AN INTEGRATIVE APPROACH TO SOCIAL LEARNING AND BEHAVIORAL TRADITIONS IN PRIMATES

A collection of 30 years of research work (1979 to 2009)

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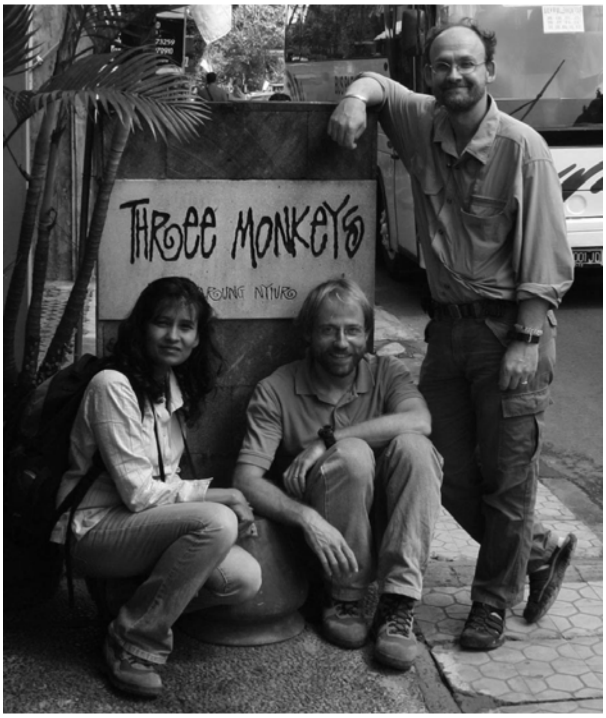

C.A.D. Nahallage, J.-B. Leca, and M.A. Huffman (Ubud, Bali, Indonesia, August 2008)

About the authors

Michael A. Huffman earned an MSc (1985) and a D.Sc. (1989) from the Department of Zoology, Kyoto University under the direction of Professors Junichiro Itani and Toshisaa Nishida (who joined the laboratory ca. 1987). He started his primatological career in 1979 as an undergraduate, with work on female mate choice and partner preference in Japanese macaques (the topic of his graduate degrees). Huffman is now an associate professor at the Primate Research Institute of Kyoto University. His research experience covers a wide range of species including chimpanzees in East Africa (Tanzania, Uganda) and in captivity (Japan, Italy) as well as macaques in Japan, Bali, Sri Lanka and India. He has published on a wide range of topics spanning from reproduction and sexual behavior, parasite ecology, social learning and primate self-medication. Jean-Baptiste and Charmalie are his two key collaborators in the current work on stone handling, joining his laboratory as a post doc and graduate student, respectively.

Jean-Baptiste Leca earned a Ph.D. in Ethology (2002) from the University Louis Pasteur, Strasbourg, France, and was a Post-Doctoral Fellow at the Primate Research Institute, Kyoto University for 4 years between 2003-2004 and 2008-2009. His research explores the biological, social, and ecological foundations of behavioral traditions in non-human primates. More specifically, he is interested in the determinants of behavioral innovations as well as the constraints on their diffusion and long-term maintenance within social groups. Among the various traditional behaviors reported in Japanese macaques, he mainly focuses on stone handling behavior in multiple troops across Japan. From 2003, he has been taking an integrative approach to studying stone handling through the combination of comparative, longitudinal, and experimental methods. Recently, he also provided an update about the maintenance of the fish-eating behavior in the Japanese macaques living on Koshima Islet, and reported the first case of dental flossing behavior by a Japanese macaque at Arashiyama.

Charmalie A.D. Nahallage, earned a Ph.D. in Primatology (2008) from the Primate Research Institute, Kyoto University, Kyoto, Japan, and now is a senior faculty member at the Department of Sociology and Anthropology, University of Sri Jayewardenepura, Sri Lanka. Her initial research was to explore the effects of biological and environmental factors for the maintenance of a behavioral tradition in a social group. Later by long term research she was able to demonstrate the acquisition and development process of a behavioral tradition by socially biased learning. Then she shifted to compare the interspecies difference in the same traditional behavior using three macaque species performing it, namely Japanese macaques, rhesus and long-tailed macaques. Currently she is analyzing the grip patterns of object manipulation in Japanese macaques.

About this document

The following compilation of scientific research articles is the result of the first 30 years of fruitful collaborations from people of different nations, backgrounds, interests and cultures. We believe that these collaborations have provided new insights into the understanding of the appearance, diffusion, and long-term maintenance of behavioral traditions in monkeys, as well as some of the underlying social learning mechanisms involved in the evolution of primate culture.

In the quest for cultural versus alternative explanations of behavioral variation within and between groups of the same species, there has been a heated conceptual and methodological debate among field and laboratory researchers. According to the environmental conditions of study, the species attributes, and the behavioral domain under investigation, the questions addressed and the methods used to answer them vary considerably. However, when considered alone, each of them has its limitations and even flaws. An integrative approach could then compensate for this shortcoming. By addressing the influence of environmental, socio-demographic, developmental, and phylogenetic constraints on the emergence, diffusion, and maintenance of behavioral traditions in the genus *Macaca*, a major part of the present research aims at contributing to this ongoing debate.

Among the various behavioral innovations and traditions reported in Japanese macaques (*Macaca fuscata*), stone handling (SH) is a form of solitary object play consisting of the non-instrumental manipulation of stones by performing various behavioral patterns, such as gathering stones into a pile, clacking stones together, or repeatedly pounding a stone on a substrate. We used a standardized observation procedure to systematically compare the context of occurrence, frequency and form of SH in 10 troops of Japanese macaques. More specifically, we compared four captive troops housed at the Kyoto University Primate Research Institute and Japan Monkey Centre, Inuyama, and six free-ranging provisioned troops living at four geographically isolated field sites in Japan, namely Arashiyama (Kyoto Prefecture), Koshima (Miyazaki Prefecture), Shodoshima (Kagawa Prefecture), and Takasakiyama (Oita Prefecture). Recently, we extended our comparison to five additional field sites in Japan, namely Funakoshiyama (Hyogo Prefecture), Katsuyama (Okayama Prefecture), Minoo (Osaka Prefecture), Miyajima (Hiroshima Prefecture), and Tsubaki (Wakayama Prefecture). We also extended our comparison of SH to two other macaque species, namely rhesus macaques, *M. mulatta* (one captive group housed at Kyoto University Primate Research Institute) and long-tailed macaques, *M. fascicularis* (one free-ranging provisioned troop in the Sacred Monkey Forest Sanctuary, Padangtegal, Ubud, Bali, Indonesia). We collected longitudinal data on the appearance, early diffusion, and long-term maintenance of SH within one free-ranging group of Japanese macaques and across generations at several points in time over a 30-year period. In the semi-controlled conditions of an outdoor enclosure, we focused on mother-infants dyads, and evaluated the influence of early exposure to environmental and social stimuli in the acquisition of SH during the first six months of life. We conducted field experiments to test the effect of SH artefacts (e.g., piles of stones left on the ground by previous stone handlers) on the subsequent performance of SH.

The combination of the comparative, longitudinal, and experimental approaches to studying SH behavior allowed 1) to establish the comprehensive repertoire of 45 SH patterns in Japanese macaques, 2) to reveal substantial variation in SH between troops, referred to as SH cultures, 3) to show a geographic distribution of clear troop-dependent clusters of SH variants suggestive of the notion of cultural zones, based on inter-troop observation and possibly males transferring SH patterns when migrating from one troop to another, 4) to rule out simple alternative explanations for such behavioral variability, such as genetic determinants or some obvious environmental differences, 5) to indicate that group size and composition in age classes, as well as group spatial cohesion may impact the prevalence of SH, 6) to provide evidence for the role of social factors in the acquisition of the behavior and the maintenance of the tradition, which may involve not only direct social influences through the observation by naïve infants of their mothers as SH demonstrators, but also indirect social inputs through the stimulating effect of SH artefacts, 7) to interpret some intra-group variability in the performance of SH patterns from the viewpoint of developmental constraints, 8) to show that in several troops, this behavioral tradition has reached its transformation phase, with an increase in the SH repertoire and an expansion of the contexts in which SH is practiced, also referred to as "ratchet effect" or "cumulative culture", 9) to argue that food provisioning by humans may be a key factor in the innovation and transformation phases of the SH tradition, and 10) to discuss the role of phylogenetic constraints and behavioral predispositions in the evolution of the SH culture in the genus *Macaca*.

In sum, our integrative approach to SH emphasizes both the product (via the comparative method to assess which differences are observed in the form of behaviors) and the mechanisms (via the longitudinal and experimental methods to determine which specific processes are involved in producing such differences) of the cultural phenomenon. SH is probably the longest studied and best-documented cultural behavior in monkeys to date. The methodology we used and the findings we obtained may have implications for various fields, including anthropology, psychology, ecology, ethology, and evolutionary biology. We draw an overall picture of rich cultural diversity in a particular type of object-play behavior in macaques, and suggest that multiple factors should be jointly considered to identify the sources of behavioral variation in animals. Our comprehensive dataset provides valuable empirical information to test predictions and fit models generated from theories about the role of cultural processes in human evolution. Our findings will contribute to the understanding of the biological foundations of non-human primate culture and the role behavioral traditions might have played in the emergence of hominid material culture through stone-tool technology (for stone-tool use in macaques, see also Malaivijitnond et al., 2007: Am. J. Primatol. 69, 227-233 and Gumert et al., 2009: Am. J. Primatol. 71, 594-608).

In addition to this major focus on SH behavior, we also studied, in Japanese macaques, fish-eating behavior on Koshima island, and dental flossing behavior at Arashiyama, as well as leaf swallowing behavior in chimpanzees (*Pan troglodytes*). We addressed the determinants of behavioral innovations and the constraints on their diffusion and maintenance within social groups of primates. Many new behaviors have been reported to appear in primate troops, but were either idiosyncratic, or independently adopted by very few individuals, or their performance was restricted to a small class of the population, and for some reason, they never widely spread within the group by social means to become traditions. We used longitudinal, cross-sectional, and experimental data to explore the history, describe the propagation, and assess the current prevalence of these behaviors at the group-level. We examined the factors that may have favored these innovations, including the environmental context, the individual characteristics of the innovator, and the structural and functional aspects of the behavior. Group size, kinship, and dominance are socio-demographic factors that are likely to limit the opportunities for any group member to observe the innovator, and thus constrain the diffusion or maintenance of these potential candidates for behavioral traditions. We discussed the role of the conformity process in the cultural transmission of behavioral variants. Identifying the determinants of innovations and the constraints on their diffusion within social groups of non-human primates is of special interest to understanding cultural evolution in hominids.

The research articles compiled in this document were ordered chronologically by year of publication, and then alphabetically by name of the first author. Related and complementary information, including additional theoretical background, methodological materials, maps of the field sites, galleries of pictures, the pdf files of most articles, and the curriculum vitae of the authors, can be found online at the following address:
http://www.primatecultures-stonehandling.pri.kyoto-u.ac.jp/

This work would not have been possible without the contribution of many people who helped in many ways during the course of our research. We wish to thank the researchers, students, staff, and friends who provided permission to work, support, assistance, and valuable specific information about the history, demography and environmental conditions of the troops at the different study sites and general information from other field sites. We are grateful to the following people in Japan: S. Asaba, J. Hashiguchi, T. Kawashima, S. Kobatake, and S. Tamada (Iwatayama Monkey Park, Arashiyama), S. Hanamura (Kyoto University Laboratory of Human Evolution Studies), F. Kanchi and T. Suzumura (Koshima Field Station), H. Kurita (Takasakiyama Natural Zoo), M. Matsubara, T. Matsuzawa, A. Mori, Rizaldi, H. Takemoto, and K. Watanabe (Kyoto University Primate Research Institute), M. Nakamura and Y. Takenoshita (Japan Monkey Centre), and M. Shimada (Teikyo University of Science and Technology). We also thank our Balinese colleagues from Udayana University's Primate Research Center, Denpasar, and more particularly A. Rompis, G. Soma, and N. Wandia. For her major participation in different stages of the research, including logistic assistance, contribution to data collection, entering, and analysis, as well as insightful comments during manuscript writing, we sincerely thank N. Gunst (University of Georgia, USA). For fruitful discussion and for providing us with longitudinal data on the Arashiyama-E troop, we thank P.L. Vasey (University of Lethbridge, Canada). For occasional assistance with data collection, we thank K.J. Petrzelkova (Academy of Sciences of the Czech Republic), M. Sakakibara and T. Harasaki (Gifu University, Japan), N. Tworoski (University of Minnesota, USA), and B. Detta and R. Manullang (Udayana University, Bali, Indonesia). We thank A. Jacobs (University of Strasbourg, France) for designing the website. JB is indebted to the Enomoto family for generously providing him with logistic assistance at Arashiyama during his study periods.

