# Mechanisms of expression of object play: A comparative study of stone handling in two captive groups of long-tailed macaques (*Macaca fascicularis fascicularis*)

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**Keywords:** *Macaca fascicularis*; material culture; solitary object play; stone handling

**Abstract**

Stone handling (SH) is a form of solitary object play that is socially learned and culturally maintained. We studied two captive groups (Modena, N = 20; Padova, N = 20) of common long-tailed macaques housed in a sanctuary in Italy. Our research goal was two-fold: (1) establish the first SH repertoire in captive-raised long-tailed macaques, and (2) explain major differences in the expression of SH between the two study groups. Despite being of identical size and sharing similar environmental conditions, we found that SH was performed by most group members in Modena, whereas SH was absent in Padova. We aimed to explain this inter-group variation by exploring the role of proximate factors that are known to affect the occurrence of SH: demography, dominance, stone availability, activity budget, and food provisioning. The atypical age structure of Padova (i.e., no immature individuals) may have impaired the emergence of SH in this group. In Modena, we found no significant effect of hierarchical rank on SH frequency and duration and no temporal relationship between SH and feeding. Regarding the activity budget, SH filled in for a portion of affiliative and resting behaviours in Modena. Our findings lend support to the cultural nature of SH.

**Keywords:** *Macaca fascicularis*; material culture; solitary object play; stone handling

## 1. Introduction

Stone handling (SH) is a form of solitary object play that is acquired via social means and culturally maintained in its daily performance (Huffman, 1984; Leca et al., 2010a; Nahallage and Huffman, 2007a). SH was observed for the first time more than 40 years ago in a free-ranging group of Japanese macaques (*Macaca fuscata*) at Arashiyama-Kyoto, Japan (Huffman, 1984). Since then, SH has been identified and reported in three other macaque species in captive and free-ranging settings: Rhesus macaques (*Macaca mulatta*), long-tailed macaques (*Macaca fascicularis*), and Taiwanese macaques (*Macaca cyclopis*) (Nahallage et al., 2016). Recently, SH has been reported in a captive group of gelada baboons (*Theropithecus gelada*; Cangiano et al., 2020) and in captive otters (*Lutrogale perspicillata* and *Aonyx cinereus;* Allison et al., 2020; Bandini et al., 2021).

SH behaviour consists of the non-instrumental manipulation of stones. Stone handlers perform various behavioural patterns, such as gathering stones into a pile, rubbing stones together, or repeatedly pounding a stone on a substrate. Arising as a behavioural innovation by a particular juvenile female Japanese macaque in 1979 at Arashiyama (Huffman, 1984), SH spread horizontally among immature peer playmates within a few years, and then when the female members of this cohort became mothers, the behaviour was transmitted vertically to their infants, and so on across generations (Huffman and Quiatt, 1986). SH is now considered one of the longest-studied culturally-mediated object play behaviours in non-human primates, at both proximate and ultimate levels of causation (Leca et al., 2012; Nahallage et al., 2016).

Cross-species comparative studies of SH within the genus *Macaca* showed similarities and differences in SH repertoires (Nahallage and Huffman, 2008a; 2012; Pelletier et al., 2017). The behavioural repertoires of two captive macaque groups (rhesus and Japanese macaques) housed under similar conditions were identical except one SH behavioural pattern was not reported in Japanese macaques, and this minor difference was brought about by a slight difference in the climbing structures available to each group (Nahallage and Huffman 2008a). Moreover, inter- and intra-group variation in SH behavioural patterns were charted in Japanese macaques, demonstrating that within the same species, a given object play activity, and even some of its behavioural variants, can be customary in certain populations and rare or even absent in others, although they are ecologically possible (Leca et al., 2007a; Nahallage et al., 2016). These comparisons of SH repertoires in macaques are consistent with the view that an interactive triad of phylogenetic, environmental, and social factors can contribute to cultural variation (Huffman and Hirata, 2003).

In Japanese macaques, inter-group comparative studies focusing on major socio-demographic and ecological factors (e.g., group size, age structure, dominance, observational learning, stone availability, activity budget, and food provisioning) produced several results that are relevant to the present research. First, group size was positively correlated with the proportion of individuals exhibiting SH simultaneously (Leca et al., 2007b). Second, groups with an atypical age structure (i.e., missing age class) showed a lower proportion of stone handlers and a lower frequency of SH than groups in which all age classes were present (Leca et al., 2007b). Third, even though SH was mainly practiced by young individuals, it continued to be exhibited well into adulthood, making SH one of the very few forms of object play behaviour to be routinely performed by adult individuals (Huffman, 1984; Leca et al., 2007b, 2011). Fourth, in most groups studied, SH bouts were more frequent but shorter in immature than in adult individuals (Leca et al., 2007b; Nahallage and Huffman, 2007b). Fifth, the SH behavioural patterns performed by mature individuals (aged 7 years and over) were structurally more complex than those performed by immature individuals (up to 6 years) (Leca et al., 2007b). Sixth, on average, aging individuals (16 years or more) performed less diverse, less bimanual, and less coordinated SH behavioural patterns than younger individuals (up to 15 years; Leca et al., 2007b, 2011; Nahallage and Huffman, 2007b). Seventh, there was a positive correlation between geographic proximity among groups with overlapping home ranges and their cultural similarity in SH repertoires, measured by the number of SH behavioural patterns showing similar frequencies at the group level; this phenomenon labelled "cultural zones" may be attributed to inter-group observational learning or inter-group transfer of males (Leca et al., 2007a). Eighth, even though SH is almost exclusively a terrestrial activity, site-specific stone availability was not significantly associated with inter-group differences in SH frequency, which suggests that the motivational processes underlying SH activity are more diverse and more complex than the mere environmental opportunity of encountering stones on the ground (Leca et al., 2008b). Ninth, SH has never been reported in non-provisioned populations of macaques. Indeed, this activity probably emerged as a behavioural by-product of free time and relaxed selective pressure on foraging afforded by food provisioning in free-ranging and captive groups (Huffman, 1984; Leca et al., 2008a). In captive groups of Japanese macaques, SH occurred throughout the day, regardless of the food provisioning schedule; however, in free-ranging and frequently provisioned groups such as Arashiyama and Takasakiyama, there was a clear temporal connection between food provisioning and SH. Most SH activity occurred during the 30-minute post-provisioning period – which led researchers to argue that, in these environmental circumstances, handling stones may be an extension of foraging-like behaviours, a continuation of manipulatory actions while chewing provisioned food (Huffman and Quiatt 1986; Leca et al., 2008a).

Moreover, in the free-ranging and provisioned group of Japanese macaques living at Arashiyama, a preliminary analysis showed a negative correlation between hierarchical rank and SH frequency: the most frequent stone handlers tended to be lower-ranking individuals (Nishie, 2002). Thus, it was suggested that SH could be proximately triggered, during the post-provisioning period, by an emotional conflict between an unsatisfied feeding drive and the motivation to avoid aggressive interactions on the feeding ground, particularly in subordinate individuals (Nishie, 2002). If this interpretation is correct, then SH in free-ranging, crowded, and provisioned groups of Japanese macaques, in which food competition is intense, could be viewed as a displacement activity or a stress-coping behavioural strategy taking the form of a culturally-maintained and outwardly playful object manipulation. However, in partial contrast to this view, a long-term study of a captive group of Japanese macaques showed that stressful situations (e.g., intra-group aggressive interactions, human interventions, cold temperatures), rather than high hierarchical status, were associated with a significant decrease in SH frequency (Nahallage and Huffman, 2008b). Therefore, the putative relationship between dominance and SH, possibly mediated by stressful environmental conditions, is not fully understood.

Within the genus *Macaca*, Japanese macaques and rhesus macaques exhibit the highest degree of nepotism and have the most asymmetrical aggressive interactions (grade 1 according to Thierry et al., 2000), whereas long-tailed macaques are considered a slightly less despotic species (grade 2 according to Thierry et al., 2000). However, long-tailed macaques are still more despotic than those species ranked as grade 3 or 4 on Thierry's scale, which have much more relaxed dominance hierarchies. It is noteworthy that SH has not been reported in grade 3 or grade 4 macaques. From this perspective, social structure, and particularly dominance, should be taken into account, when exploring the proximate causes underlying the expression of SH in macaques. In sum, research on the proximate and ultimate causes of SH in Japanese macaques has benefitted from longitudinal and inter-group comparative studies conducted both in captive settings and in more natural, even though human-influenced, environmental conditions.

More recently, the SH ethogram of a free-ranging and provisioned population of common long-tailed macaques (*Macaca fascicularis fascicularis*), living in Ubud, Bali, Indonesia, has been reported, with a total of 38 SH behavioural patterns (Cenni et al., 2021; Pelletier et al., 2017). Like in Japanese macaques, SH in Balinese long-tailed macaques appears to be a socially influenced, structurally complex, and playfully motivated manipulative activity, hypothetically linked to the foraging behaviour system, and with an exaptive potential of being co-opted into stone tool use (Cenni et al., 2020, 2021; Leca and Gunst, in review; Pelletier et al., 2017; Pellis et al., 2019). The long-tailed macaque is thus an excellent candidate species to explore the putative relationships between playful and instrumental manipulation of stones because the behavioural variability associated with the performance of SH may be a predictor for the emergence of stone tool use in *Macaca fascicularis* (Cenni et al., 2020, in press; Leca & Gunst, in review).

Such a research endeavour may be facilitated by investigating the proximate causes of SH in the controlled conditions of captive settings. However, to date, there are no studies of SH in long-tailed macaques that were born and raised in captivity. The overarching goal of the present study was to contribute to the existing database of SH in *Macaca fascicularis*, by examining the origins and mechanisms of expression of SH behaviour in captive common long-tailed macaques. In 2019, V.A. started studying two groups of captive common long-tailed macaques of identical sizes but contrasting age structures, both housed in similar enclosures at a sanctuary in Semproniano, Italy. V.A. noticed the occurrence of SH in one, but not the other group, even though other forms of object-directed play were present in both groups. Our research objective was two-fold. We first aimed to provide the first descriptive report of SH displayed by captive individuals, that never lived in a natural habitat. To do so, we used and adapted the existing SH ethogram in this species (Cenni et al., 2021; Pelletier et al., 2017). We then sought to explain one of the main inter-group behavioural differences: the occurrence versus absence of SH by exploring the roles of two endogenous factors (i.e., demography and dominance) and three exogenous factors (i.e., stone availability, activity budget, and food provisioning) that are known to affect the emergence, social diffusion, daily expression, maintenance, and transformation of this cultural behaviour (Cenni et al., 2021; Huffman, 1984; Huffman and Quiatt, 1986; Leca et al., 2007a,b, 2008a,b; Nahallage et al., 2016; Pelletier et al., 2017).

