Thus, the following is a reasonable scenario: since a Takahama troop member spends, on average, more time with stones in its hands than a member of other captive troops (Leca et al., 2007a), it is more likely to have at least once accidentally released and propelled a stone through the air during an agonistic interaction or a playing episode. When stones are thrown, individuals in the line of trajectory will often move aside to avoid being inadvertently hit (Nahallage, pers. observ.). This reaction of others to stone-throwing, if recognized by the displayer, may encourage it to repeat the behavior for the same effect in the future. This would in turn make this individual likely to become a stone-throwing initiator for others.

Third, although social influence on the dissemination of stone-throwing was not quantified in this study, it is possible to imagine that, once invented, social conditions particular to the Takahama troop, such as a relatively relaxed dominance style, may have allowed numerous group members to perform stone-throwing even when higher-ranking individuals were nearby. With more available stone-throwing demonstrators, naïve individuals were likely to have more opportunities to observe and learn the novel behavior, thereby facilitating its spread within the group. On the other hand, previous findings suggest that when a behavioral practice is restricted to very few group members or individuals with a particular social status, the behavior is likely to disappear at the group level (Candland et al., 1978; Nishida et al., 1999; Leca et al., 2007c). Because younger individuals have been observed to integrate throwing into playful stone handling contexts, it is likely to spread more widely within the group. Unfortunately, since we did not witness the appearance and initial dissemination of the stone-throwing behavior, we can only speculate about the emergence of the stone-throwing tradition. Further investigation, including experimentally-elicited stone-throwing, may help to determine the learning process by which this behavior is transmitted within the group.

To our knowledge, this is the first study to report a stone-tool-use tradition in Japanese macaques, and to address a single type of behavior in a non-human primate species, by taking a multi-troop comparative approach, presenting analyses borrowed from physical anthropology (in terms of motor patterns, body postures, handedness, and ballistic motion), exploring a psychological perspective (motivational aspects of throwing behavior), and discussing a longitudinal view (dissemination over time of the throwing tradition). Overall, our findings are consistent with the comparative data using modern non-human primate species to model the structural processes and functional aspects of throwing evolution in early hominids.

Our results and interpretations also support the view that tool-use evolves in stages from initially non-functional behaviors, such as object play (Beck, 1980; Huffman and Quiatt, 1986), a categorization that perfectly suits the SH activity (Huffman, 1984). Food provisioning and captivity have relaxed selective pressures on foraging and created favorable environmental conditions under which SH may simply serve the function of maintaining in some populations a set of behaviors that could evolve into tool-use in a different environment. As an unselected but eventually beneficial trait, the SH tradition would be an exaptation (cf. Gould and Vrba, 1982). Given the lack of information on spontaneous use of stone-tools by macaques (Beck, 1980; but see Malaivijitnond et al., 2007), this report is of direct relevance to questions regarding the evolution of stone technology in hominids.

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