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Michael A. Huffman, Jean-Baptiste Leca, and Charmalie A.D. Nahallage, Inuyama, Japan,
December 7, 2009

Every study has a beginning, and this is ours

M. A. Huffman

After the first semester of my freshman year as an undergraduate at Ft. Lewis College, Durango Colorado, I arrived in Japan in early February 1978 for what was supposed to be a 3-month study abroad program between my university and the Kansai University of Foreign Language Studies (Kansai Gaidai), Hirakata, Osaka. I stayed on until August 1980. Through a fateful chain of events, starting with an introduction from the Dean of Student Affairs at Kansai Gaidai, I met with Dr. Masao Kawai at the Primate Research Institute, Kyoto University (KU) and his colleague in Kyoto, Dr. Junichiro Itani, in the Laboratory of Physical Anthropology, Department of Zoology (KU). In my heart I was convinced after my meeting with Itani sensei that Japan was where I was meant to be and that this was the place to study primates. Itani sensei invited me to attend the lab's seminar every Friday and introduced me to Yukio Takahata, who was then just finishing his MSc research on the reproductive biology and socio-sexual behavior of the Arashiyama Japanese macaques.

My observations of the Arashiyama B troop first began on August 2, 1979. Every Friday after seminar, I went to Arashiyama, and slept up on the mountain several days a week for the next 12 months. During my introduction to Japanese society and the society of Japanese macaques, I was befriended by so many distinguished primatologists in Japan, and indeed from around the world that came to visit Professor Itani in the laboratory of Human Evolution. Their friendships lasting to this day and the tireless guidance offered along the way had an important impact on my life and my thinking. I reluctantly left Japan in August of 1980, stopping off in Kenya for a few weeks to observe baboons at Gilgil with Fred Berkovitch and his wife Denise.

Mike Huffman (22 yrs.) at Arashiyam in the early summer of 1980

Back in the US and totally reverse culture shocked, I spent the next two and a half years in Colorado finishing up my undergraduate degree, thinking of nothing but returning as quickly as possible to resume my research at Arashiyama and to continue with my life in Japan. I received word in the summer of 1983 that I was granted a Japanese Government scholarship for graduate studies at Kyoto University. I quit a part-time job at a Japanese restaurant, *Arigatou*, in Durango, and prepared for the big adventure.

October 1983, Iwatayama Monkey Park, Arashiyama
On my first day back in Kyoto after reporting to Itani sensei, now my official graduate advisor, I took the bus and local train from Kyoto University to the Hankyu Arashiayama Railways station and rushed up to the provisioning grounds on top of Iwatayama. It had been three long years back in the US, finishing up my undergraduate degree. I had long waited for this day to come, working over-time back in Colorado to finish up my Bachelor of Science degree at Ft. Lewis College, Durango.

I climbed up the mountain with great anticipation, eager to see how my friends, both human and monkey, had been in my absence. I first greeted ‘Encho san’ (Nobuo Asaba, Director of the Park) and caught up on the latest news on the mountain. He had been like a second father, treating me like family, and providing every kind of support in my study of the Japanese monkeys. He allowed me to live up on Iwatayama in the small building he had constructed as an office and meeting place for the Arashiyama Natural History Society. Every few weeks he would say “Mike san, your looking a bit thin, we need to go get you something good to eat!” Working to support myself, I was on a tight budget. I became famous for discovering and eating good things that the monkeys ate in the forest as well as the fresh fruits and vegetables that Encho san and his staff gave to the monkeys. During my stay in 1979, I would usually spend four consecutive days a week up on the mountain. Most of the time waking up before the monkeys arrived at first light, going to bed late in the night after having followed the monkeys to their sleeping sites, sometimes returning again later in the evening to see what they did at night, and pouring over the literature Encho san had accumulated on research work done at Arashiyama since 1954.

Now back again on the mountain in 1983, nothing much had changed during my absence. The adult monkeys I had spent many hours with in 1979 had gotten a little older, some had died or migrated out of the troop, but of course there were many new young faces that I had to learn before starting up observations again.

It was time for the 12:00 feeding. Encho san and I were talking in his office about future plans for my research, what the monkeys had been up to etc… Suddenly a curious loud banging sound coming from the metal roof above us caught my attention. Curious, I rushed outside to see what was going on. Many young monkeys were up on the roof with handfuls of stones, rubbing them across the metal surface, gathering them together and scattering them about again. I had never observed the monkeys up on the roof with stones like this at Arashiyama before, and so I asked Encho san when this had started. He said that he was aware of this behavior for at least the two years (started to be noticeable sometime in 1981). He added that it had became particularly more noticeable after he dumped a large pile of stones on the side of the provisioning grounds, that had been left over from some trail repairs he had made.

After thinking about all this for a bit, I suddenly remembered a curious observation I had made during my first stay, of a young female playing with stones at the feeding site one day in December of 1979. Excited about the prospects of having possibly witnessed the start of a new cultural behavior for Japanese macaques I returned to the lab that afternoon and told Itani sensei what I had seen and heard at Arashiyama. He was very interested and encouraged me to look into it in more detail. A few days latter, after I had un-packed all my books and field notes, I found the field diary, in which I recorded in more detail that day’s events from my field notes. I then went through my photo and slide files and found a picture of the young female in action!

Field Diary entry: December 7 1979, Iwatayama Monkey Park, Arashiyama Kyoto
A few minutes after the 12:00 feeding time: *My attention is drawn to a young individual out in the center of the feeding site, a few minutes after the group is provisioned with wheat and soy beans. The 3-year old female, Glance 6476 is stacking and rearranging blocks of stones. I am struck by this human infant-like behavior. I quickly take a few photos then continue to watch her.*

Glance 6476 (Arashiyama, December 7, 1979)

She scatters the block like stones around with open hands, and scoops them together into a pile. I find it interesting that these stones could not have been collected from the immediate area because the feeding grounds were routinely swept clean of all debris (feces, liter etc.) after each feeding time for the tourist traffic. The rocks were deliberately gathered and brought to the center of the feeding site by this female from the forest at the edge of the provisioning ground. At one point when she was disturbed by other monkeys she picked up as many stones as possible, holding them against her chest with her arms and some clutched in both hands, she then moved off to a location about 5 meters away.

I picked up the remaining stones and brought them to her to see what she would do. She quickly took them, mixed them in with the other stones, and continued to play.

Two weeks after this first observation of stone handling in 1979, I traveled down to Kyushu on December 22 to spend New Years in Kagoshima Prefecture at the home of a friend (my future wife). Along the way, we stopped at the Takasakiyama Monkey Park, in Beppu (Oita Prefecture, northern Kyushu), famous as one of the earliest study sites of Japanese macaques by Junichiro Itani and colleagues. We stayed there for two days. Talking with park employees I learned that they too had seen monkeys handling stones for the first time in 1979. I was intrigued as to how this could happen. After I returned to Arashiyama on January 5 1980, I kept my eyes peeled for more incidences of this behavior. However, during the course of my entire study of the troop between August 1979 and August 1980 I saw stone handling only this one time.

Back to the future: Fall 1983 onward. My main topic of research at Arashiyama for my masters and doctorate was a study of female mate choice and partner preference in the Japanese macaques. This was a continuation of one of my study topics in 1979. My main focus of observations was mating activity of the troop, and this meant that my observations of stone handling couldn't start in earnest until the early spring of 1984, after the end of the mating season.

In December of 1984, Duane Quiatt, a professor from the University of Colorado's Denver Campus came to visit me in Japan. We had met in Colorado when I was an undergraduate and he was quite interested in observing the behavior of Japanese macaques since he had also observed rhesus monkeys on Cayo Santiago of the cost of Puerto Rico. We spent several weeks together observing the monkeys at Arashiyama. We also traveled to observe stone handling at Takasakiyama with Itani sensei, and then traveled on to Yakushima to see the sub-species *Macaca fuscata yakui*. Duane was the first to join me in the study of stone handling and together we began to conceptualize some of the implications for the long-term study of this behavior.

At the time, little did I know what and were this was going to lead to. These opportune events and guidance from senior colleagues at the beginning of my career set the stage for a very productive study that had led us on a study that has lasted now for more than 30 years. Most of the early work I did alone, but it is clear to me that the real advances began after collaboration with others. The first census of 1990 at Arashiyama was possible with the help of Ms. Connie Cagampang, an under-graduate from Berkley who came for the summer to assist in data collection and data entry. She volunteered her time in exchange for the opportunity to see if primatology was what she wanted to pursue for her graduate studies. She was a great help, and a source of motivation to systematically observe every individual in the troop. She went on to study law. She will certainly make more money!

Many advances in our understanding of this behavior and its implications for the study of social learning and culture in animals have been made in the last few years, thanks to the beautiful collaborations with my two junior colleagues and co-compilers of this document JB and Charmalie. It is through the tireless efforts that we own our understanding of the details of transmission, social learning and cultural variation between sites of stone handling behavior.

Junichiro Itani and Mike Huffman, co-chairing a satellite symposium on Culture as part of the 1990 IPS Congress in Kyoto, Japan

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Stone-Play of *Macaca fuscata* in Arashiyama B Troop: Transmission of a Non-adaptive Behavior

Stone-play, a directly non-adaptive behavior, was observed in the free-ranging Arashiyama B troop of Japanese macaques near Kyoto, Japan. Stone-play was classified into eight types characterized by gathering, picking up, scattering about, rolling in hands, rubbing in hands, clacking, carrying, or cuddling, of stones. The behavior, first observed in 1979, spread throughout 49% (n = 236) of the troop by 1984. Infants and juveniles of both sexes accounted for 80% (n = 92), while the remaining 20% were young adult males (6) and females (6) or adult females (11). Unlike other reported cases of novel cultural behaviors, this non-adaptive behavior initially diffused among younger individuals and was then later transmitted in form of tradition from these individuals to their offspring or younger sibs and playmates.

1. Introduction

The acquisition and transmission of new behaviors in Japanese macaques (*Macaca fuscata*) have been well documented (Itani & Nishimura, 1973). These behaviors all share in common a relation to feeding and are thus positively reinforced by the direct benefits acquired through its practice. The acquisition of stone-play, which involves the collecting, scattering, or carrying of stones, cannot be explained in these terms. Stone-play is not the means to an end in which apparent benefits are acquired. This article describes stone-play behavior and its transmission in the Japanese macaques of Arashiyama. The significance of this phenomenon in Japanese macaques and its implications for the study of hominid cultural evolution are discussed.

2. Method and Materials

Japanese macaques have been provisioned and studied since 1954 at the Iwatayama Natural Park, Arashiyama, Japan. (Baldwin *et al.*, 1980; Koyama, 1967; Takahata, 1982). The following observations were made during two periods (July 1979–September 1980 and November 1983–June 1984) on the Arashiyama B troop (Figure 1). *Ad libitum* observations were recorded with pen and note pad, occasionally supplemented with VHS video recording.

3. Observations

Description of Behavior

The sizes of a sample of 43 stones used in play, ranged from 11 mm × 11 mm × 11 mm weighing about 2 g to 110 mm × 110 mm × 70 mm^3 weighing 730 g. The mean measure of the three dimensions (arbitrarily determined) gives the size of an ordinary stone used in play as: 44 mm × 31 mm × 20 mm.

Stone-play was most predictably observed on clear, warm days and less frequently on rainy days. The number of players appeared to be fewer on overcast days. Stone-play could be most predictably observed after the provisioning of wheat and corn, a time when most

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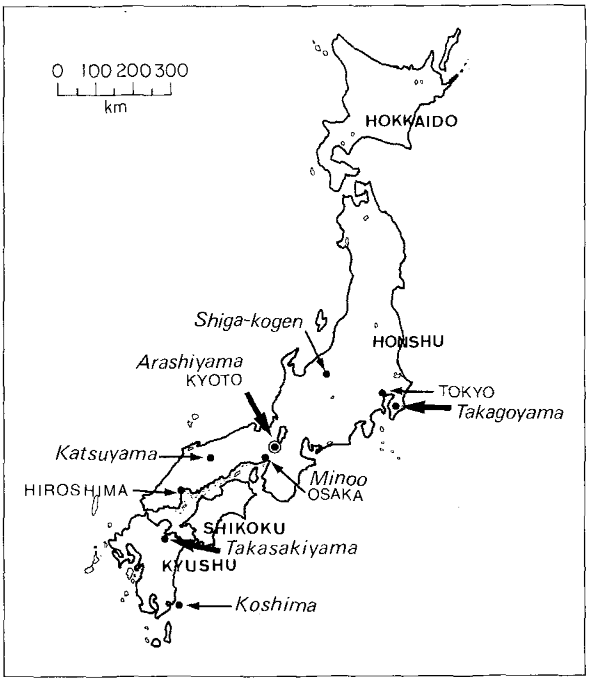


Figure 1. Map of Japan and location of primate study sites.

individuals are engaged in resting, grooming, or social play. Individuals seen stone-playing after feeding always had their cheeks filled with grain and showed no signs of distress or any emotional expression. Likewise, individuals stone-playing at other times of the day appeared calm while in the play activity. Individuals stone-played at or away from the feeding station.