We tested five hypotheses that each corresponded to one of these five factors (Table 1). First, the "Demography and SH" hypothesis (after Leca et al., 2007b; Nahallage and Huffman, 2012) holds that (1) the age structure of the group affects the innovation and early stages of the social diffusion of the behaviour, which typically occur among immature individuals, and (2) there are age-specific effects on the frequency and form of SH (Hypothesis 1). As per the first part of this hypothesis, we predicted a more multi-layered demographic structure in the group in which SH occurred and a more atypical demographic structure – with missing age classes, particularly the immature class – in the group in which SH was absent (Prediction 1a). In line with previous research on age-related differences in SH (Leca et al., 2007b, 2011; Nahallage and Huffman, 2007b), we also predicted, in the group in which SH occurred, more frequent (Prediction 1b) but shorter (Prediction 1c) SH bouts in immature than in mature subjects. Finally, we predicted less diverse (Prediction 1d) but more complex (Prediction 1e) SH behavioural patterns in mature than in immature subjects.

Second, the "Dominance and SH" hypothesis (after Nishie, 2002) holds that hierarchical rank affects SH frequency and duration via a stress-coping mechanism (Hypothesis 2). We predicted a negative correlation between hierarchical rank and SH frequency (Prediction 2a), and a negative correlation between hierarchical rank and SH duration (Prediction 2b). Third, the "Stone availability and SH" hypothesis (after Leca et al., 2008b) holds that, if loose stones are present on the ground, group-specific SH frequency is not strictly determined by local availability of stones (Hypothesis 3). To test this hypothesis, we assessed whether the difference between the SH and non-SH groups was associated with a significant variation in local stone availability. Fourth, the "Activity budget and SH" hypothesis (after Leca et al., 2008a) holds that SH is a form of solitary object play that tends to fill in for essential activities (e.g., foraging, social interactions, resting) when free time under relaxed selective pressures are afforded by food provisioning in captive settings (Hypothesis 4). We predicted higher rates of foraging (Prediction 4a), social (i.e., aggressive and affiliative interactions; Prediction 4b), and resting activities (Prediction 4c) in the non-SH group than in the SH group. Fifth, the "Food provisioning and SH" hypothesis (after Leca et al., 2008a) holds that, in captive groups of macaques, there is no clear temporal connection between SH and food provisioning (Hypothesis 5). We predicted that SH would occur throughout the day, regardless of the food provisioning schedule (Prediction 5a) and the monkeys' feeding activity (Prediction 5b).

## 2. Material and methods

### *2.1. Statement of ethics*

This project followed the protocols approved by the European Parliament and Council's Directive 2010/63/EU of 22 September 2010 on the protection of animals used for scientific purposes. It also followed the institutional guidelines for the care and management of primates established by the International Primatological Society and the LAV Onlus.

*2.2. Study subjects and housing conditions*

We studied two groups of common long-tailed macaques (*Macaca fascicularis fascicularis*) (see Appendix A) that have been housed in a sanctuary for exotic animals in Semproniano, Italy, since 2016 (Modena) and 2017 (Padova). Prior to their arrival at the study site, the members of both groups had similar histories and backgrounds associated with comparable laboratory conditions. They were all born and raised in captivity. The subjects born before 2015 were caged in small groups comprised of a few individuals. As far as we know, the subjects did not have access to outside enclosures with loose stones on the ground, nor did they benefit from a standardized environmental enrichment. The subjects were kept in different laboratories for biomedical purpose, but none was involved in medical trials and invasive procedures.

The first group, named "Modena", was comprised of 20 individuals of various age and sex classes, including three old juvenile males (aged 4 years) and two adolescent females (aged 4) that were born in the sanctuary, as well as seven young adult males (aged 7 and 8), three young adult females (aged 7 to 9), two middle-aged adult females (aged 11 and 15), one old adult male and two old adult females (aged 20 to 22) that were born in the laboratory (for age classes in macaques, including long-tailed macaques, see Brotcorne et al., 2015; Cenni et al., in review; Leca et al., 2007b). The second group, named "Padova", also totalled 20 individuals, but had a significantly less diverse age structure; it was comprised of 18 middle-aged females, one old adult male, and one old adult female (Table 2). We do not have any genealogical information about this group, but we know that they never bred in the laboratory because males and females were always kept in separate cages.

At the sanctuary, each group's enclosure was comprised of (1) an outside compartment (250 $m^2$) furnished with wooden structures, hammocks made of firehose and a pool (25 cm deep), and (2) an inside compartment (18 $m^2$) that was divided into two different sections and furnished with platforms. The floor of the inside compartments was covered with sawdust. Compartments and sections were connected through movable hatches that remained open 24/7. In wintertime, an air heating system maintained a stable temperature (15-20 °C) in the inside compartments. The ground of the outside compartments was covered with loose travertine stones that are naturally present in this area. The closest fences of the two groups' enclosures were 15 meters apart. The members of each group were in auditory contact, but only partial visual contact because there were tall trees between the two enclosures, and one was located below the other. Therefore, the members of each group could only see each other when they are on the highest structures of the outside compartments, a location in which SH was never recorded.

In January 2020, (i.e., at the beginning of the study period), three Modena group members (i.e., one middle-aged adult female, one old adult male, and one old adult female) were separated from the rest of the Modena group (Table 2). They were housed as a subgroup that remained in visual contact with the main Modena group and with the group of Padova, but only when they were in the outside compartment (Appendix B). The ground of the outside compartment of the Modena subgroup was also covered with many loose travertine stones, that are naturally present in this area.

The animals were provisioned three times a day with commercial pellets in the morning (Kasper Fauna Food- Primate PT1), fruit and vegetables at midday, and carrots in the afternoon. In addition, nuts and dried fruit were provided at least twice a week.

*2.3. Data collection*

Observations of the main behaviours of interest were conducted by V.A. and R.B. from July to December 2020, from 8:00 to 18:00 on observation days (N = 169). During each 1-hour observation session, we used a combination of two behavioural sampling techniques: (1) 3-min instantaneous group scan sampling every 10 minutes, and (2) behaviour-dependent sampling focused on SH behaviour (Martin and Bateson, 2007). The same observation procedure was used in the two study groups; we collected behavioural data on the Modena subgroup at the same time as the main Modena group because they were both in the same area). All the behavioural data were collected from outside the enclosures, through the wire mesh. The average distance between the observers and the study subjects was 3 metres (range: 2-8 metres).

During an instantaneous group scan sampling session, the observers recorded the activity of each visible group member within the following behavioural categories (see Appendix C for operational definitions): abnormal, foraging, aggressive interaction, affiliative interaction, locomotion, object manipulation, play in the water, self-grooming, SH, and resting. The observer systematically walked in the same direction from the inside compartment to the outside compartment and recorded these behavioural data with pen-and-paper. The maximum duration of a group scan sampling session was 180 seconds (mean ± SD: 130.71 ± 1.32 sec). All the subjects that were not detected within this 180-sec window were labelled as "not recorded". We collected 540 group scan samples for the Modena group, and 526 group scan samples for the Padova group. In the Modena group, the average number of sampled subjects was 19.95 (± SD 0.24; range: 18-20), whereas in the Padova group, the average number of sampled subjects was 19.94 (± SD 0.25; range: 17-20).

If no SH was recorded in the group scan sample, the observer started a 10-min behaviour-dependent sampling session focused on SH behaviour. This behavioural sampling technique was reliable because (1) our study groups were relatively small (20 subjects), (2) the visibility was optimal, and (3) SH is a conspicuous behaviour. If an individual started engaging in SH during this 10-min period, its SH activity was continuously video-recorded with a digital video camera (Panasonic HC-V180). When this individual stopped performing SH, its video recording was extended for five minutes, independently of its activity. If SH resumed during the last two minutes of this 5-min extension, the video recording was extended for five minutes (see Huffman, 1996). If the group scan sample contained at least one stone handler, the observer completed the group scan sampling session, and started a continuous video recording (as per the aforementioned video-recording rules) of the first stone handler that was recorded in the group scan sample. We collected 129 hours of cumulative group scan sampling and behaviour-dependent sampling for the Modena group, and 107 hours of cumulative group scan sampling and behaviour-dependent sampling for the Padova group.

To determine the dominance hierarchy within a social group, we conducted all-occurrence sampling (Martin and Bateson, 2007) of agonistic behaviours (see Appendix D for operational definitions) from January to April 2021, and from 8:30 to 16:30, with pen-and-paper. This data collection protocol was only applied to the Modena group (i.e., main group and subgroup, separately) because it was the only group in which SH occurred. We only recorded unidirectional dyadic agonistic (i.e., dominance-submissive) interactions (e.g., lunge, slap, grab, bite, stare, open-mouth threat, chase, avoidance, escape) with a clear winner-loser outcome.

To assess the local availability of stones for each study group, we used the quadrat method (Krebs, 1999). A total of ten 1-$m^2$ quadrats were drawn on the floor of each outside compartment. In each quadrat, we counted the number of stones bigger than 1 cm x 1 cm x 1 cm. We estimated the site-specific availability in stones by calculating the average number of stones per meter square, based on a total of ten 1-$m^2$ quadrats surveyed for each group.

*2.4. Data analysis*

V.A. used *The Observer XT 12* (i.e., a video scoring/analysis software by Noldus) to score all the video-recorded SH bouts. We defined a SH bout as the display of SH activity with possible pauses of no longer than 120 seconds (see Huffman, 1996). The total number of SH bouts is comprised of the bouts collected during the group scan sampling and the behaviour-dependent sampling. We obtained the frequency of SH bouts (i.e., SH frequency) at the individual level by dividing the total number of SH bouts recorded during behaviour-dependent sampling and instantaneous group scan sampling for the total observation time.