Stone-play was classified into eight basic types.

Gathering: several stones (2–20) are collected, gathered into a pile or separate piles. These separate piles are formed when the individual picks up several stones, puts them down and collects new stones (see below). Similar collecting and carrying of sticks or peanut shells at the same time is also observed among certain individuals.

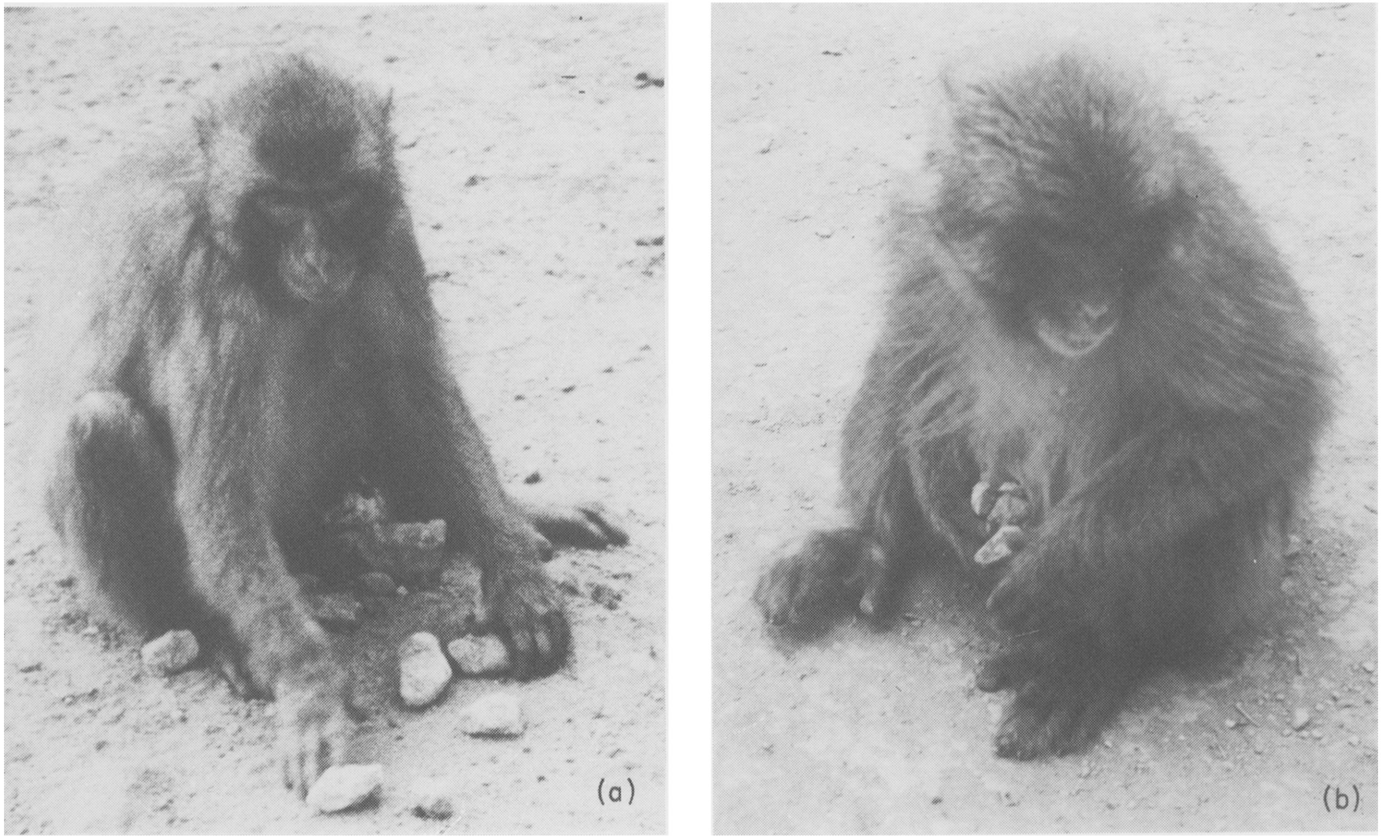
Pick up: one to several (5–7) stones are picked up and held in one hand. The stones are dropped and the procedure is repeated; the same stones are picked up, new stones are picked up from the same area, or new stones are picked up elsewhere.

Scatter about: stones which have been collected and placed in front of oneself are scattered about on the ground with open palm(s) in a circular or side-to-side sweeping motion [Figure 2(a)].

Roll in hands: one or two stones are picked up, and with an opposing directional movement of the forearms, rolled about rapidly between the hands.

Rubbing stones: two stones are collected, holding one in each hand, and rapidly rubbed against each other. Sometimes a smaller stone is held with one or both hands and rubbed on a larger stationary stone or similar flat object in a forward and backward motion.

Figure 2. (a) Individual scattering several stones about. (b) Individual cuddling several stones in both hands.



Clacking: two stones are collected, holding one in each hand, and rapidly struck together producing a clacking noise.

Carrying: stones (1–3) are picked up and carried. The stones are not manipulated in any particular fashion, but instead are held close to the body with a hand or foot.

Cuddling: usually one large stone, but sometimes several smaller stones are picked up and held closely to the body [Figure 2(b)]. The stone is carried around frequently when an individual changes resting positions, but usually the individual just sits in one place holding the stone. In such situations the individual is sometimes seen in social interaction with others, i.e., grooming, huddling, etc. *Cuddling* usually follows more active types of stone-play behavior.

Stone-play lasts from 30 seconds to over 20 minutes at a time with frequent periods of rest or change in play type. These behavioral types are performed individually or sequentially. The observed relative frequencies of the above behaviors are given in Table 1. The data is taken from 17 days of observation. The following excerpt from field notes exemplifies the sequential performance of stone-play behaviors in an eight-year-old, B1-596475.

> April 3, 1984. 10:42, B1-596475 is in brush below feeding grounds. *Pick up, rubbing stones, gathering.* 10:46′33″–:51′26″, she changes positions, *pick up, rubbing stones.* 10:51′26″–:52′12″, stops and grooms own leg. 10:52′28″–:58′28″. *Carrying, pick up, carrying, rubbing stones.* She stops several times and looks toward me. I act as if my attention were focused elsewhere and she resumes stone-play. 10:58′43″–:59′31″, B1–596475 moves across the slope *carrying* several stones with her. She sets the stones down in front of her and begins to feed off a small clump of grass. 10:59′31″–11:00′32″, she moves in between small brush isolated from other monkeys and the observer. *Gathering, pick up,* 11:00′32″–:00′47″, B1–596475 moves out into open and feeds on grass. 11:00′47″–:02′30″, *pick up, scatter about, rubbing stones, gathering.* 11:02′30″–:05′18″, feeding on grass frequently pausing to groom herself. 11:05′18″–:05′40″, *Pick up, gathering.* 11:05′40″–:06′24″, B1–596475 feeds on grass then moves out in open area and sits with others. Her three year old male offspring B1–59647580 approaches and both walk off.

When engaged in stone-play, others' attention was often drawn and one's stones were occasionally stolen. When approached, an individual would pick up as many stones as he could carry and run off bipedally or tripedally, to resume play elsewhere. Stones left behind were often picked up by the individual who approached, or by other individuals nearby who in turn would begin to play with the stones. In other instances, stone-playing

Table 1 **Observed frequencies of stone-play behavior at Arashiyama**

Behavior	Frequency ($n = 391$)
Gathering	42
Pick-up	91
Scatter about	83
Roll in hands	39
Rubbing stones	34
Clacking	7
Carrying	78
Cuddling	17

Data collected during 17 days from 169 instances.

individuals would be displaced and the intruder would begin to play with the stones. Occasionally an infant or juvenile would be approached by several playmates initiating chase or a wrestling bout. In some instances such individual would evade his playmates and resume stone-play. In other instances the individual ceases stone-play and joins in play with others.

In general, stone-play is a solitary activity with individuals spaced at least 1–3 m apart, but occasionally two to four individuals (mother–infant, siblings, playmates) would sit side by side while playing. Stone-play was also seen in social interactions where the playing individual was being groomed, would intermittently groom, or sit next to someone else briefly. Individuals would also forage off the surrounding vegetation.

Diffusion

Until 7 December 1979, stone-play was never seen at Arashiyama. The first individual discovered to display this behavior was G1-6476, then three years old. She was seen *scattering about, picking up* and *carrying* stones in the open space of the feeding area. By November 1983, stone-play occurred frequently (Table 1).

It is difficult to determine exactly to what extent stone-play behavior has spread throughout the troop, since it is impossible to test each individual for the acquisition of this spontaneous behavior. However, a general picture can be drawn from observations. Figure 3 shows the extent of observed diffusion. A total of 115 (49%) individuals were seen to exhibit stone-play behavior. Of these individuals, 92 (80%) were born between 1980 and 1983, after this play was first innovated. The remaining 20% was composed of six young adult males (4·5–8·5 yr), six young adult females (3·5–4·5 yr) and 11 adult females (5+ yr).

Frequently observed individuals not seen to exhibit stone-play behavior represented 24% (n = 57) of the troop. These individuals were all seven years or older. The remaining

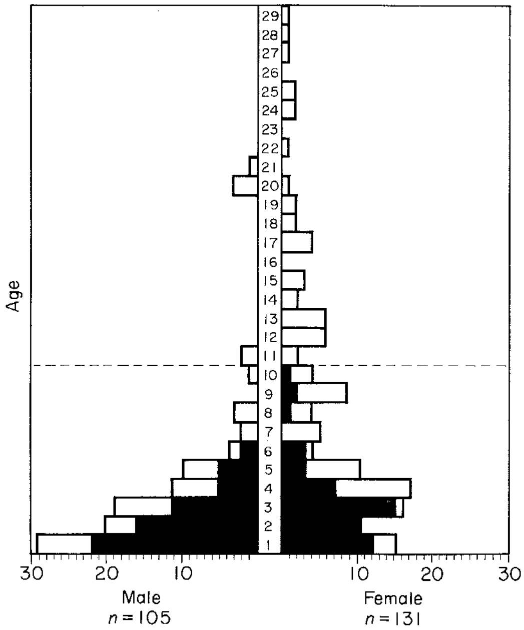


Figure 3. Histogram of Arashiyama B troop. Black areas represent number of individuals seen to exhibit stone-play behavior.

unaccounted for individuals (62) all under 10 years of age, have not directly been observed to play with stones or are peripheral individuals seldom seen with the troop.

The first individual seen to exhibit stone-play, G1–6476, was the only individual of her age in the troop seen to exhibit this behavior during the second observation period. Three older females, G1–6775 and G1–6774 of the same Glance lineage group, and B1–596475, were the only members of the troop older than G1-6476 seen to exhibit this behavior. In the acquisition of stone-play, like that of potato-washing or wheat-washing, observed on Koshima islet (Kawai, 1965), both age and positive nature of the individual appear to be related factors. These three females probably acquired this behavior as early as 1979, suggesting that older individuals do not acquire this behavior.

Although it is unknown which one of the four females originated this stone-play behavior, it is likely that she was a member of the Glance (G1) lineage group. Figure 4 shows the Glance lineage members seen to exhibit stone-play.

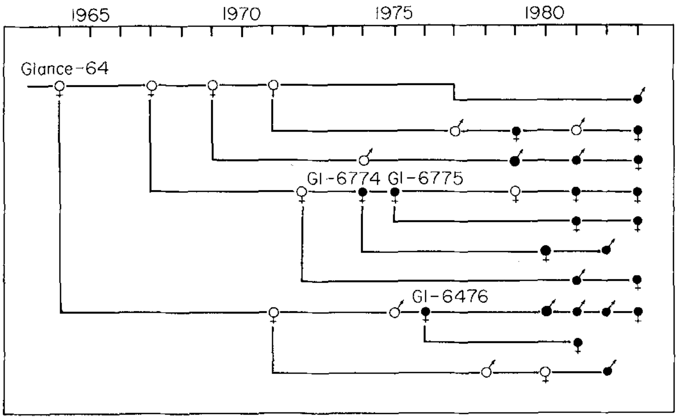


Figure 4. Glance lineage group. ♂, ♀: individuals seen to exhibit stone-play behavior.

No individuals over 10 years old were seen to exhibit stone-play behavior. In 28 out of 39 mother-offspring units (in which the mother was older than 10 years and the offspring were younger than six years), one or more offspring stone-played. This suggests that stone-play was transmitted at least partially between sibs. There were six mothers, 10 years or younger, seen to exhibit stone-play; G1–6774, G1–6775, B1–596475 (mentioned above), Op–7078 and Mo–5978. In all of these cases, all of their offspring born before 1984 were seen to exhibit stone-play. During the 1984 birth season, infants were born to B1–596475, G1–6474, and for the first time Op–626878. These females were all seen to stone-play within two to five days after giving birth. On 1 July, 12:59 B1–596475 was seen stone-playing while her infant sat to the side. The infant approached and sat down in front of her. As B1–596475 began grooming the infant, it started to grasp, rub, and try to lift a stone its mother had previously been using. The above observations suggest that the behavior was also transmitted from mother to offspring. Non-sib playmates were seen stone-playing together, suggesting that transmission may also occur through these channels.

4. Discussion

The above observations, as in the studies on the transmission of sweet-potato-washing, wheat-washing, and other cultural behaviors (Kawai, 1965; Itani & Nishimura, 1973), show that play in innovative, young, and frequently female individuals can be responsible for the initiation of new cultural behaviors into the troop. Frisch (1977) points out that play is a very important element in the occurrence of inventive behavior. He states that inventions are not the product of necessity, rewarded by food, mating, or status, but are rather the byproduct of play.

The manipulation of stones appears to be a relatively unreported phenomenon in macaques. A few brief descriptions of stone manipulation have been reported for enclosed groups of Japanese macaques, including methodical manipulation, tossing, and carrying among infants and juveniles, throwing as a form of display in young adult males, and use as a grooming tool on her infant by one adult female (Eaton, 1972; Candland, 1978, 1981).

Similar behaviors can arise independently among spacially separated groups of the same species because they share a common capacity to perform the behaviors (see Figure 1). In January of 1979 and 1984, stone-play was observed at Takasakiyama and is believed to have started almost at the same time as at Arashiyama (Huffman, unpublished data). Stone-gathering was observed also at Takagoyama (troop 1) in 1974 while the troop was still being provisioned (Hiraiwa, 1975). The stone-play described by Hiraiwa is equivalent to five behavioral types; *gathering, cuddling, pick up, rubbing stones,* and *roll in hand,* reported here. Hiraiwa reports that, at that time stone-gathering was observed at a frequency of 15 times in nine out of 31 days. Compared with Arashiyama, the frequency of occurrence was low (Table 1). At Takagoyama, stone-play was seen in individuals up to three years of age. No adults were seen to stone-play at that time. At present stone-play is infrequently seen in a few individuals at Takagoyama after provisioning has been abandoned (T. Fujita, pers. comm.). Aside from stone-play, other peculiar behaviors like this can be found in several different troops. The following are examples. Snowball construction by enclosed Japanese monkeys captured near Hiroshima and now in Oregon was reported by Eaton (1972). This novel behavior can also be observed among the free-ranging Japanese monkeys of Shiga-kogen (Figure 1), Japan (N. Okayasu, pers. comm.). Sweet-potato-washing behavior at Koshima reported by Kawai (1965) has been observed among a few individual monkeys at Takasakiyama and Arashiyama (Huffman, unpublished data).

Although the relationship between feeding and stone-play is not yet fully understood, the individuals involved clearly distinguish food objects from play objects. Except a few infants, stones were never seen to be put either in the mouth or up to the nose like provisioned or unfamiliar food objects.

Because of an overpopulation problem in provisioned troops, the volume of daily rations was decreased gradually over a few years in several areas including Takasakiyama, Takagoyama, and Arashiyama. The initial effect this may have had on the behavior of individuals in these troops is unknown. However, with the exception of Takagoyama at which provisioning has been abandoned all together, the amount of daily rations has not been further decreased in the last four to five years at Takasakiyama and at least six years at Arashiyama. At Arashiyama rations are widely distributed throughout the feeding area insuring that the lower ranking individuals have equal access. The most representative age class of stone-players, one to four years of age, have not experienced any change in provisioned rations.

Behavior similar to stone-play has been observed at Arashiyama before provisioning was started in 1955. Before provisioning of the troop at the present location, the monkeys inhabited an area further west along the Katsura river. According to Eiji Oota, a naturalist and educator in the area, there were several citris trees of the species *Poncirus trifoliata* in the troop's old range. The round fruit, about 4 cm in diameter is hard and was rarely eaten by the monkeys (Murata & Hazama, 1968). Oota (pers. comm.), who has watched the troop since 1948, saw the monkeys collecting, carrying, and scattering about the fallen fruits, but rarely did they attempt to eat it. After provisioning at Arashiyama similar behavior with provisioned food has not been reported.

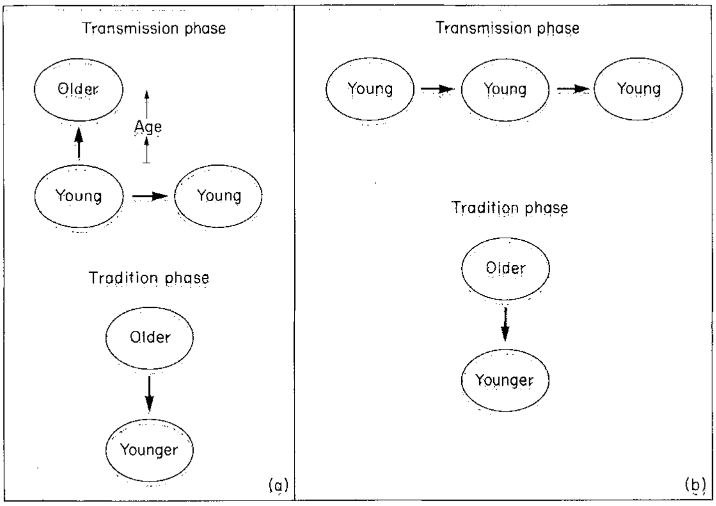
The behavior described in this article is considered to be a form of object-play in Candland's (1978) terminology. Stone-play is a motor activity rather than a sensory activity and the behavior occurs under low arousal conditions. Solitary or object-play in adults of other free-ranging macaques have not been reported. As for the documentation of adult play in free-ranging macaques there is little (Brueggeman, 1978; Caine & Mitchell, 1979). At Arashiyama however, in adults both solitary and social play were observed in the form of stone-play. In general adult stone-play at Arashiyama consists of more complex movement and manipulation of stones (e.g., *clacking* and *rubbing stones*), than younger individuals, and occasionally included the collecting and rubbing of sticks. This greater complexity can possibly be attributed to two factors: (1) experience and (2) greater neuro-motor development.

Menzel (1976) earlier reported that free-ranging Japanese macaques at Takasakiyama, Katsuyama, and Minoo, Japan, showed indifference to objects in their environment other than food (Figure 1). He stated that object manipulation lasted no more than 30 seconds, but that an object possessed by another individual becomes of more interest. At Arashiyama, individual stone-play lasted for several minutes at a time. Unlike food, these stones have no survival value, yet they are a sought-after commodity; especially when another monkey is playing with them. A positive reinforcement for the continuation of such play might be considered to be its popularity value. An object or play with that object is valued because it is desired by others. A similar phenomenon reported by Susan Isaacs in human children is discussed by Levi-Strauss (1969, pp. 85–86) in the context of the framework of social life with which universal institutions can be connected. The study of such behaviors in non-human primates may also provide data for application in similar studies.

There are many similarities between the nature of the transmission of stone-play and other cultural behaviors studied previously. However, there appears to be a fundamental difference in the direction of initial transmission. This is probably influenced by the nature of these behaviors. That is, one is play related and the others are feeding related. Thus the social networks involved are different. These differences in transmission are schematized in Figure 5.

As described by Kawai (1965), the initial direction of transmission of sweet-potato-washing, wheat-washing, and other cultural behaviors was from the young to the older; predominantly infant–mother and secondly among sibs. Listed above as transmission phase (a), Kawai calls this the "period of individual propagation". Once the younger individuals become older, the behavior is transmitted in the reverse direction. Kawai says it is always transmitted from the mother to child, and refers to this phase as the "period of pre-cultural propagation".

Figure 5. Channels of the transmission of (a) previously studied cultural behaviors and (b) stone-play.



Itani (1958) uses the term "tradition" as opposed to propagation, for the mother to infant or older to younger channel of cultural behavior acquisition. Here this is called the tradition phase. As was found in this study, behavior can be acquired by a young individual regardless of whether or not its mother exhibits the behavior. The transmission phase (b) of Figure 5 represents the channels in which stone-play is considered to have followed. Looking at Figure 3 it can be seen that no individuals over 10 years of age acquired the behavior. Initially, the behavior was transmitted between young females of the same Glance lineage and then to same age playmates of other lineages. The rate of diffusion increased greatly when younger sibs or other younger playmates and then finally one's own offspring began to acquire the behavior.

In a test designed to analyze the process of novel behavior acquisition, Itani (1958) discovered that the rate of acquisition of caramel-eating behavior was highest among individuals between one and three years of age. Similar results were obtained in the present study. Itani found that by six months of age 70% of the infants had acquired the behavior. In another study, Itani (Itani & Nishimura 1973) found that almost all the naturally occurring foods eaten by the Takasakiyama troop were acquired by infants in their first year.

The research on culture in non-human primates which began with the Japanese macaque, has analyzed the transmission of behaviors relative to subsistence; many concerning the acquisition of new foods (Kawamaura, 1959, 1965; Itani, 1958), methods of feeding (Kawamura, 1954; Kawai, 1965), or the manufacture of tools for use in foraging (Goodall, 1963; Nishida, 1973; Sugiyama, 1979). It has been generally thought that these new behaviors were acquired and transmitted because they were of direct benefit to the individual. However, Imanishi (1952), who first suggested the presence of culture in non-human primates, did not limit cultural transmission to "adaptive" behaviors only. Stone-play, reported here, can be said to demonstrate that even behaviors of no direct benefit to the individual are subject to cultural transmission. An area paid particular attention to by Imanishi (1957*a, b*), that of troop oriented behaviors such as the traditional transmission of leadership or troop leading related behavior have not yet been investigated. This topic should be given special attention in the future, collecting information from several areas before coming to any conclusions.

Frish (1976) states that "culture replaces random genetic mutation as the chief means by which the organism adapts itself to the environment". As shown here such behaviors do not necessarily have to be of direct adaptive value to be passed on from generation to generation. Sometimes even behaviors of apparent advantage or benefit fail to be propagated throughout the group (Kawai, 1965). This suggests that perhaps the mode of introduction (e.g., *play*) and the direct stimulus for the continuance of the behavior within a group (e.g., *popularity*), may be as important as "intrinsic" or envisaged adaptive value when considering the transmission of early hominid cultural behavior. When fixed in a group as tradition, what form the behavior takes after further individual accretion is also a topic worthy of further investigation.

In order to fully comprehend the process of early hominid evolution, it is necessary to understand the mechanism and full potential of their culture. The study of the transmission of learned behaviors such as stone-play by Japanese macaques may provide new insights into understanding the process of early hominid cultural evolution.

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Stone Handling by Japanese Macaques (*Macaca fuscata*): Implications for Tool Use of Stone

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ABSTRACT. Stone-play, a newly innovated cultural behavior, has been observed among the free-ranging Arashiyama B troop Japanese macaques near Kyoto, Japan since 1979. Conditions in which the non-purposeful handling of stones might possibly give rise to tool behavior are discussed. The progression of this behavior is traced through three phases: transmission, tradition, and transformation. During the first two phases, through social learning, the behavior was established within the group as a regular item of their behavioral repertoire and was most frequently observed after eating provisioned grain. In the third phase, observations suggest a "faddish" shift in the practice of certain behavioral sub-types between 1984 and 1985. During this period young individuals increasingly began to carry stones away from the feeding station, mixing stone manipulation with forage-feeding activities in the forest. Observations suggest under such conditions, stone handling is likely to lead to the occasional use of stone as a tool. This conclusion probably can be applied to species other than *Macaca fuscata*. Consideration of the eco-setting and social learning correlates of stone handling suggests how the instrumental use of stone might emerge from a tradition of non-instrumental manipulation.

Key Words: Japanese macaque; Play; Diet and behavior; Tool behavior evolution; Cultural transmission.