We defined the total duration of group scan sampling time as the sum of duration of each scan sample for each group. We defined the total duration of behaviour-dependent sampling as the sum of all the time windows during which we observed each group outside of the group scan sampling time. To further investigate the expression of SH at the individual level, we calculated the number of different SH behavioural patterns per hour of observation time (i.e., frequency of SH patterns).

To examine the form of SH, we assessed "SH pattern diversity" by counting the total number of different SH behavioural patterns performed in each age class (immature and mature) and more specifically in each age-sex class. We followed previous categorization by Leca et al. (2007b) and grouped the SH behavioural patterns into three levels (namely, simple, intermediate, and complex) based on the four categories of general activities (i.e., investigative, locomotive, collection, and complex manipulative; after Nahallage and Huffman, 2007b) (Table 3). All the variables that have been used are listed in Table 4.

We grouped the age-sex classes used for descriptive analysis in two main age classes: immature (up to 6 years) and mature (over 7 years). We ran nonparametric Mann-Whitney U to test the differences between the two age classes in terms of frequency of SH bouts and duration of SH bouts for each subject. We ran a Chi-square test of independence to assess the relation between age class and the different categories of SH pattern complexity (simple, intermediate, and complex).

Hierarchical (or dominance) rank was calculated with the "EloRating" package (Neumann et al., 2011) in R (R Core Team, Vienna, Austria, version 3.5.0), considering all dyadic agonistic interactions with a clear winner-loser outcome. We excluded non-dyadic interaction (i.e., cases in which multiple senders or receivers were involved). We used Spearman rank-order correlation tests to evaluate the correlation between dominance rank and SH bouts and duration of SH bouts within the group of Modena.

To gain information regarding the activity budget, we calculated the frequency of each activity performed by each subject by dividing it for the total time of instantaneous group scan sampling in both groups. Then we calculated the mean ± SD for each activity within the group.

We counted the number of SH bouts recorded immediately before (pre-feeding) and within 30 minutes (post-feeding) from food provisioning in the group of Modena by each subject.

All analysis were performed with IBM SPSS (version 24) and JASP statistical software (version 0.16), which uses R-packages, unless otherwise noted. We used an alpha level of 0.05 as cut-off for significance. To measure inter-scorer reliability, J.-B.L. transcribed a total of 139 minutes of videorecords (i.e., 18.8% of the data set). The comparison of the transcriptions obtained from V.A. and J.-B.L. for the frequency of SH behavioural patterns analysed in this study yielded strong inter-scorer consistency ($k$ = 0.95).

## 3. Results

*3.1.* SH ethogram

We identified 32 SH behavioural patterns in the Modena group (see Appendix E). A video illustration of this SH repertoire is available at: https://youtu.be/GyxS7ZKc34s. The most frequently performed SH behavioural patterns were Hold, Bite, and Wrap, whereas the least frequently performed ones were Throw, Toss-Walk, and Pound. Some SH behavioural patterns were exclusive to one age class: Cuddle and Pick-and-Drop were only performed by immature subjects, whereas Push-Through, Shift-in-Hands, and Toss-Walk were only performed by mature subjects (Figure 1). Compared with previously reported SH ethograms in this species (Pelletier et al., 2017; Cenni et al., 2021), a number of SH behavioural patterns were not displayed by our study subjects (i.e., Clack, Flint, Pound-Drag, Rub Together, Shake-in-Hands, Slap-Roll, and Toss-and-Catch) while one SH behavioural pattern (i.e., Flip), previously only reported in Japanese macaques, was recorded in the Modena group (Table 5). We did not record any SH bouts in the Padova group.

3.2. "*Demography and SH" hypothesis*

Regarding SH prevalence (i.e., percentage of stone handlers in a group),90% of the Modena subjects (i.e., 18 out of 20 subjects) were verified stone-handlers and 10% (2 out of 20 subjects) were verified non-stone handlers. These two verified non-stone handlers were old adults belonging to the Modena subgroup. In the Padova group, 100% of the subjects (i.e., 20 out of 20 subjects) were verified non-stone handlers (Figure 2). This result revealed a considerably higher percentage of stone handlers in the group with a multi-layered demographic structure (i.e., Modena: all age classes were present) than in the group with an atypical demographic structure (i.e., Padova: missing immature class).

Regarding SH frequency, we recorded a total of 184 SH bouts over 129.07 hours of total observation time in the Modena group. The average number of SH bouts (± SD) per individual and per hour of total observation time in the Modena group was 0.07 ± 0.05. In the Padova group, we did not record any SH bouts over 107.39 hours of total observation time. SH frequency was significantly higher in the group with a multi-layered demographic structure (i.e., Modena: all age classes were present) than in the group with an atypical demographic structure (i.e., Padova: missing immature class) (Mann-Whitney *U* test, $U = 32.73$, $P < 0.001$, 95% CI [0.05, 0.90]). Therefore, Prediction 1a was supported.

Contrary to our expectations, we found no statistically significant differences in the Modena group between immature and mature individuals in frequency of SH bouts ($U = 36.50$, $P = 0.965$, 95% CI [-0.05, 0.07]) and the duration of SH bouts ($U = 37.00$, $P = 1.000$, 95% CI [-0.60, 0.50]). Therefore, Predictions 1b and 1c were not supported. However, a careful examination of the frequencies and durations of SH bouts, across more narrowly defined age classes, showed that the highest values were ascribable to adolescent and young adult subjects, whereas the lowest values were ascribable to middle-aged and old adult subjects (Table 6).

Regarding the diversity of SH behavioural patterns, we found that the immature subjects performed a higher number of different SH patterns (mean ± SD: 17.8 ± 5.35) compared with mature ones (mean ± SD: 15 ± 7.9) (Figure 3). However, this difference was not statistically significant ($U = 42.50$, $P = 0.693$, 95% CI [-0.43, 0.62]). Therefore, Prediction 1d was not supported.

We found a statistically significant association between age class and SH pattern complexity ($\chi^2 = (2, n = 20) = 219.93$, $P < 0.001$). Specifically, immature subjects performed more complex SH behavioural patterns (*adjusted residual* = 12.6, $P < 0.01$) and more intermediate SH behavioural patterns (*adjusted residual* = 3.6, $P < 0.01$) than simple SH behavioural patterns (*adjusted residual* = -14.8, $P < 0.01$), whereas mature subjects performed more simple SH behavioural patterns (*adjusted residual* = 14.8, $P < 0.01$) than intermediate SH behavioural patterns (*adjusted residual* = -3.6, $P < 0.01$) and complex SH behavioural patterns (*adjusted residual* = -12.6, $P < 0.01$) SH patterns). Therefore, Prediction 1e was not supported.

In Appendix F, we listed the total amount of SH behavioural patterns performed by each age class and categorized according to the level of complexity and the general activity pattern.

*3.3. "Dominance and SH" hypothesis*

We collected 263 unidirectional dyadic agonistic interactions within the subjects of the Modena group. The correlation between SH frequency and dominance rank was not statistically significant ($r_s$= -0.129, $P$ = 0.586, 95% CI [–0.54, -0.33]). Therefore, Prediction 2a was not supported. The correlation between SH duration and dominance rank was not statistically significant ($r_s$ = -0.056, $P$ = 0.816, 95% CI [–0.48, -0.39]). Therefore, Prediction 2b was not supported.

*3.4."Stone availability" hypothesis*

The average number of stones assessed in the outside compartments of the Modena group was not statistically different from the average number of stones assessed in the outside compartments of the Padova group ($U$ = 40.00, $P$ = 0.46, 95% CI [-0.61, 0.30]), neither between Modena and the subgroup ($U$ = 27.50, $P$ = 0.09, 95% CI [-0.76, 0.03]) nor between Padova and the subgroup ($U$ = 61.50, $P$ = 0.40, 95% CI [-0.63, 0.27]). In other words, the difference between the SH and non-SH groups was not associated with a significant variation in local stone availability. Therefore, this result is consistent with Hypothesis 3.

*3.5."Activity budget and SH" hypothesis*

When comparing the mean frequencies of each activity performed by the two groups, we found that the Modena group performed significantly more abnormal behaviours ($U$ = 395.00 $P$ = < 0.001, 95% CI [0.94, 0.98]) and object manipulation ($U$ = 372.00, $P$ = < 0.001, 95% CI [0.73, 0.93]) than the Padova group (Table 7). However, we found no statistically significant difference between the two groups in the frequency of foraging activities (*U* = 222.00, *P* = 0.56, 95% CI [-0.24, 0.44]; Table 7). Therefore, Prediction 4a was not supported.

We found significantly higher rates of affiliative behaviours in the Padova group than in the Modena group (*U* =105, *P* = 0.011, 95% CI [-0.70, -0.15]), but no statistically significant differences in the rates of aggressive behaviour (*U* = 213.00, *P* = 0.733, 95% CI [-0.29, 0.40]). Therefore, Prediction 4b was only partly supported. Finally, we found significantly higher rates of resting activities in the Padova group than in the Modena group (*U* =125.00, *P* = 0.044, 95% CI [-0.63, -0.03]; Table 7). Therefore, Prediction 4c was supported.

### *3.6. "Food provisioning and SH" hypothesis*

We scored only two SH bouts during pre-feeding time and one SH bout during post-feeding time, which represent 1.63% of the total number of SH bouts recorded. These results clearly indicate a lack of temporal connection between food provisioning and SH activity. Therefore, Predictions 5a and 5b were supported.

## 4. Discussion

Our study contributed to the existing SH behaviour database in long-tailed macaques. We provided the first evidence that SH can emerge and become prevalent among members of this species that were born and raised in captivity (see Nahallage and Huffman, 2007b for similar results in Japanese macaques). Moreover, the striking contrast between one group routinely exhibiting SH and the other in which this behaviour was completely absent allowed us to make inferences about the proximate causes of innovation, transmission, daily expression, and long-term maintenance of SH. The fact that these two groups had similar histories and lived in similar physical environments enabled us to investigate the effects of two endogenous factors (i.e., demography and dominance) and three exogenous factors (i.e., stone availability, activity budget, and food provisioning).