INTRODUCTION

BENJAMIN B. BECK has suggested that "the most important set of determinants in the origin of learned tool use...(may be) associative experience with objects in free play or non-problem settings" (BECK, 1980). Prior familiarity with the material properties and relations of objects in an animal's environment could increase the likelihood of their employment in a problem setting; and, on a more basic level of likelihood, fortuitous reward of some pattern of object manipulation requires at least that that pattern occur.

Experience with objects gained early in development may be essential to later proficient instrumental manipulation (RUMBAUGH, 1970, cited by BECK, 1980). MENZEL, on the basis of experimental data drawn from comparisons of wild-born and lab-born chimpanzees, has suggested that full realization of developmental potential for tool behavior depends on "early experience of a very general sort" (MENZEL et al., 1970; see also GOODALL, 1968). However, "...Tool using ability does not lie in the hands alone, in the central nervous system alone, or in the environment alone...but in some lucky interaction and isomorphic fit between them..." (MENZEL et al., 1970). As BECK has made clear (BECK, 1980), the relations between experience, setting, learning and evolution of tool behavior are complex and interesting. The case of Japanese macaque stone handling provides a nice opportunity to examine some of those relations.

Collection and manipulation of small stones by provisioned Japanese macaques was first reported at Takagoyama by HIRAIWA (1975). Stone handling was observed at Arashiyama and Takasakiyama in 1979, and its popularity at those two sites increased through 1984. Stone handling can be characterized, following CANDLAND's terminology, as a form of object play (CANDLAND et al., 1978), with inventive variations transmitted in a context of social facilitation and observational learning, individual repertoires influenced in part by matriline and other associations (HUFFMAN, 1984). HUFFMAN compared the cultural transmission of stone handling with that of feeding innovations well documented for Japanese macaques, e.g., sweet potato washing and wheat washing (KAWAI, 1965; HUFFMAN, 1984). Those behaviors are directly contingent on provisioning and presumably are directly reinforced by food rewards—food which washing makes more palatable or easier to ingest. Stone play, however, appears to be self-rewarding, with no apparent instrumental function, at least in its manifestation to date.

Stone play differs, too, from sweet potato washing and wheat washing in the manner of its early diffusion. Once introduced, sweet potato washing and wheat washing were acquired by older relatives of the innovator (in each case the same young female) as well as by age-mates. Stone play, on the other hand, was first transmitted solely among peer playmates aged 3–5 (HUFFMAN, 1984). At Arashiyama and Takasakiyama, where stone play continues to be observed, the original players have grown to adulthood. Stone handling now is acquired ordinarily a few months after birth by infants whose mothers handle stones. The behavior is widely diffused at both sites, but so far there has been no evidence for its adoption by adults. This tends to support our notion of it as a kind of play. However, since we are not in this paper concerned with the question of what constitutes play, or how play *per se* may contribute to the transmission and evolution of behavior, we will keep to a more neutral terminology: hence *stone handling*.

The behavior at issue involves repetitive manipulation of stone in a variety of ways (HUFFMAN distinguished eight subcategories in his 1984 paper, and we discuss changes in distribution of these, by age, in a later section). Stone handling is readily distinguishable in form and activity context from the occasional pick up, examination, and discard of a stone or other object by a monkey or ape engaged in exploration. Stone handling is essentially a solitary activity; although young monkeys may compete for stones and steal them from one another, stones are not the focus of social play—as when possession of an unusual found object triggers reciprocal chase-and-seizure games—nor is the manipulation of stones incorporated into social displays. In those features which involve collecting, scattering, and regrouping of stones, stone handling resembles the collection of inedible fruits, twigs, or leaves which is infrequently described as behavior idiosyncratic to one or a few related individuals in a group (OOTA, pers. comm. cited by HUFFMAN, 1984; QUIATT, unpub. data on *Macaca mulatta*, Cayo Santiago). What is perhaps most striking about stone handling by Japanese macaques, at Arashiyama and Takasakiyama, is the time and energy which individuals devote to it and its steady increase in popularity.

MATERIALS AND METHODS

This study was conducted on the Arashiyama B troop at the Iwatayama Natural Park, Arashiyama, Japan, over three periods (by one or both of the authors); July 1979–September 1980 (M.A.H.), November 1983–June 1984 (M.A.H.; D.Q. in January), September 1984–

February 1985 (M.A.H.). Observations were made *ad libitum*, by scan sampling and with VHS video. The feeding station area was scanned for stone playing individuals after each feeding when the behavior could most predictably be observed. In scan sampling, the area was scanned only once during any given feeding, moving across the grounds in a set direction to avoid sampling the same individual twice during the same sample session. Behavioral sub-types were recorded and individuals identified by name or age.

THEORETICAL CONSIDERATIONS

We will consider stone handling from two perspectives: (1) from a general standpoint, looking at this behavior as a kind of fad which, whatever its origins, can appear, flourish for a while, and then likely as not disappear again from the repertoire of a group; and (2) from a particular historical standpoint, focusing on Arashiyama at the present moment, and on stone handling there as a cultural phenomenon with its own history of adoption and transmission—asking how the specific contexts of stone handling may have changed (as opposed to what we will suggest is a conductive general context, provisioning with hard-coated grain foods), whether there have been important changes in character and distribution of manipulative subcategories, and, most important, whether there is any basis for predicting what is likely to happen next. The views from these two standpoints overlap, bringing into relief certain implications of Japanese macaque stone handling for the evolution of tool behavior.

THE GENERAL PERSPECTIVE: STONE HANDLING IN RELATION TO TOOL BEHAVIOR

BEN BECK, in his comprehensive review of animal tool behavior (BECK, 1980), noted that captive animals frequently are observed to use tools not just because they are frequently observed but because, caged, provisioned, and with plenty of "free" time, they are likely to spend some of that time exploring their restricted habitat and whatever objects it may contain. Thus, they are likely to become thoroughly familiar with the properties of those objects and, through random manipulation, to develop motor patterns some set of which may eventually be rewarded by attainment of food and thereby reinforced in practice.

The importance of observation and repeated imitative practice for mastering even so seemingly simple an exercise as probing for termites is well documented (e.g., GOODALL, 1968; MCGREW, 1977; see also BARD & VAUCLAIR, 1984). PARKER and GIBSON, in a discussion of the evolution of language and intelligence in early hominids, maintain that developmental acquisition of skills essential to the tool-using procedures which early hominids are likely to have practiced must have required a long period of juvenile dependency (PARKER & GIBSON, 1977). Similarly, LANCASTER and LANCASTER, speculating about the role and character of parental investment in early hominids, argue that "for early hominids, the evolution of a protected period of juvenile dependency...could have led to major improvements in tool-using and tool-making techniques even before any significant change in brain size or organization, because of the creation of leisure time to be spent in play, object manipulation, and the development of skilled performances without a need to participate in the food quest" (LANCASTER & LANCASTER, 1983).

We do not mistake Japanese macaques for early hominids, nor do we propose to develop the parallel, implicit in LANCASTER and LANCASTER's discussion, between cages of captive animals and putative home bases of "central places" (Isaac, 1971, 1983) of early hunter-gatherer hominids. It is important to keep in mind, too, that the evidence so far for tool-use and tool-making by small-brained hominids prior to 2.6 million years ago comes strictly from comparative primate behavior and comparative and functional anatomy, not from the earth. We especially want not to equate Japanese macaque stone handling with tool using. But we agree with Beck that "tool use, in terms of topography function, or causal dynamics, dovetails imperceptibly with other categories of behavior," and it seems to us that frequent *handling* of stones, if to employ a stone as a tool entails having some familiarity with the properties of stone, must be likely to increase the probability of stone tool *use* being initiated within a group.

Beck's comments on the random manipulation of objects by captive animals may yield insight into the occurrence of stone handling among Japanese macaques provisioned with hard-coated grains—as at Arashiyama, Takasakiyama, and, for a time at least, Takagoyama. About the precise connection between provisioning and stone handling, *in its original occurrence and initial stages of adoption*, we can only speculate. But, at least until recently, "stone-play could be most predictably observed after the provisioning of wheat and corn" (Huffman, 1984), and monkeys seen handling stones typically are engaged simultaneously in chewing grain from cheek pouches.

In nature, for Japanese macaques and indeed for most primates, foraging is a time-consuming whole-body activity. Collection and processing of natural foods involves a complex conjunction of integrated activities, reaching out, grasping, holding, plucking, chewing, moving to a new position, etc., operations in which there would seem to be reinforced an accustomed synchrony of mastication and other body movements, particularly arm and hand movements directed toward manipulation of foodstuffs. Under provisioning and in close competition with group associates, Japanese macaques collect food as rapidly as possible, with minimal pre-ingestive processing. Time spent on internal processing of pouched grain foods far outweighs that devoted to collection and pre-processing.

It seems reasonable therefore to speculate that, since hard-coated grains require considerable processing subsequent to collection and pouching, monkeys so provisioned and engaged in long bouts of a strenuous but not particularly preoccupying activity (chewing) might feel a need to be "doing something" with their hands—grooming, for instance, or (once tradition has made it a possibility) handling stones. From this standpoint, to suggest that stone handling may be self-rewarding is not to beg the question of cause but to raise the question whether such a need, given a particular set of diet and foraging constraints, might not be physiological.

Rather than speculate further about what it is that could make this repetitive, ritualized manipulation of stones so popular an activity in the contexts in which it has been observed and recorded, we will simply reemphasize the original connection with corn and wheat provisioning. In Takagoyama, where provisioning was discontinued in March of 1976, stone handling is reported to be now much reduced in frequency (Fujita, pers. comm. cited by Huffman, 1984). While we lack the quantitative data needed to document thoroughly this rise and fall in popularity, the history of stone handling at Takagoyama, as reported, is suggestive. Of course, it should not suggest anything like a *necessary* correlation with provisioning; we do not want to argue that stone handling can occur *only* in conjunction with provisioning or that, once having been introduced into a group, it must then persist for as long as provisioning is maintained.

At Takasakiyama there appears to have been, in recent months, a decline in the frequency of stone handling bouts. If that decline should continue, it will seem reasonable to inquire whether there may not have been concomitant persistent changes in the pattern of provisioning or in some context features associated with provisioning. However, as noted, features of stone handling which interest us mightily are its faddishness, the apparent lack of instrumental function, the disinclination of adults to adopt it, and the inventive variations in patterns of display—there seems to be nothing "necessary" about this behavior, and, apart from the obvious fact that familiarity with an object in some sense must underlie its purposeful employment (SCHILLER, 1957), stone handling cannot be posited as a *necessary* precursor to stone tool use.

It makes sense to look at the evolution of stone tool behavior in terms of a Markov progression. The coincidence of stone handling with provisioning, and, in particular, with provisioning of hard-coated cereal grains, suggests some distribution of probabilities for the occurrence of stone handling in nature (assuming that stone handling can occur in nature) in correlation with a limited range of dietary circumstances. Similarly (and disregarding dietary circumstances) it seems reasonable to assign higher probabilities of eventual tool use to groups in which stone handling has come to be practiced on a regular basis.

Thus, what we see from the general standpoint is a kind of object play, weaving in and out of the manifest repertoire of a species' behavior, more likely to be in when certain diets prevail and, when it *is* in, tending to increase the likelihood of stone tool use. This raises the question whether we can outline, without considering the specific purposes to which stone tools will be put, some conditions in which stone handling could be expected to give rise to tool behavior. To deal with this question, we will move to the historical particular standpoint and look at one manifestation of stone handling—at Arashiyama—as a prolonged cultural phenomenon with its own history of adoption, transmission, and change.

THE HISTORICAL PERSPECTIVE: STONE HANDLING AT ARASHIYAMA

HUFFMAN has outlined the diffusion of stone handling at Arashiyama from its first appearance in 1979 through the spring of 1984 (HUFFMAN, 1984; Fig. 1 below), breaking it into two phases, in part to facilitate comparison with previously studied diffusions of innovated behaviors (ITANI, 1958; KAWAMURA, 1959; KAWAI, 1965). The conventional distinction drawn between "transmission" and "tradition" phases in the propagation of innovations seems to us meaningful and illuminating. However, these terms connote a processual conservatism which does not quite fit the case of stone handling (see below) and events at Arashiyama suggest that it may prove useful, where stone handling is concerned, to recognize a third phase.