In the first part of our discussion, we address the hypotheses and predictions pertaining to the comparison between our two study groups, namely Prediction 1a, Hypothesis 3, and Predictions 4a to 4c. Indeed, this part of our study had a number of empirical limitations due to the absence of SH in the Padova group. Our data were consistent with Prediction 1a pertaining to the potential effect of a group's demographic structure on the frequency and prevalence of SH (Table 1). SH was performed by 90% of the members of the group with a multi-layered age structure (Modena) whereas this behaviour was completely absent in the group of the same size but with an atypical age structure (Padova). These results are consistent with previous inter-group comparative research in Japanese macaques suggesting that the age structure of a group may affect the emergence and spread of SH (Leca et al., 2007b).

First, group composition influences the likelihood of individual behavioural innovation (Leca et al., 2010b). This is particularly true for SH, an object play behaviour that was shown to be first invented by a juvenile female before being transmitted horizontally among this individual's similar aged kin and peer playmates during the initial stages of SH tradition in the Arashiyama group of Japanese macaques (Huffman, 1984). Therefore, in our study groups of long-tailed macaques, the presence of immature members in Modena and their absence in Padova may contribute to explaining the occurrence of SH in the former and the non-occurrence of SH in the latter.

Second, like social parameters, demographic structure is likely to impact the possible range of behavioural options available for naïve individuals to acquire, thereby influencing the probability of subsequent transmission of a novel behaviour (Huffman and Hirata, 2003; Leca et al., 2007b). Because SH is known to spread through pivotal group members and follow a diffusion pathway determined by the age class to which the innovator belongs (Huffman and Quiatt, 1986), the multi-layered demographic structure in the Modena group could have facilitated the wide spread of SH across individuals from all age-sex classes. On the other hand, even though we cannot rule out the possibility that SH might have emerged at some point in the Padova group, the atypical age structure (i.e., no immature individuals) may have impaired the emergence and early diffusion of

SH in this group. It is unlikely that the atypical sex structure in Padova (i.e., one male and 19 females) played a substantial role in the lack of SH in this group. Indeed, previous studies in multiple groups of Japanese and long-tailed macaques found no significant sex differences in the frequency and form of SH (Leca et al., 2007b; Nahallage and Huffman, 2007b, 2012).

We also found that the only two members of the Modena group that were never recorded performing SH were the oldest individuals (aged 21 and 22). This result is in line with those obtained in previous longitudinal studies of SH in the Arashiyama population of Japanese macaques, where the behaviour has been followed over time since in its innovation in 1979: in 2008, out of 132 group members, and despite sufficient sampling effort, only the four oldest individuals, aged 28 years and older had never been observed performing SH (Huffman, 1984, 1996; Leca et al., 2012). Even though these four individuals were infants or juveniles during the phases of innovation and early diffusion of SH, their mothers were not part of the earliest stone handlers (Huffman, 1984). Moreover, they did not belong to the matrilineages that engaged in SH between 1979 and 1984, that is the 5-year critical period upon which the acquisition of SH by naïve individuals is contingent in this population (Huffman, 1996). Indeed, no individuals over 5 years old when SH was innovated at Arashiyama ever acquired the behaviour (Huffman, 1984, 1996).

In the case of the Modena group of long-tailed macaques, we do not know exactly when SH was innovated, but it was between 2016 (i.e., when the animals arrived at the study site and had access to stones for the first time) and 2019 (i.e., when V.A. first noticed the performance of the behaviour in this group). If we assume that SH was innovated and started to spread within the group in 2019, then the two oldest individuals, who are also the only verified non-stone handlers, were 20 and 21 years old at that time. This is consistent with the view that, even though SH may become an established behavioural tradition in a group of macaques, it is not acquired by the oldest portion of the group. However, of the 18 stone handlers in Modena, 13 were over 5 years old and that time: three were 6, six were 7, and the remaining four were aged 8, 10, 14, and 19. If we push the innovation year back to 2016, then three individuals were still beyond the 5-year critical period, namely 7, 11, and 16 years of age.

There are several and non-mutually exclusive interpretations for this discrepancy between our results and these findings pertaining to the demography of SH. Because long-tailed macaques are more manipulative than Japanese macaques (Heldstab et al., 2016; Leca et al., 2011; Pelletier et al., 2017; Torigoe, 1987), their critical period for the acquisition of SH may extend well beyond 5 years. Due to differences in spatial distribution, captive individuals (like in our study group) may have more regular opportunities to observe SH in conspecifics than free-ranging individuals (like in the Arashiyama population), which could further contribute to extending the critical period of SH acquisition. Finally, it is noteworthy that the 5-year critical period has never been presented as an immutable sensitive phase beyond which it is impossible for any macaque to learn SH. This age-related threshold could not be confirmed in nine other groups of Japanese macaques in which SH was practiced because this behaviour had emerged in these groups long before observations began (Leca et al., 2007b). Future studies aiming to systematically test the effect of demographic factors on intergroup variation in the occurrence, prevalence, frequency, and form of SH should use longitudinal designs to compare groups with differential demographic structures living in similar environments. When ethically possible, individuals belonging to different age and sex classes may be translocated from a SH group to a non-SH group in order to test the differential demographic influence of seeding stone handlers into naïve groups. Finally, even though our data support the "Demography and SH" hypothesis, we cannot rule out the possibility that the recent ancestors of some Modena subjects were wild born and members of a population in which SH was an established behavioral tradition. This may have led to a residual genetic signal of object-directed manipulative propensities in the descendants of these stone handlers which could explain part of the inter-group difference currently observed. Future studies aiming to compare SH occurrence across captive groups should include a genealogical survey pertaining to the origins and stone-related activities of ancestral group members.

Our data were consistent with the “Stone availability and SH” hypothesis in that the occurrence (or lack thereof) of SH in our study groups was not associated with a significant variation in local stone availability. This result is in agreement with an inter-group comparative study in Japanese macaques showing that the performance of SH and the motivation to engage in this activity are not readily explained by the number of stones available in the local environment (Leca et al., 2008b). It is also in line with another study on captive Japanese macaques showing no significant correlation between the age of SH acquisition in infant cohorts and the number of stones encountered per hour from birth to the moment SH was first performed (Nahallage and Huffman, 2007a). Nonetheless, the role of stone availability in the emergence and early of diffusion of the SH behavioural tradition in a group should not be underestimated. Indeed, the rapid social transmission of SH within the Arashiyama population of Japanese macaques may have been enhanced by local construction projects when a large pile of stones was left at the edge of the provisioning area in clear view of all monkeys at feeding time (Huffman and Hirata, 2003).

Our data were partly consistent with the “Activity budget and SH” hypothesis which holds that, in selective pressure-free environmental conditions such as those afforded by food provisioning in captive settings, frivolous activities (like SH) would take the place of essential activities, including foraging, socializing, and resting. As expected, we found that group-level affiliation (Prediction 4b) and resting (Prediction 4c) were lower in Modena (i.e., the group in which SH is an established behavioural tradition) than in Padova (i.e., the non-SH group). Combined with higher rates of object manipulation in Modena than in Padova, these results suggest SH and the environmental conditions associated with this form of self-rewarding object play behaviour may contribute to shift a group’s activity budget away from other pleasurable and relaxing activities, like grooming and resting. These interpretations are consistent with findings obtained in an inter-group comparative study of SH in Japanese macaques focusing on the influence of food provisioning regimes on group-level activity budgets (Leca et al., 2008a). Admittedly, the higher rates of affiliation behaviours and resting in Padova could be also attributed to the demographic composition of this group. In terms of sex ratio, Padova was comprised of 19 females and one male; because long-tailed macaques are a female-philopatric species (di Fiore and Rendall, 1994), higher allogrooming frequencies are expected in groups with female-biased sex ratios. Regarding age structure, Padova was comprised of only adult members aged 11 and older, which could contribute to explaining higher resting rates.

Contrary to our expectation, SH did not take the place of foraging activity in Modena, as both groups did not significantly differ in the time they devoted to foraging (Prediction 4a). This result could reflect the high frequency and quality of the provisioned food in our two study groups, compared to all the groups of Japanese macaques previously studied in relation to SH (Leca et al., 2008a). In addition to commercial pellets, a twice-a-day provisioning of fruits and vegetables supplemented with a twice-a-week delivery of nuts and dried fruits may be sufficiently attractive to maintain a stable food-related activity budget, even in a group in which SH is practiced.

In the second part of our discussion, we address the predictions pertaining to the SH group (i.e., Modena; Predictions 1b to 1e, 2a and 2b, as well as 5a and 5b) because they provide stronger evidence for the mechanisms underlying the expression of SH. Contrary to our expectations, immature individuals did not perform SH significantly more often (Prediction 1b) and for significantly shorter periods of time (Prediction 1c) than mature individuals. In fact, there was no marked age differences in SH frequency and duration. Even though this result is at odds with previous findings obtained in Japanese macaques (Leca et al., 2007b, 2011; Nahallage and Huffman, 2007b), it is noteworthy that the sample analysed in the present study is considerably smaller than the ones analysed in Japanese macaques. Therefore, it is difficult to completely rule out any age-related effects on SH performance in the Modena group of long-tailed macaques. Alternatively, the lack of significant age differences in SH frequency and duration in this study could result from long-tailed macaques being more likely to manipulate objects than Japanese macaques (Heldstab et al., 2016; Leca et al., 2011; Pelletier et al., 2017; Torigoe, 1987), and thus SH being even more performed by adults in the former than the latter species.

Contrary to our expectations, mature individuals did not exhibit a significantly higher diversity (Prediction 1d) and complexity (Prediction 1e) in their SH performance than immature individuals. There are at least three reasons to account for the unexpected result that older subjects performed less complex SH behavioural patterns than younger subjects. First, the mature age class was comprised of two verified non-stone handlers, which reduced the pool from which to draw potential SH complexity. Second, all the subjects belonging to this age class were born and raised in a stone-free environment; the ontogenetically delayed exposure to stones might have negatively affected the complexity of their SH performance. Third, the more complex, thus possibly more vigorous, SH performance in younger individuals is in line with the "Surplus Energy" hypothesis holding that playful activities (like SH; Leca et al., 2007b, Nahallage and Huffman, 2007a) enable the adaptive expenditure of metabolic energy, which tends to be higher in immature than mature mammals (Barber, 1991).

With no significant correlation between hierarchical rank and SH frequency (contrary to Prediction 2a) and no significant correlation between hierarchical rank and SH duration (contrary to Prediction 2b), our data were not consistent with the "Dominance and SH" hypothesis (after Nishie, 2002). This result contrasts with a previous study of Japanese macaques indicating that more frequent stone handlers tended to be lower-ranking individuals and arguing that the expression of SH is an outlet for feeding frustration experienced by subordinate individuals with limited access to food provisioning site (Nishie, 2002). However, this interpretation was based on a small subset of a large free-ranging population and might not be generalizable to groups in which the food regime is less competitive, including captive individuals with *ad libitum* access to large amounts of food, like our study group. Additionally, a field experimental study conducted in the Arashiyama population of Japanese macaques showed low-ranking and middle-ranking individuals significantly preferred SH artefacts (i.e., piles of stones replicating physical traces of SH activity) over randomly scattered stones to start engaging in SH, whereas this preference was not detected in high-ranking individuals (Leca et al., 2010a). More data are needed to address the putative relationships between dominance, competition (for food, for stones) and SH in macaques (Huffman and Hirata, 2003; Leca et al., 2010a).

Finally, and as expected in a captive group of macaques (Leca et al., 2008a), our data were consistent with the "Food provisioning and SH" hypothesis. Indeed, we found no marked temporal connection between SH and food provisioning (Prediction 5a) and between SH and feeding activity (Prediction 5b). This pattern is typical of macaques that are provided with large food items (i.e., that require some manual processing) and in such large amounts that some of the food is still available hours after provisioning (i.e., all group members were able to eat until satiated). Specifically, for environmental enrichment purposes, our study subjects were mainly provisioned with foods that required a multi-stepped behavioural sequence before being eaten, including climbing on top of the enclosure, retrieving large pieces of fruit stuck in the wire mesh, and bringing the food item to a comfortable place where it could be processed. Because the monkeys could continue to move around and manipulate food items with their hands while chewing, their naturalistic post-feeding foraging-like behaviours were expressed. Therefore, they did not have to handle stones shortly after feeding as an extension of manipulatory foraging actions. Therefore, we can confidently conclude that the expression of SH in the captive Modena group of long-tailed macaques was not underlain by motivational processes associated with foraging.

This phenomenon contrasts with findings obtained in large free-ranging provisioned groups of Japanese macaques that were given with small-sized food items (i.e., cereal grains scattered on the ground and that could only be put in mouth without any manual processing) and in such small amounts that the food patch was quickly depleted. In these groups, there was a strong temporal connection between SH and food provisioning, with SH being primarily expressed within 30 minutes after food provisioning (Huffman, 1996; Leca et al., 2008a). In these specific cases, SH did not meet the criteria of *anticipatory* misdirected foraging as reported in captive oriental small-clawed otters (*Anonyx cinerea*) engaging in more object play while waiting for food provisioning at the usual time (Pellis, 1991). However, this form of SH met the criteria of *post-provisioning* misdirected foraging in the sense that handling stones may be an extension of foraging-like behaviours via the continuation of manipulatory actions directed towards non-edible objects (stones) while chewing provisioned food that did not require further food-processing (Huffman and Quiatt 1986; Leca et al., 2008a; Nahallage et al., 2016).

## 5. Conclusion

Through a systematic comparison of two groups of long-tailed macaques with similar histories and living conditions, we explored some of the main proximate causes (i.e., socio-demographic and environmental factors) underlying the emergence, social diffusion, daily expression, maintenance, and transformation of SH, while controlling for experiential components of innovation and learning. By doing so, we lent further support to the cultural nature of this behavioural practice. Future studies will focus on the role of social networks in the occurrence, absence, and performance of SH at the group level. This captive setting will allow us to test whether SH facilitates the acquisition of experimentally-induced stone tool use in Modena compared to the Padova group (see Leca and Gunst, in review).

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| Hypothesis | Prediction | Hypothesis/Prediction description | Supported |
|---|---|---|---|
| H1. Demography | Prediction 1a | More multi-layered demographic structure in the SH group, and more atypical demographic structure – with missing age classes, particularly the immature class – in the non-SH group | Yes |
| | Prediction 1b | More frequent SH bouts in immature subjects | No |
| | Prediction 1c | More shorter SH bouts in immature subjects | No |
| | Prediction 1d | Less diverse SH behavioural patterns in mature subjects | No |
| | Prediction 1e | More complex SH behavioural patterns in mature subjects | No |
| H2. Dominance | Prediction 2a | Negative correlation between hierarchical rank and SH frequency | No |
| | Prediction 2b | Negative correlation between hierarchical rank and SH duration | No |
| H3. Stone availability | Not applicable | If loose stones are present on the ground, group-specific SH frequency is not strictly determined by local availability of stones | Yes |
| H4. Activity budget | Prediction 4a | Higher rates of foraging activities in the non-SH group than in the SH group | No |
| | Prediction 4b | Higher rates of social activities in the non-SH group than in the SH group | Partially |
| | Prediction 4c | Higher rates of resting activities in the non-SH group than in the SH group | Yes |
| H5. Food provisioning | Prediction 5a | SH should occur throughout the day, regardless of the food provisioning schedule | Yes |
| | Prediction 5b | SH should occur throughout the day, regardless of the monkeys' feeding activity | Yes |

*Table 1.* Summary of hypotheses, predictions, and outcomes.

| Group | Age classes (years) | | | | | | | **N total** |
|---|---|---|---|---|---|---|---|---|
| | Juvenile males (4) | Adolescent females (4) | Young adult males (6-10) | Young adult females (5-10) | Middle-aged adult female (11-15) | Old adult (16-) | | |
| | | | | | | Male | Female | |
| Modena | 3 | 2 | 7 | 3 | 1 | 0 | 1 | **17** |
| Modena subgroup | 0 | 0 | 0 | 0 | 1 | 1 | 1 | **3** |
| Padova | 0 | 0 | 0 | 0 | 18 | 1 | 1 | **20** |
| ***Total*** | **3** | **2** | **7** | **3** | **20** | **2** | **3** | **40** |

*Table 2.* Number of individuals across age classes in the two main groups and the Modena subgroup.

| Level of complexity | Category | Behaviour |
| --- | --- | --- |
| Simple | Investigative activities | Bite, Hold, Lick, Move Inside Mouth, Sniff |
| | Locomotive activities | Carry, Grasp-Walk, Move and Push/Pull, Toss-Walk |
| Intermediate | Collection (gathering) activities | Cuddle, Dislodge, Gather, Grasp, Pick And Drop, Pick Up |
| Complex | Complex manipulative activies | Cover, Flip, Groom, Insert Into Cavity, Pound, Push-Trough, Roll, Roll In Hands, Roll With Fingers, Rub, Rub With Hands, Scatter, Shift In Hands, Slap, Tap, Throw, Wrap |

*Table 3.* SH behavioural patterns performed by the study subjects, categorized according to their general activity patterns (after Nahallage and Huffman, 2007b), and their level of complexity (after Leca et al., 2007b).

| SH variables | Definition | Used for prediction |
|---|---|---|
| SH occurrence | Number of verified stone handlers (i.e., subjects that were observed performing SH at least once during the observation time) and number of verified non-stone handlers (i.e., subjects that never performed SH during the observation time) | 1a |
| SH frequency | Number of SH bouts per hour of observation time | 1b, 1c |
| SH duration | Duration of the total number of SH bouts observed for each subject | 1d |
| SH pattern diversity | Number of different SH behavioural patterns performed by members of a given age class | 1e |
| SH pattern complexity | Total number of SH behavioural patterns performed by members of a given age class and categorized by levels of complexity | 1f |

*Table 4.* SH variables, their definitions, and the predictions they were used in.

| SH Behavioural Pattern | LTM in Semproniano, Italy | LTM in Ubud, Bali |
|---|---|---|
| Bite | X | X |
| Carry | X | X |
| Clack | - | X |
| Cover | X | X |
| Cuddle | X | X |
| Dislodge | X | X |
| Flint | - | X |
| Flip | X | - |
| Gather | X | X |
| Grasp | X | X |
| Grasp-Walk | X | X |
| Groom | X | X |
| Hold | X | X |
| Insert Into Cavity | X | X |
| Lick | X | X |
| Move and Push/Pull | X | X |
| Move Inside Mouth | X | X |
| Push-Trough | X | X |
| Pick and Drop | X | X |
| Pick Up | X | X |
| Pound | X | X |
| Pound-Drag | - | X |
| Roll | X | X |
| Roll in Hands | X | X |
| Roll With Fingers | X | X |
| Rub | X | X |
| Rub Together | - | X |
| Rub With Hands | X | X |
| Scatter | X | X |
| Shake in Hands | - | X |
| Shift In Hands | X | X |
| Slap | X | X |
| Slap-Roll | - | X |
| Sniff | X | X |
| Tap | X | X |
| Toss And Catch | - | X |
| Toss-Walk | X | X |
| Throw | X | X |
| Wrap | X | X |

*Table 5.* Comparative presence (X) and Absence (-) of SH behavioural patterns in our study subjects (i.e., captive long-tailed macaques in Semproniano, Italy) and the free-ranging population of long-tailed macaques (Ubud, Bali; Cenni et al., 2021; Pelletier et al., 2017).