RESULTS

TRANSMISSION PHASE

The introduction and early dissemination of stone handling presumably is similar from group to group in the character of its occurrence. A young monkey (at Arashiyama, *Glance 6476*) collects and manipulates stones, does so again, and over time continues to repeat that activity for increasingly extended periods. Sibs and unrelated playmates aged 3 or less

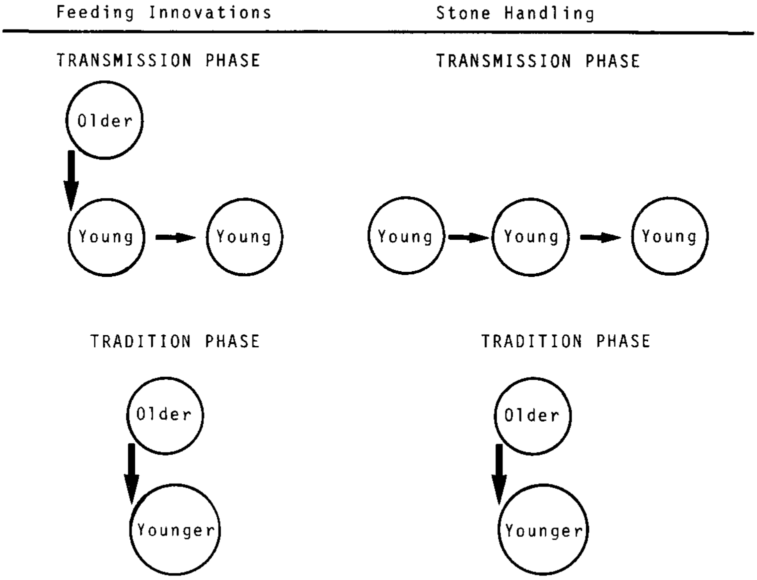

Fig. 1. Direction of transmission of feeding innovations and stone handling (after HUFFMAN, 1984). Note the difference in the transmission phase between stone handling and previously studied innovations in feeding behavior.

observe and imitate the behavior. This repetitive, stereotypical manipulation of stones is transmitted initially to a network of spatial-interactional associates which is specific to the innovator(s) and characteristic of the behavior context (i.e., play). As innovators grow older, their social networks are extended; younger sibs and new peer-associates become stone handlers. Observational learning plays an important role, as in, e.g., chimpanzees (GOODALL, 1968) and forest baboons (*Mandrillus sphinx*, CAMBEFORT, 1981). The relation between social facilitation and imitative learning in this process of transmission has been discussed by CAMBEFORT (1981); individual learning and cultural transmission of behavior have been compared by NISHIDA (1986); and KURLAND and BECKERMAN (1985) have remarked on the complexity of relations between accident, invention, and observational learning.

TRADITION PHASE

When female stone handlers reach reproductive maturity, as many now have at Arashiyama, a new phase is opened. In this *tradition* phase the rate of diffusion is approximately equal to the birth rate: an infant will learn stone handling from mother, from an infant playmate whose mother handles stones, or from an older sib who has learned stone handling from a playmate. This observational learning occurs very early in development. Infants as young as 3 weeks show interest in handling of stones—approaching, grasping at, mouthing, and picking up stones being handled by mothers (HUFFMAN, unpub. data from Spring 1985). At this stage, as long as there are stones available, stone handling may persist as a tradition within the group, though there can be no guarantee that it will persist. The case of Takagoyama suggests that persistence may be contingent on diet and foraging circumstances, which is consistent with the view presented here. Stone handling at Takagoyama appears never to have reached a high frequency, and it is likely that the *tradition* phase had not been attained before provisioning was discontinued.

The monkeys at Arashiyama are now in the *tradition* phase, with stone handling propagated via observational learning from mothers to infants as well as laterally among playmates. Currently, there are indications of change which should not only strengthen the tradition but, in theory at least, increase the likelihood of stone tool use occurring as an indirect outcome of non-purposeful manipulation.

TRANSFORMATION PHASE

For at least some young individuals, practice and acquired familiarity with the properties of stones are likely to extend the repertoire of motor sequences employed in stone handling. In terms of the group, this means an accumulation of variety available via observational learning to new stone handlers. That variety is available in practice primarily to 1- to 3-year-olds. Older individuals do not seem as quick to pick up on change, but within that younger age-group innovation, exchange, and replacement of manipulative patterns are free-flowing. This faddish cycling of motor activities is difficult to document, much less interpret. However, continued observation of stone handling at Arashiyama has yielded a number of new behavioral sub-types, most of which so far appear to reflect behavior predominantly of individuals born since 1980. Furthermore, comparison by age of subject of observed stone-play behaviors shows an interesting distribution (Table 1): *Gather*, *Pick-up*, and *Scatter*, categories representing what might be called the generic pattern of stone handling, are broadly distributed across age classes, while categories which reflect a more specific attention to one or two stones as well as to the activity at hand are limited almost exclusively to 1- to 3-year-olds.

In January 1984, when we spent two weeks videotaping sequences of stone handling, there were heavy snowfalls at Arashiyama; the monkeys spent most of each day at the feeding station, where on sunny days the thaw was quicker and where food and stones were plentiful. The next winter (1984–1985), when there was an abundance of acorns and no snow on the ground through January, the troop spent less time at the feeding station and more in the woods. Table 2 shows an interesting shift in behavior frequencies from 1984 to 1985 (because sampling procedures were revised in 1985, tests of significance cannot be applied, but patterns of difference are not much affected).

Table 1. Distribution by age and behavioral sub-type for stone handling sampled in the fall and winter of 1984–85.

Stone handling sub-types	Year of birth 1984	1983	1982	1981	1980	1979	1978	1977	1976	1975	1974	Total
Gather	5	12	5	4	19	2	12	—	1	1	—	61
Pick-up	11	15	9	1	18	5	20	—	3	4	—	86
Scatter	2	15	11	8	4	4	12	—	—	2	—	58
Roll in hands	—	3	2	1	—	—	—	—	—	—	—	6
Rub	23	41	11	6	1	—	1	—	—	2	—	85
Clack	—	2	1	—	—	—	—	—	—	—	—	3
Carry	11	24	9	4	—	1	6	—	1	—	—	56
Cuddle	6	13	6	1	—	1	—	—	—	—	—	27 ($N = 382$)

Data collected during 113 days between September 22, 1984 and February 15, 1985 from 95 identified individuals.

Table 2. Relative frequencies of stone handling sub-types compared for 1984 and 1985.

Stone handling sub-type	1984	1985
Gather	.11	.14
Pick-up	.23	.20
Scatter	.21	.14
Roll in hands	.10	.03
Rub	.09	.27
Clack	.02	.02
Carry	.20	.14
Cuddle	.04	.05
	1.00 ($N = 391$)	.99 ($N = 681$)

Data was collected during 17 days from 169 instances in 1984 and 22 days from 204 instances in 1985.

Some behaviors—*Gather*, *Pick-up*, *Clack*, and *Cuddle*—show very little change in frequency. *Gather* and *Pick-up* of course are activities basic to stone manipulation and probably should not be expected to change much. Other behaviors show marked change in frequency; most outstanding is *Rub*, which appears to be the going fad (note however that certain individual "specialists" account for a high proportion of *Rub* bouts—HUFFMAN, unpub. data). *Carry*, *Clack*, *Cuddle*, and *Rub* are behaviors displayed most frequently by young individuals (Table 1). In 1985, the youngest stone players showed an increased tendency to take stones into the woods on leaving the provisioning station and to mix stone play with feeding. For these troop members, the range of sites and situational contexts in which they practice stone handling was significantly expanded. The expansion may be attributed in part to (or at least is nicely correlated with) change in weather conditions and increased abundance of natural foods (acorns).

Two incidents from the winter of 1985 will serve to illustrate the conjunction of activities just noted. HUFFMAN observed a 3-year-old male, a life-long stone player, rubbing stones, his mouth full of acorns after foraging in the woods. He rubbed stones together, paused, removed an acorn from his cheek pouch, took the shell part way off, rubbed the acorn against one of the stones, and ate the now wholly shelled meat. In the second incident, a monkey was reported to have rubbed a dirty sweet potato with a rock before eating it.

Note that we do *not* submit these as instances of tool use. In our view, their significance lies precisely in their ambiguity, in the fact that they cannot readily be categorized by formal criteria (i.e., apart from assumptions as to cognition and intent). They return us to BECK's observation that tool use dovetails with other categories of behavior (BECK, 1980). The repetitive, stereotypical character of stone handling in its initial forms has been invaded by lability, and more and more at Arashiyama the motor patterns of stone play are being integrated with those of other activities. Stone handling in its original manifestation was, and is, an exercise which affords experience with the properties of stones. When stones are handled in conjunction with other materials, while feeding for instance, a basis is established for relating the properties of stone to those of other materials—for an understanding, in effect, and in terms of accumulated sensory experience, not just of the properties of things but of relationships between them.

SUMMARY AND CONCLUSIONS

Propositions about the importance of play and diet to animal tool behavior arise from the observation that there is an inverse relation between time spent foraging and time available for object play, and that playing with an object increases the likelihood of putting it to instrumental use. That tool behavior is more common among captive animals than among wild conspecifics may be explained largely by the fact that the former are provisioned and have more time to explore their environment. As BECK points out, captive animals are also likely to come in contact with novel objects as well as atypical foods. He further states that, atypical foods may stimulate atypical feeding responses—so that, altogether, (1) provisioning promotes the exploratory manipulation of objects; and (2) "object manipulation provides a pool of behavioral variants which, if fortuitously reinforced, can become tool patterns" (BECK, 1980).

Our examination of stone handling by free-ranging but provisioned Japanese macaques supports BECK's argument. Stones are encountered by monkeys foraging in nature (especially when digging for subsurface food items), hence they cannot be considered novel objects when they occur in numbers at a provisioning site. Nevertheless, that they do occur there in numbers and in conjunction with novel foods (i.e., hard-coated grains) is atypical.

Whether or not such foods are seen as stimulating atypical feeding responses must depend on what one considers typical for *Macaca fuscata*. Japanese macaques, like other forest-dwelling macaque species, forage much of the time off the ground. This requires a greater investment of both time and overall body activity in procurement and processing, *prior* to pouching, than does picking up harvested grain cast on the ground. Conversely, the latter requires a considerable amount of active processing *subsequent* to initial intake and pouching. It appears as if there is a systematic relation between prolonged chewing of grain and the manipulatory activities involved in grooming and stone handling.

Stone handling raises other interesting issues. As noted, stone play in its initial manifestation (i.e., in the transmission and tradition phases) involves a distinctive set of apparently self-rewarding operations. They appear to be highly absorbing and, in that sense, self-contained, detached in their exercise from other more ordinary activities. To the extent that it is coupled temporally with ingesting provisioned food, stone handling may be reinforced by food gratification, and so likely to become habitual in development. However, it is difficult for us to imagine how a specific operation might be fortuitously instrumental and selectively rewarded. On the other hand, if at Arashiyama young animals continue to carry stones away from the feeding station, and if stone handling continues to be integrated with other activities in what we have called, perhaps prematurely a *transformation* phase, then it is easier to see how the application of stone to another material could be rewarded and lead to the learning of tool use (HAMILTON, 1973; BECK, 1980). The food-rubbing incidents cited earlier suggest how this might occur. Where quadrupedal monkeys are concerned, skeletal-muscular constraints associated with habitual posture and locomotion are likely to direct the effective instrumental manipulation of stone to rubbing or scraping operations rather than to hammering.

It is important also, where tool behavior is concerned, to keep in mind the distinction between learning and evolution. Manipulation and instrumental use of an object may be learned by individual animals and transmitted as a feature of culture over generations. From the standpoint of biological evolution, what evolves is not tool behavior *per se* but the facility for learning, neural coordination, and—in the unique case of hominids—complex anatomical accommodation to a niche which has been radically transformed by habitual conversion of various materials to objects of use. Though we anticipate that stone handling at Arashiyama and Takasakiyama is likely to give rise to the occasional use of stone as a tool, we of course do *not* predict niche transformation and further evolution of tool behavior in this sense. The most likely outcome for stone handling at Arashiyama and Takasakiyama is continued cultural transmission of the trait until some change in the environment, e.g., long term food shortage (HAMILTON, et al., 1978, cited by BECK, 1980) or change in diet make it maladaptive. Environmental opportunity is critical for behavioral evolution.

The affirmation of the importance of environmental opportunity seems to us an important lesson to be gained from considering the context of stone handling in Japanese macaques. It encourages us not to think of the invention of stone tools either as a serendipitous solution to problems set by nature or as the automatic endpoint of a natural chain of events: non-instrumental manipulation of stones→use of stones as tools→manufacture of stone tools.