| Age-sex classes | Subject | Age class | Number of SH bout per hour of observation time | Mean frequency of SH bouts per age/sex class ± SD per hour of observation time | Total duration of SH bouts per minutes of observation time | Mean duration of SH bouts per age/sex class ± SD per minutes of observation time |
|---|---|---|---|---|---|---|
| Juvenile male | Giorgio | Im | 0.04 | 0.06 ± 0.03 | 3.07 | 21.92 ± 16.40 |
| | Pasqualino | Im | 0.09 | | 32.99 | |
| | Pietro | Im | 0.04 | | 29.69 | |
| Young adult male | Furby | Ma | 0.09 | 0.11 ± 0.04 | 36.93 | 66.61 ± 38.02 |
| | Dalì | Ma | 0.20 | | 121.20 | |
| | Ingegnere | Ma | 0.06 | | 53.92 | |
| | Piccolo | Ma | 0.09 | | 32.11 | |
| | Monky | Ma | 0.10 | | 93.86 | |
| | Occhiolino | Ma | 0.10 | | 25.72 | |
| | Pepito | Ma | 0.11 | | 99.02 | |
| Old adult male | Alfa* | Ma | 0.00 | 0.00 ± 0.00 | 0.00 | 0.00 ± 0.00 |
| Adolescent female | Paprika | Im | 0.17 | 0.11 ± 0.09 | 83.17 | 24.42 ± 19.22 |
| | Iside | Im | 0.05 | | 24.55 | |
| Young adult female | Sbuccia | Ma | 0.02 | 0.06 ± 0.05 | 9.71 | 15.00 ± 20.83 |
| | Macchia | Ma | 0.11 | | 46.17 | |
| | Psiche | Ma | 0.05 | | 17.38 | |
| Middle-aged female | Wika | Ma | 0.05 | 0.03 ± 0.03 | 29.73 | 12.40 ± 17.53 |
| | Buddha | Ma | 0.01 | | 0.28 | |
| Old adult female | Siddharta | Ma | 0.05 | 0.03 ± 0.04 | 24.79 | 0.21 ± 0.292 |
| | Agata* | Ma | 0.00 | | 0.00 | |

*Table 6.* Frequency and duration of SH bouts across subjects of the Modena group and by age-sex class (* Subjects of the Modena subgroup. Im:immature. Ma:mature).

| | Modena (mean ± SD) | Padova (mean ± SD) |
|---|---|---|
| Abnormal | 1.47 ± 0.85 | 0.18 ± 0.11 |
| Foraging | 5.12 ± 1.61 | 4.79 ± 1.32 |
| Aggressive interaction | 0.09 ± 0.07 | 0.11 ± 0.10 |
| Affiliative interaction | 5.40 ± 1.67 | 6.79 ± 1.43 |
| Locomotion | 4.55 ± 1.68 | 3.85 ± 1.27 |
| Object manipulation | 1.90 ± 0.95 | 0.50 ± 0.43 |
| Play water | 0.11 ± 0.15 | 0.07 ± 0.13 |
| Self-grooming | 1.70 ± 1.26 | 1.41 ± 0.65 |
| Stone handling (SH) | 0.07 ± 1.26 | 0.00 ± 0.00 |
| Resting | 7.05 ± 1.98 | 8.23 ± 2.21 |
| Not recorded | 0.07 ± 0.07 | 0.29 ± 0.83 |

*Table 7.* Mean frequency of each activity performed in the two study groups (mean ± SD) per hour of observation time.

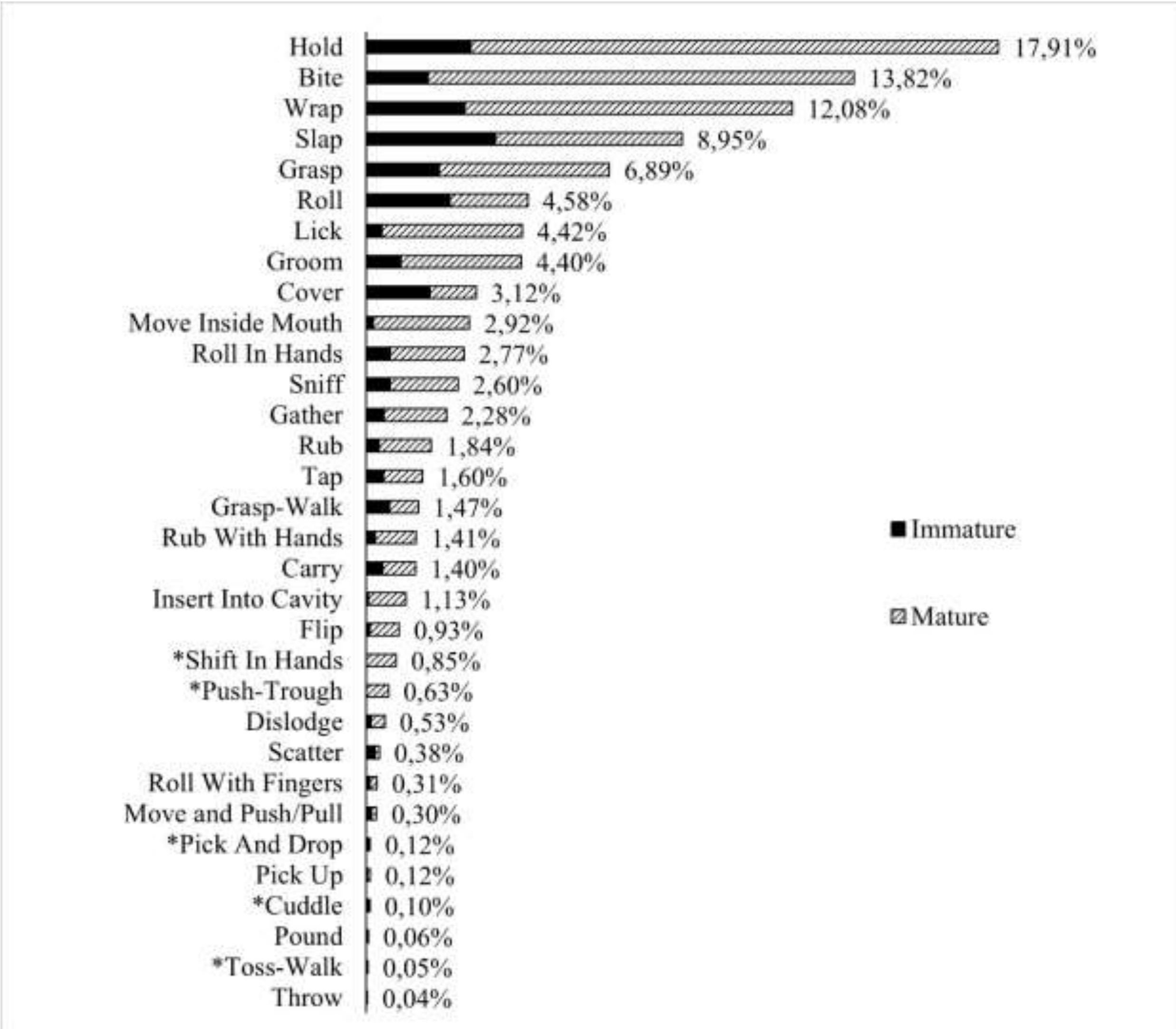



*Figure 1*. Quantitative assessment of SH behavioural patterns (expressed in % over the total number of SH behavioural patterns expressed) performed by members of the Modena group. *SH behavioural patterns that were exclusive to one age class.

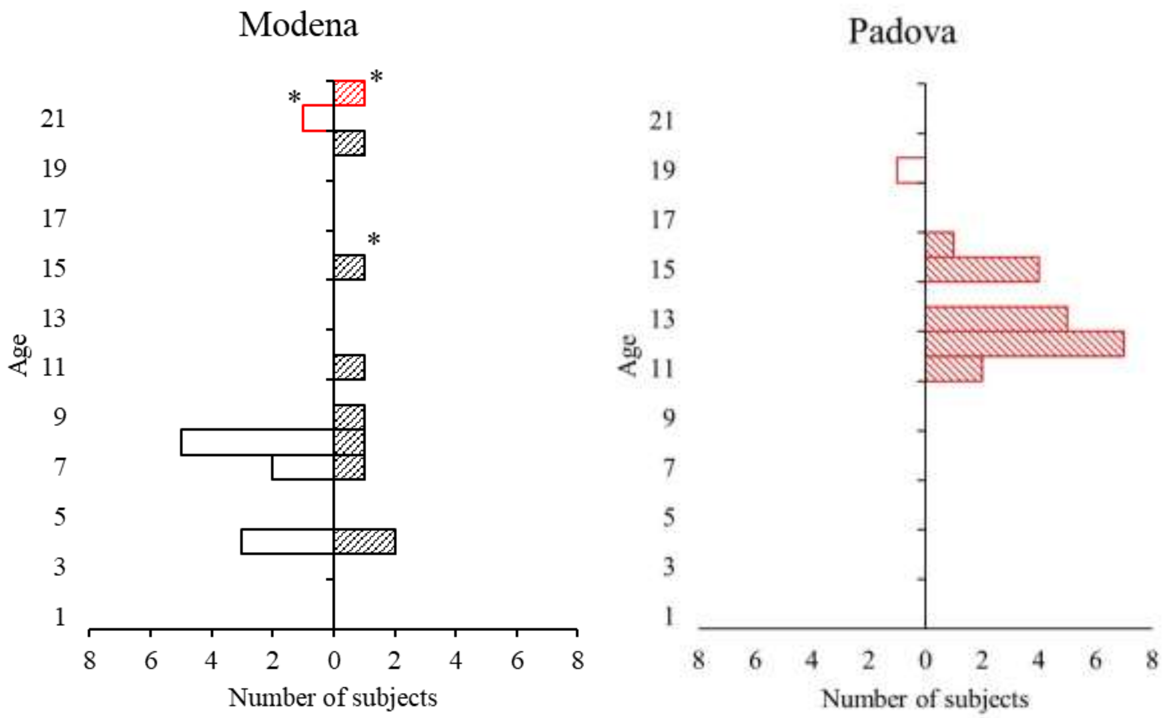



*Figure 2.* Histograms representing age-sex structure, verified stone-handlers (black), and verified non-stone handlers (red) in each study group (clear bars: males; hatched bars: females) * Subjects of the Modena subgroup.

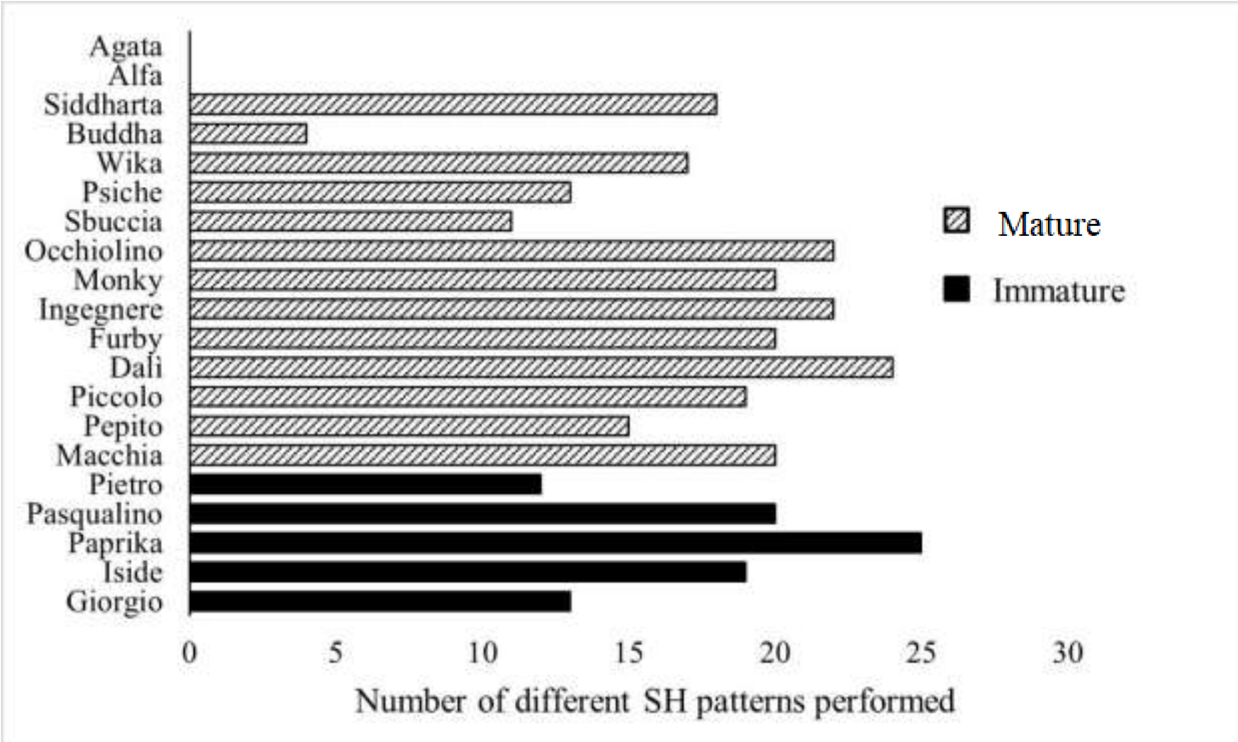


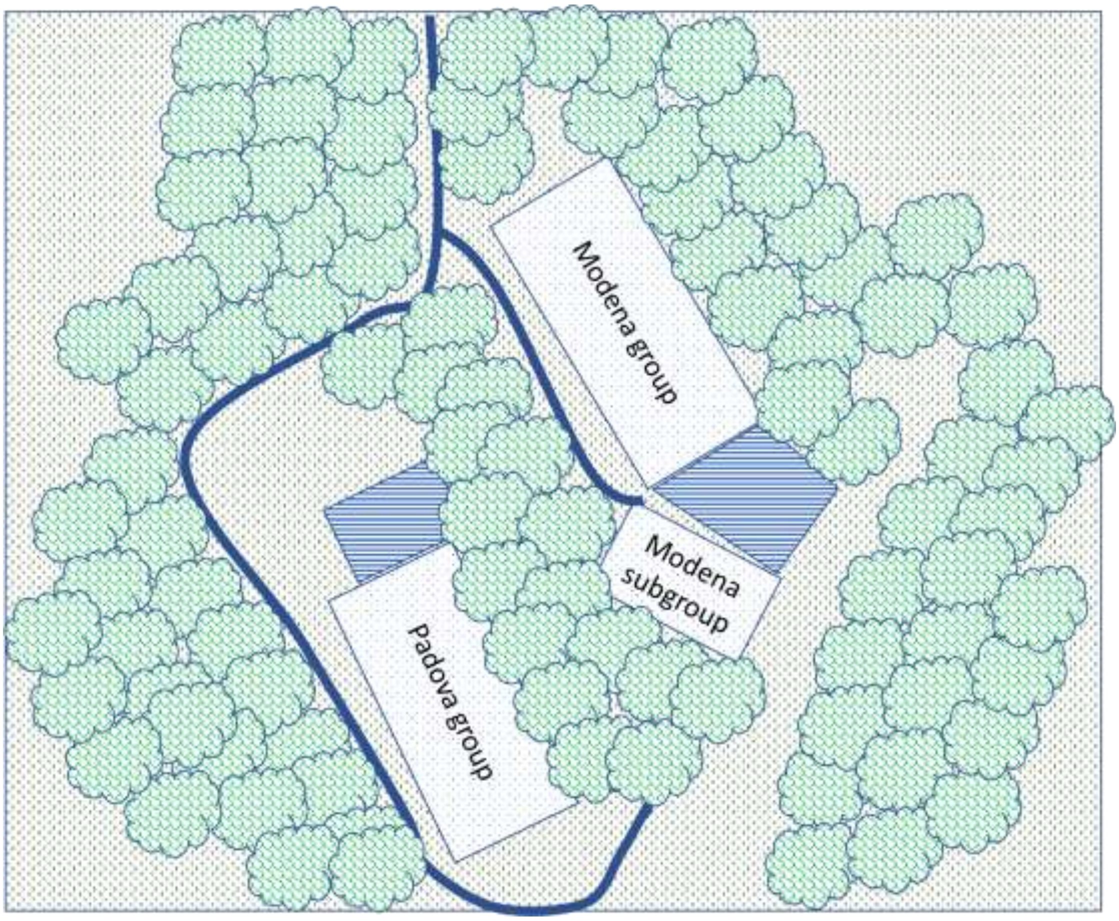

*Figure 3.* Diversity in SH behavioural patterns among the two main age classes in the Modena group (subject listed from older on the top to younger on the bottom).

## Appendices

Appendix A

**List of the study subjects and their respective age (years in 2020), age class (Ma:mature. Im:immature), sex (M:male. F:female), and group membership (Ms: Modena subgroup, Mo:Modena, Pa:Padova)**

| Subject | Age (years) | Age class | Sex | Group |
|---|---|---|---|---|
| Agata | 22 | Ma | F | Ms |
| Alfa | 21 | Ma | M | Ms |
| Buddha | 15 | Ma | F | Ms |
| Dalì | 8 | Ma | M | Mo |
| Furby | 8 | Ma | M | Mo |
| Giorgio | 4 | Im | M | Mo |
| Ingegnere | 8 | Ma | M | Mo |
| Iside | 4 | Im | F | Mo |
| Macchia | 7 | Ma | F | Mo |
| Monky | 8 | Ma | M | Mo |
| Occhiolino | 8 | Ma | M | Mo |
| Paprika | 4 | Im | F | Mo |
| Pasqualino | 4 | Im | M | Mo |
| Pepito | 7 | Ma | M | Mo |
| Piccolo | 7 | Ma | M | Mo |
| Pietro | 4 | Ma | M | Mo |
| Psiche | 9 | Ma | F | Mo |
| Sbuccia | 8 | Ma | F | Mo |
| Siddharta | 20 | Ma | F | Mo |
| Wika | 11 | Ma | F | Mo |
| Alabat | 12 | Ma | F | Pa |
| Amy | 15 | Ma | F | Pa |
| Becky | 12 | Ma | F | Pa |
| Bella | 13 | Ma | F | Pa |
| Buffon | 12 | Ma | F | Pa |
| Carina | 13 | Ma | F | Pa |
| Cebu | 13 | Ma | F | Pa |
| Cocò | 11 | Ma | F | Pa |
| Darwin | 19 | Ma | M | Pa |
| Edera | 15 | Ma | F | Pa |
| Elfo | 13 | Ma | F | Pa |
| Ester | 16 | Ma | F | Pa |
| Etna | 12 | Ma | F | Pa |
| Fifa | 12 | Ma | F | Pa |
| Heidi | 15 | Ma | F | Pa |
| Honey | 13 | Ma | F | Pa |
| Kenza | 11 | Ma | F | Pa |
| Manila | 12 | Ma | F | Pa |
| Orsetto | 12 | Ma | F | Pa |
| Pox | 15 | Ma | F | Pa |




Appendix B. Map of the outside compartments of the main Modena group, Modena subgroup, and the Padova group.

Appendix C

| Behaviour | Description |
|---|---|
| **Abnormal** | Prolonged or excessive contact of tongue with the wire mesh of the enclosures |
| **Foraging** | Ingest or looking for food. This pattern also includes the action of drinking. |
| **Aggressive interaction** | Physically attack another individual or to vocally threaten without physical contact. |
| **Affiliative interaction** | Express affiliative behaviours (allo-groom, hug, social play) towards another individual. |
| **Locomotion** | Move from one place to another; this pattern include walking, galloping, running, jumping, and climbing. |
| **Object manipulation** | Manipulate artificial objects. |
| **Play water** | Swimming, jumping or walking inside the pool or playing with the water contained in the drinking sites (immersing the arms or the head) |
| **Self-grooming** | Pick through own hair with hands or mouth. |
| **Stone handling** | Form of solitary object play consisting of the manipulation of stones by performing various behavioural patterns. |
| **Resting** | The subject is still and either sleeping or dozing. This pattern can be performed in different positions (sitting, standing quadrupedally, lying down, climbed on the mesh); both awake and with eyes closed. |
| **Not recorded** | Subjects that were separated from the group during the scan sample (i.e., for medical reasons), or subjects that were recorded after the time limits for the instantaneous scan sampling (3 minutes). |

Appendix D

| List of agonistic related behaviour scored during all-occurrence sampling | |
|---|---|
| Behaviour | Description |
| Lunge | Quick and sudden rush against another individual. |
| Slap | Hitting with the hands another individual. |
| Grab | Took hold of a body part of another individual. |
| Bite | Seize with the teeth the body part of another individual. |
| Stare | A fixed gaze directed to another individual and accompanied by a rigid posture. |
| Open-mouth threat | The eyes are widely open, the eyebrows are raised, the ears are pulled back, and the mouth is open; the lips are tensed forming a rounded opening and the teeth are not visible. |
| Chase | Run after another individual with hostile intention. |
| Avoidance | Moving away to avoid the interaction with another individual |
| Escape | Running away from an individual that is approaching |

Appendix E

**Ethogram comprised of 32 stone handling behavioural patterns performed by the long-tailed macaques in the rescue centre of Semproniano, Italy (modified after Pelletier et al., 2017; Cenni et al., 2021; Leca et al., 2007b).**

1. **Bite:** To bring a stone to the mouth and place it between the teeth.
Comments: This pattern is typically performed using one or both hands. This pattern may also occur when an individual brings their face down to a stone that is placed on a surface or wrapped into a cloth.