Manipulation of stones is, to begin with, an oddity of behavior for most primates. In the case of Japanese macaques, it appears that only exceptional environmental circumstances are likely to provide "room" for non-instrumental manipulation of stones as a regular item of daily behavior. Even where stones are handled daily, and where stone play has become a popular, time consuming feature of behavior, our observations indicate that it is unlikely to give rise to instrumental manipulation until the material and some of the operations of this behavioral fad have been integrated into other, more basic life activities. Integration may be furthered by minor and temporary environmental changes (e.g., climatic variation from one year to the next, as witnessed at Arashiyama between 1984 and 1985); but, alternatively, change in the environment may tend to reduce or eliminate what might be called the source behavior, the habit of non-instrumental handling of stone (as we suggest may have been the case at Takagoyama). Thus, stone handling could occur, disappear, and reoccur any number of times as an apparently regular item of a group's manifest repertoire of behavior, culturally transmitted from generation to generation and even from group to group, and never once be practiced in a context providing fortuitous reward and shaping instrumental use. Handling stones on a regular basis of course increases the likelihood of fortuitous reward, subsequent learning, and transformation to the next stage of instrumental use of stones as tools. But even then the process is reversible, and furthermore, it is most unlikely that a group of Japanese macaques or any species of monkey would progress to a stage of tool manufacture. Only long-term perpetuation of just the right conjunction of circumstances could bring about the change of niche which we must have in mind when we think about the evolution of stone tool manufacture from habitual use of stone as tools. Events at Arashiyama and Takasakiyama shed no light on this end result; however, they contribute to understanding of the process by suggesting how, in a specific eco-setting, free handling of stone can give rise to instrumental use.

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On Home Bases, Nesting Sites, Activity Centers, and New Analytic Perspectives

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cent discussions on Piltdown and Keith's possible involvement (CA 33:243–93).

First, although it has often been regarded as a depiction of Keith's reconstruction of the Piltdown skull, one of us (P.V.T.) has shown recently that the cover figure represents the Piltdown I hominoid fragments superimposed on the outline of a modern English skull often used by Keith for purposes of comparison (CA 33:281).

Secondly, a curious contradiction has emerged as to the words embossed alongside it: "Piltdown Skull" according to Kennedy (p. 269), "Piltdown Fragments" according to Tobias (p. 281). Further researches by us on the various editions and impressions of *The Antiquity* have revealed that both of us were right, albeit in respect of different impressions of the first edition.

We have found that "Piltdown Skull" appeared on the cover of the first impression of the first edition (October 1915) and "Piltdown Fragments" on the second (December 1915), the third (February 1916), and the fourth (March 1920), as well as on the second edition (January 1925). The change from "skull" to "fragments" was thus effected between the first and the second impression of the first edition.

The original wording was misleading and, as we have seen, did indeed mislead some scholars. It is possible that Keith realised how misleading it was and instructed his publishers, Williams and Norgate, Limited, to change the cover for the second impression. Or a colleague might have pointed it out to him. Possibly a reviewer of the book might have drawn attention to it, but this is the least likely, for there was a lapse of only two months between the first and the corrected second impression.

Postscript. Carmel Schrire has kindly drawn our attention to an American printing of the 1915 edition published by J. B. Lippincott. The cover bears the label "Piltdown Skull," and we assume it was based upon the first impression published in England. We have been unable to trace whether Lippincott published a second impression.

On Home Bases, Nesting Sites, Activity Centers, and New Analytic Perspectives

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Japanese macaques have been observed to engage in "stone play" or "stone handling," carrying about and manipulating stones in a variety of contexts both in captivity and in free-ranging circumstances, both in provisioned groups and, for a short period of time, in one unprovisioned one. In groups in which stone handling is popular and culturally well-established, transmitted over several generations, individuals may engage in this noninstrumental manipulation of stones on a regular basis and for long periods of time. Is Japanese macaque stone handling relevant at all to the use of stone implements by early hominids and the formation of sites resembling home bases or food-processing locations? Our studies of stone handling (Huffman 1984, Huffman and Quiatt 1986, Derr and Quiatt 1992) incline us toward a positive answer, and that inclination is reconfirmed by our reading of Sept's (CA33:187–208) response to the challenge issued some years ago by Isaac: (1986:237): "Can we conceive of patterns of behavior and adaptation that could lead to the formation of familiar-looking patterns of archaeological evidence, and yet which were behaviors unfamiliar to us in that they were structured differently from recent and present-day human ones?"

Sept asks whether the accumulation from year to year of remains from chimpanzee foraging and nest construction might not establish a physical pattern similar in its local concentration to that which suggested to Isaac the use of home bases by early hominids. To test her hunch she looks at the accumulation of nest remains over a two-year period of a small population of chimpanzees on the Ishasha River (p. 195):

> If the chimpanzees had left durable residues of their manipulative activities wherever they constructed a nest, for example, sites could have been buried and preserved by the overbank sediments of the Ishasha River. Such "sites" would not have formed as a result of home-base behavior or other communal activity patterns; they would have formed because something about the local forest structure and composition—perhaps fruit density or canopy height—favored frequent reuse of the locality for chimpanzee nesting or feeding and debris accumulated there through time.

Sept concludes that her research "supports arguments that early archaeological sites could have formed as byproducts of a system of subsistence and ranging very different from a home-base or central-place foraging system."

Chimpanzees do not manufacture and use stone tools in nature, but Sept (p. 204) wonders whether it is possible to "imagine a behavioral mechanism that could account for the occasional transport of stone or bone to favorite patches of fruiting or nesting trees without invoking cooperative foraging and food sharing." The answer, of course, is yes. As Boesch and Boesch (1984) have shown, chimpanzees carry nut-cracking stones up to several hundred meters. It may be, as Potts (1984, 1987) has argued, that some concentrations of stone artifacts and bone in Bed I Olduvai represent tool caches, stone having been transported to refuge areas in conjunction with a scavenging pattern of subsistence. But it may be, too, that the ancestors of those putative scavengers transported stone to the same or similar refuge areas for quite other purposes—for processing vegetal foods or, for that matter, for purposes not directly connected with food processing.

The questions put by Isaac and now Sept need not and probably should not be addressed solely from a chimpcentric perspective; stone handling by free-ranging Japanese macaques provides a challenging example of how activities can combine to produce clumpings of artifacts that would be unlikely subsequently to yield insights about origins. Since stone play and stone transport became established as a daily practice of the younger generations of the Arashiyama and Takasakiyama troops (five in total), piles of stones have begun to accumulate in certain areas of the forest surrounding the provisioning grounds. These "play stations," revisited daily, are occasionally located near forest foraging sites, because the behavior is often intermixed with or followed by (but in no way directly related to) foraging for acorns, grass, and leaves. Stones are transported from one station to another and deposited on stone slabs (fig. 1) at the bases of large trees and sometimes even in trees. Stones are occasionally modified, scratched, or chipped in handling, and recycling can produce repeated modification.

FIG. 1. *Stones left on flat stone surface by free-ranging stone handler(s) at Takasakiyama, Japan. (Photo Michael A. Huffman.)*

McGrew and Moore take issue with Sept's rejection of "referential models" on grounds, following Stanford and Allen (1991), that the distinction drawn by Tooby and DeVore (1987) between "referential" and "conceptual" models "is artificial and misleading" (Moore, p. 199). McGrew adds (p. 198) that while "referential models have their drawbacks (no species *is* another species), . . . they have one big advantage: Living organisms can provide us with both behaviour and artefacts, while concepts supply neither." We agree strongly with both observations and would like to remind readers, further, that Stanford and Allen were critical not just of Tooby and DeVore's advocacy of "conceptual" over "referential" models but of what they saw as a return under new banners to the unreconstructed ground of male-centric hunting/scavenging.

As Stanford and Allen remind us, although male cooperation in the hunt and use of stone implements to procure and/or process meat may have had great adaptive significance at some stage of human evolution, there is little support for the notion that hominid culture can be traced to an original association of these two "historical occurrences." Indeed, the one documented instance to date of tool-assisted predation on vertebrates by chimpanzees in the wild is the very recent observation at Mahale of an adolescent female's using a modified branch to capture a large adult squirrel hiding in a hole in a tree (Huffman and Kalunde 1993). Chimpanzee tools are virtually never used in conjunction with meat procurement, and although females may participate infrequently in hunting parties at Gombe and Mahale (in 4% of hunts observed at Gombe [Goodall 1986]), females at the Tai National Park, where stone and wooden hammers are used to crack nuts (as they are not in either Gombe or Mahale), are both more active hunters (13% of all individuals observed hunting [Boesch and Boesch 1989]) and more active nut-crackers, just as Gombe females are more active termiters (McGrew 1981). Tai females are more active sharers of meat than females at Gombe, sharing with males as well as with offspring and other females. "Most food sharing among chimpanzees involves plant foods shared between mother and infant (de Waal 1989, McGrew 1981), and so models of human social evolution based on meat procurement may apply only to a very recent stage" (Stanford and Allen 1991).

Just as it is heuristic now and then to decouple our speculations about male cooperation, hunting (and scavenging), and tool use, so it may be heuristic to decouple our thoughts concerning object manipulation and transport, tool use, and food procurement. The implication of Sept's mapping of the physical residues of chimpanzee behavior, expressed tentatively by Sept and more strongly by various commentators, is that lithic remains at early hominid sites may have been transported for use in processing vegetal rather than animal foods. Lithic raw materials found at sites located up to 10 km from source deposits need not have been transported there in "a single, goal-directed journey" (McGrew, p. 197). Tai forest chimpanzees regularly transport stones over short and not-so-short distances, and, as McGrew goes on to note, repeated carrying "over decades, or centuries, or millennia" may eventually have built up concentrations of stones at sites some distance from their original source. "This," says McGrew, "is a topic ripe for computer modelling, and specification of *which* 'by-products of other behaviors' " (i.e., behaviors other than hunting/scavenging) may be required. We agree, and, since we agree too with McGrew, Moore, and Stanford and Allen concerning the utility of "referential" models, we would add only that it may be helpful, when considering those "by-products of other behaviors," to look at the behavior of, for instance, Japanese macaques.

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CHAPTER

13

Acquisition of Innovative Cultural Behaviors in Nonhuman Primates: A Case Study of Stone Handling, a Socially Transmitted Behavior in Japanese Macaques

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THE STUDY OF NONHUMAN PRIMATE CULTURE IN JAPAN

The question of whether or not animals have culture, and if they do, how does animal culture differ from that of humans has long been a topic of interest and debate (see Halloway, 1969; Kummer, 1971; Dobzhansky, 1972; Mann, 1972; Weiss, 1973; Moore, 1974; Harris, 1979; Galef, 1992). The pioneering studies of Japanese macaques have brought us closer to answering these questions and have played a significant part in bringing to light the importance of social learning in nonhuman primates.

At the time the Kyoto University Primate Research Group, under the leadership of Denzaburo Miyadi and Kinji Imanishi, began investigations of Japanese macaques in 1948, culture was considered to be a uniquely human trait (e.g., Kroeber & Kluckhohn, 1952). Imanishi, often called the father of Japanese primatology, was one of the first to explicitly suggest the presence of culture in animals. In a paper entitled "The evolution of human nature," Imanishi (1952)

Social Learning in Animals: The Roots of Culture

discussed instinct and culture, emphasizing that unlike instinct, culture could be viewed as the expression of nongenetically inherited acquired behaviors. He reasoned that if one defines culture as learned by offspring from parents, then differences in the way of life of members of the same species belonging to different social groups could be attributed to culture. Imanishi also stipulated that cultural behaviors can be maintained only in species living in perpetual social groups. Imanishi further suggested that if the above requirements are met whether by wasps or monkeys, we should recognize the existence of culture in a species.

While Imanishi was proposing his definition of culture, members of the Primate Research Group were beginning to investigate Japanese macaques

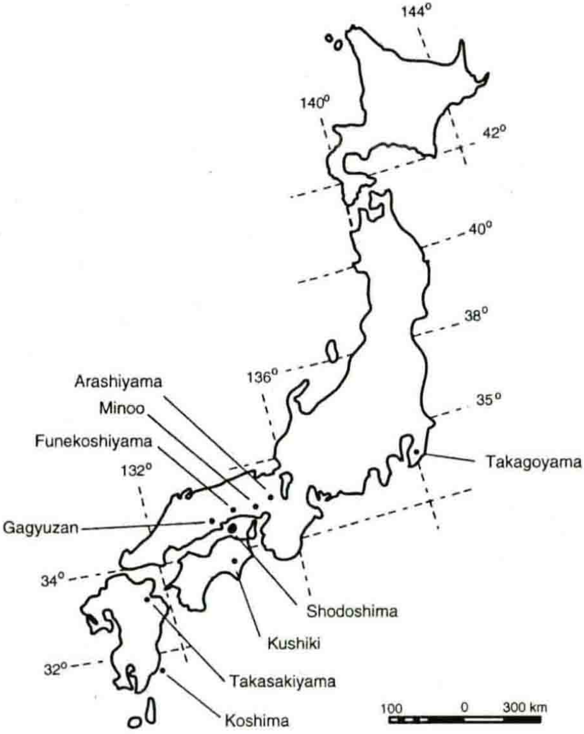


Fig. 1. Japanese macaque study sites in Japan.

throughout Japan (Fig. 1). As time went on, researchers became aware of differences between groups in both social patterns and feeding behavior. For example, while adult males at Takasakiyama regularly displayed paternal care toward 1- to 2-year-olds, such behavior was seldom seen at Arashiyama (Itani, 1959). At Shodoshima the monkeys ate unhusked rice from fields, while monkeys of the Kushiki troop in Tokushima Prefecture did not. Also, monkeys in the Minoo troop in Osaka were observed to dig up and eat the tubers and bulbs of several plant species that monkeys at Takasakiyama would not put into their mouths (Kawamura, 1954, 1965).