2. **Carry:** To hold or cradle a stone while moving from one place to another.
Comments: This pattern can be performed by using either the hands or mouth to grasp the stone. Stones are either held or cuddled against the body while the individual moves in a bipedal, tripedal, or quadrupedal manner.

3. **Cover:** To lightly place an object upon or over a stone with the hands.
Comments: This pattern often resembles a peek-a-boo type of activity, where the stone is fully covered, and then frequently uncovered. Items regularly used to perform this activity are dry leaves and cloth.

4. **Cuddle:** To take hold of, grab or cradle a stone against the chest.
Comments: This pattern was performed by only two young individuals.

5. **Dislodge:** To (presumably attempt to) remove a stone embedded in a substrate by scratching or rubbing it with the fingertips or mouth.
Comments: Stones are not always extracted from the substrate; indeed, they can be embedded into the mesh of the fence.

6. **Flip**: To turn a stone over with both hands (Leca et al., 2007b).
Comments: This pattern can be performed with one or both hands or only with fingertips; the stone is always flipped upside down.

7. **Gather:** To bring a stone to oneself.
Comments: This pattern is usually performed with one hand and only one stone each time is collected.

8. **Grasp:** To clutch a stone placed in front of or beside oneself, on the ground.
Comments: This pattern can be performed by both the hands or the feet, with a power grip, either tightly or loosely, and is usually performed when the individual is paying attention to something else.

9. **Grasp-Walk:** To clutch a stone in the palm of the hand while walking.
Comments: This pattern is usually performed by holding the stone in the palm of the hand while the individual moves in a quadrupedal manner.

10. **Groom:** To pick at or scratch a stone with the fingertips.
Comments: Stones may be held or grasped in the hand or foot or placed on the ground. This pattern is usually performed with the fingertips; it can also be directed toward a stone that is wrapped inside a cloth.

11. **Hold:** To pick up a stone and hold onto or clutch it for some time while keeping it away from both the body and other surfaces.
Comments: This pattern is usually performed with the hands and most frequently utilizing a power grip.

12. **Insert into cavity:** Insert a stone into a pipe or wood cavity (rhesus macaques: Nahallage and Huffman, 2012; but see Table 1 in Pelletier et al., 2017 for Balinese long-tailed macaques).
Comments: To insert the stone inside a firehose or into a gap between the ground and the hatch.

13. **Lick:** To bring a stone to the mouth and touch it with the tongue.
Comments: This pattern is typically performed right after or in combination with “Sniff”.

14. **Move And Push/Pull:** To clutch a stone that is placed on the ground with the arm(s) extended in front of oneself and walk either forward or backward while the stone is rubbed against the ground.
    Comments: This pattern can be performed using either one or both hands.

15. **Move Inside Mouth:** To insert a stone inside the mouth and move it with the tongue or the hands.
    Comments: during this activity, the stone fully disappears inside the mouth. Stones can often be seen moving through cheek when performed.

16. **Pick And Drop:** To repeatedly take a hold of a stone with the hands and let it fall to the ground or into a cavity.
    Comments: This pattern has been observed only once.

17. **Pick Up** To take hold of a stone with one hand and place it into the other hand.
    Comments: This action requires that the stone picked up be completely let go of by the original hand once placed into the open supporting hand. This pattern has been observed only once.

18. **Pound:** To strike a stone on the ground or an object by using a power grip.
    Comments: This pattern is mostly performed by pounding the stone on the metal structures of the enclosure.

19. **Push-through:** To exert force on a stone, typically with the palm of the hand or the fingers in an apparent attempt to move the stone through a cavity, like a hole or a pipe. (Cenni et al., 2021).
    Comments: This pattern may resemble "Pick And Drop", when repeatedly performed; however, when performing a "Push-Through" the stone is not dropped. It may also resemble "Dislodge", but in "Push-Through", the stone is pushed or clutched, rather than scratched or rubbed with the fingertips. Most frequently, stones are stuck in the cavity and the monkey aims to free the stone from the cavity by performing a pushing action.

20. **Roll:** To move a stone back and forth on a substrate in a rolling or rubbing motion. This pattern is performed with a loose grip or open palms.
    Comments: This pattern is most frequently performed with the hands.

21. **Roll In Hands:** To roll or rotate a stone back and forth in both hands, moving in an alternating sliding gesture, with a loose grip.
    Comments: Stones are typically rolled along the length of the hand, utilizing the palms and fingers of both hands. This action is mostly performed by keeping the hands up above the head.

22. **Roll With Fingers:** To move a stone back and forth on a substrate in a rolling motion using only the fingertips.
    Comments: This pattern differs from "Roll" as only the fingertips are used to perform this pattern rather than utilizing the palm. This pattern is most frequently performed directly in front of the individual, using both hands to presumably stabilize and guide the stone.

23. **Rub:** To slide or move a stone back and forth on a substrate utilizing a power or precision grip.
    Comments: This pattern can be performed on the ground, or other substrates, such as concrete or the metal structures of the enclosure. It is usually performed in combination with "Wrap" or "Cover" since the stone is rubbed on the ground with a cloth or dry leaf placed on it.

24. **Rub With Hands:** To hold or grasp a stone with one hand (or foot) and move the palm of the other hand along the surface of the stone while applying firm pressure.
    Comments: The hand performing the rubbing motion can either move back and forth along the surface of the stone(s) or perform the rubbing action in only one direction multiple times. Though this pattern most frequently occurs when stones are being held away from the ground or body.

25. **Scatter:** To disperse a stone with the hands in a scattering motion on a substrate, in front of oneself.
    Comments: This pattern utilizes an open hand moving in a sweeping gesture across a substrate; it can be performed also inside the water.

26. **Shift In Hands:** To completely transfer a stone from one hand to the other repeatedly, utilizing a cupping motion of the hands.
Comments: The entire hand is utilized in this activity as the curving of the fingers allows for the cupping motion required to completely pass the stone(s) off into the other hand each time. This pattern can be performed either slowly or quickly. Stones are always held away from the ground or body when this pattern is performed.

27. **Slap:** To hit a stone in a slapping motion with the palm or fingertips of the hand.
Comments: This pattern may resemble “Tap”; however, it typically occurs one to few times. and is not used to hit or move a stone towards another stone, object, or body part. This pattern can be performed while a stone is being held, grasped, or on the ground, and can be performed with one or both hands.

28. **Sniff:** To bring a stone to the nose and smell it by inhaling.
Comments: This pattern is most frequently performed by bringing a stone to the nose using the hands and it is performed most of the time in sequence with “bite”. The duration of this behavioural pattern is always very short.

29. **Tap:** To move or tap a stone in a repeated sweeping gesture using the fingertips against a substrate, object, or body part.
Comments: This pattern may resemble “Slap”; however, it occurs multiple times, and the stone is tapped against another object, stone, or body part. This pattern is mostly performed on the ground and has only been observed once on body parts (groin).

30. **Throw:** To toss a stone underhand, either in front of or behind the individual.
Comments: This pattern has only been recorded three times and in all the cases the stone was thrown with only one hand.

31. **Toss-Walk:** To lightly throw a stone, underhand, ahead of oneself while walking, then take hold of and clutch it in the palm of the hand.
Comments: This pattern differs from “Throw” as it is not performed stationary but while the individual is walking in a quadrupedal manner. The distance travelled by the stone is generally much shorter than with the pattern “Throw”, allowing the stone to be retrieved again after the tossing action occurs.

32. **Wrap:** To encase or enclose a stone in an object, using the hands, either tightly or loosely, in what appears to be an attempt to bend or fold the object around the stone.
Comments: Items frequently used to wrap stones include leaves, cloths, and bundles of dried grass. This action can be performed either while the stone is placed on the ground, or while the stone is being held. The unwrapping of a stone that was previously wrapped with an object is also classified under this pattern.

Appendix F

| Level of complexity | Category | SH pattern | Age class | |
|---|---|---|---|---|
| | | | Immature | Mature |
| **Simple** | Investigative activities | Bite | 135 | 934 |
| | | Hold | 229 | 1156 |
| | | Lick | 34 | 308 |
| | | Move Inside Mouth | 15 | 211 |
| | | Sniff | 53 | 148 |
| | Locomotive activities | Carry | 37 | 71 |
| | | Grasp-Walk | 51 | 63 |

| | | | | |
|---|---|---|---|---|
| | | Move and Push/Pull | 12 | 11 |
| | | Toss-Walk | 0 | 4 |
| **Total** | | | **566** | **2906** |
| **Intermediate** | Collection (gathering) activities | Cuddle | 8 | 0 |
| | | Dislodge | 11 | 30 |
| | | Gather | 39 | 137 |
| | | Grasp | 160 | 373 |
| | | Pick And Drop | 9 | 0 |
| | | Pick Up | 2 | 7 |
| **Total** | | | **229** | **547** |
| **Complex** | Complex manipulative activities | Cover | 140 | 101 |
| | | Flip | 9 | 63 |
| | | Groom | 77 | 263 |
| | | Insert Into Cavity | 5 | 82 |
| | | Pound | 1 | 4 |
| | | Push-Trough | 0 | 49 |
| | | Roll | 183 | 171 |
| | | Roll In Hands | 53 | 161 |
| | | Roll With Fingers | 9 | 15 |
| | | Rub | 28 | 114 |
| | | Rub With Hands | 20 | 89 |
| | | Scatter | 20 | 9 |
| | | Shift In Hands | 0 | 66 |
| | | Slap | 284 | 408 |
| | | Tap | 38 | 86 |
| | | Throw | 1 | 2 |
| | | Wrap | 216 | 718 |
| **Total** | | | **1084** | **2401** |