Soon thereafter, in the early 1950s, at both Takasakiyama and Koshima, provisioning and individual recognition of all troop members was accomplished, paving the way for long-term research on, and detailed analysis of, social networks, a cornerstone of Japanese primatology. As a result, our early understanding of the acquisition and transmission of new foods and feeding behaviors increased rapidly (e.g., Itani, 1958; Kawamura, 1954, 1959; Itani & Nishimura, 1973).

When provisioning had just begun on the island of Koshima in 1951, the researchers began to spread sweet potatoes along mountain trails and eventually down to the beach in order to lure the monkeys out into the open. By August of 1952, the monkeys, which had previously subsisted in the forest on leaves, nuts, fruits, and insects began to come out onto the beach daily and eat the food provided for them (Itani & Tokuda, 1958). In September 1953, a young female, Imo, began to carry soiled sweet potatoes to a small stream and wash off sand and dirt before eating (Kawai, 1965). The behavior itself, i.e., rubbing and rolling objects between the hands or on the ground, is a typical macaque response both to novel objects and to some common food items. The combining of sweet potatoes and a large open source of water, two previously nonoverlapping elements in macaque life, set the stage for the events that followed.

Sweet potato washing was soon displayed by a play mate of Imo, then Imo's mother and other playmates, eventually spreading to other members of the troop. Next, Imo began to wash her potatoes in sea brine instead of in fresh water and Kawai (1965) proposed that she did this for the salty taste. He classified this behavior as food seasoning.

At about the same time, researchers began to spread wheat grains on the sandy beach. It is undoubtedly a difficult task for monkeys to pick up small grains of wheat when mixed together with grains of sand as there is little necessity for such a technique in the natural foraging substrate of Japanese macaques. Again it was Imo who was first observed to take handfuls of wheat and sand to puddles on the beach or into the ocean and put the mixture into water. In doing so, the grains of wheat and sand were separated making wheat easier to pick up. This activity was named wheat-washing behavior (Kawai, 1965).

These early events have had an important influence on primatology and ethology in general as the foundation for later work on cultural behavior and social learning in animals. Since these early field studies, the criteria for recognizing culture in nonhuman primates have been refined and emphasis put on the processes by which new behaviors are transmitted from one individual to another (e.g., Kummer & Goodall, 1985; Huffman & Quiatt, 1986; Fragaszy & Visalberghi, 1989; McGrew, 1992). Previous assumptions about the way in which novel behaviors are acquired are being challenged and the processes of social facilitation and local enhancement are being examined in the laboratory (e.g., Galef, 1990; Fragaszy & Visalberghi, 1990; Visalberghi, 1993).

COMMON FACTORS OF NEWLY ACQUIRED BEHAVIORS IN JAPANESE MACAQUES

Potato washing and wheat washing are based in part on natural propensities of all members of the species as a whole, but were brought about by the introduction of stimuli new to the particular group in which they were observed. Each new behavior was initiated by a young individual and first transmitted to its mother, sibs and or peers (see Scheurer & Thierry, 1985; Machida, 1990, Higuchi, 1992, for more recent examples). When young females that had learned a behavior matured and had offspring of their own, the behaviors were acquired by their infants (Itani & Nishimura, 1973). It is important to note that many older monkeys do not acquire such new behaviors. In general, adults are quite conservative in this respect suggesting a time window within which many types of new behaviors can be acquired. This plasticity in behavior of subadults underlies the importance of their role in the transmission of new behaviors within a group.

Exceptions to this general rule are observed in the case of the spread of new feeding habits, such as seen in the spread of fish eating among the monkeys of Koshima (Watanabe, 1989). The behavior was started by adult males in the periphery of the troop and was then transmitted to dominant adult females of the group, whereupon it spread more rapidly to other members of the group. The pattern of propagation of fish eating has been suggested to be influenced by a high population density and reduction in provisioned foods on the island (Watanabe, 1989). Indeed, the route of acquisition of new foods should be more flexible than that of other behaviors because of the equal importance for all members to adapt to changing food resource availability.

Many of the behaviors mentioned above came about as the consequence of humans introducing new foods to monkeys. Thus in essence, these acquired behaviors can be considered as a product of acculturation brought about by monkeys' interaction with humans. By introducing new foods into an environment which had previously been little explored by these monkeys, as in the case of potatoes and wheat, conditions were created making it easy for social and behavioral changes to occur.

STONE HANDLING BEHAVIOR

Materials and Methods

Japanese macaques (*Macaca fuscata fuscata*) have been studied since 1954 at the Iwatayama Natural Park, Arashiyama, Kyoto and since 1950 at the Takasakiyama Monkey Park, Oita (see Huffman, 1991a; Baldwin, Koyama, & Teleki, 1980). Both groups are provisioned, During the approximately 15-year period between 1979 and 1994, I have conducted a number of investigations at both sites, focusing mainly on the Arashiyama troops (Huffman, 1991a). One main topic of my investigations has been documentation of the innovation and transmission of a newly acquired behavior called stone play (Huffman, 1984), more recently referred to as stone handling (sic. Huffman & Quiatt, 1986).

In 1986 the 246 members of the main study group at Arashiyama, B troop, underwent fission and two sister troops E and F were formed (Huffman, 1991a). After fission, the dominant E troop became the focal study group of my surveys of stone handling. E troop was selected because its members continued to come to the feeding station and could be more easily followed than could F troop which spent most of its time in the forest.

Between 1979 and 1989 observations of stone handling were recorded mainly with pen and note pad, occasionally supplemented with VHS video recording. *Ad libitum* sampling surveys were conducted with the help of park staff and coresearchers to confirm the identity of all stone handling individuals. From 1989, selected individuals were videotaped, using either a Victor-VHSC or Kyocera-8 mm compact video recorder. From an equal number of males and females of each age, a target individual was selected before each scheduled feeding time and its behavior was continuously recorded on video. The period immediately after feeding is the time in which stone handling is most likely to occur (Huffman, 1984).

Once started, stone handling was sometimes interspersed with other activities such as locomotion, foraging, grooming, etc. On the videotape, time to the tenth of a second was continuously displayed and later used for the exact measurement of the duration of all bouts of behavior. Each video record was transcribed onto a data sheet, noting name, age, and sex of subject, total duration of observation time, duration of contact with stones, and behavioral patterns displayed. This information was then entered into a computer for statistical analysis. The Spearman correlation coefficient and Mann-Whitney U tests, both corrected for ties were used for tests of statistical significance ($p > 0.05$).

Preliminary analysis of a subset of video-recorded focal follows ($n = 97$) made at Takasakiyama showed that the behavior ceased within 15 min after its initiation. Therefore, the duration of subsequent video sessions were conditionally set at 15 min after the onset of stone-handling activity. An observation was extended in the rare case that the target individual still exhibited stone handling after 15 min.

Analysis of the complete stone-handling video data set (Arashiyama: $n = 192$; Takasakiyama: $n = 71$) showed that if stone handling were to be resumed after a bout of other activity then 95% of the time it would be resumed within 120 sec or less. Therefore, to ensure that the data used for the analysis of stone-handling time was complete, only those video records lasting 120 sec or more after stone handling last occurred during the session were used (Arashiyama: $n = 169$; Takasakiyama: $n = 53$). Because the average duration of time after the last occurrence of stone handling at the end of a video session was 382.3 sec (S.D. 217.2) at Arashiyama and 535.4 sec (S.D. 238.9) at Takasakiyama, the data are considered to accurately represent complete records of stone-handling activity. The period between the beginning and the end of stone-handling activity during a video session (as defined above) is referred to below as a "stone-handling session."

First Observations

On December 7, 1979, I first observed this peculiar behavior which had never before been observed at Arashiyama. A 3-year-old female, Glance-6476, had several flat stones which she had carried out from the forest onto the open area of the feeding grounds. She first stacked the stones on top of one another in layers of 2–3 stones. She then knocked down the pile and scattered the stones about with the palms of her hands (Fig. 2). When another monkey approached she picked up several stones, moved and sat down again about 5 m away. Although I continued my observations at Arashiyama until September of 1980, this was the first and only time I saw an individual manipulating stones in this way.

By the time I resumed observations at Arashiyama in October of 1983, stone-handling behavior had become a daily occurrence. This behavior was already being transmitted from older to younger individuals.

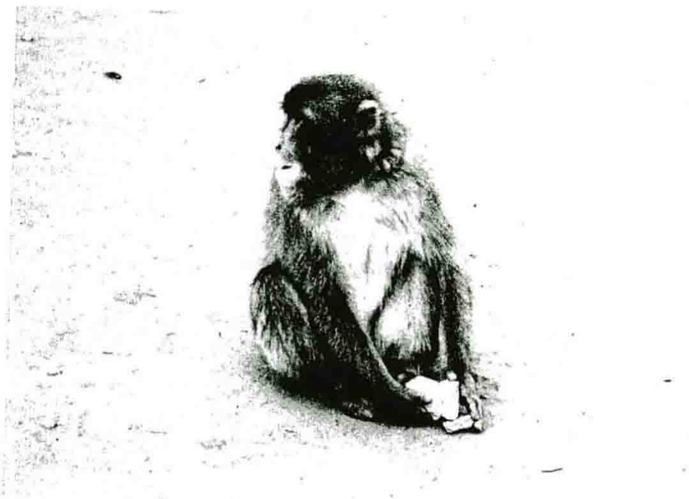


Fig. 2. First observed case of stone handling at Arashiyama (Glance-6476).

Context in Which Stone Handling Occurs

After further investigation, the circumstances under which the behavior most frequently occurred became clear. As a rule, stone handling is most frequently observed immediately after feeding time, during a period in which individuals usually rest, play, or engage in grooming activities. Individuals seen stone handling always have their cheeks filled with grain and show no signs of distress or other abnormal emotional expressions. Stone handling usually continues until all the grain in the cheek pouches has been ingested.

The stones appropriate for handling can be found almost anywhere in the forest and the brush surrounding the feeding area. Even though there is nothing particularly striking about the stones used in handling to the eye of the human observer, nearby monkeys will approach, and in some cases, snatch the stones away from a handler. It is quite common when another monkey approaches, for an individual handling stones to pick them up and move to another area to resume the activity. Quite frequently, nearby individuals will pick up stones left behind and begin to manipulate them as if they were the only stones available. Attention appears to be drawn to the stones simply because others are manipulating them.

When a stone handler is approached and solicited for example, to play or copulate, he or she will sometimes abandon the stones and join in, but more often than not, the invitee will ignore the solicitor entirely. When approached and groomed by its mother, young (1- to 3-year-olds) will continue to handle stones and stones will remain the handler's focus of attention.

Behavioral Patterns

In 1983, I classified stone-handling behavior into eight basic types: gathering (into a pile in front of ones self), pick up (place in one hand), scatter (about on the ground), roll in hands, rubbing stones (together), clacking (or striking two stones together), carry (from one location to another), and cuddling (Huffman, 1984). Excluding "clacking," all of the above behaviors are commonly exhibited by Japanese macaques when manipulating such objects as twigs and acorns collected in the forest.

Between 1984 and 1985 nine additional behavioral patterns were recognized. Six are obvious variations of the five behaviors described earlier; pick up and drop (repeated over and over), rub on surface (of roof, cement, tree etc.), flinting (strike two stones together), pick up small stones, rub with hands, and grasp with hands. The remaining three behaviors can be considered to reflect a growing familiarity with the objects and their integration with locomotor activities: toss and walk, move and push, and grasp and walk.

The younger, rather than older more "experienced," individuals were responsible for the increase in behavioral patterns observed. In 1991, the only year for which this was tested, a statistically significant difference was recognized between 1 and 4 year olds and adults in the number of behavioral patterns displayed during a stone-handling session (Mann-Whitney, 1- to 4-year-olds N1 = 32, 5 years or older N2 = 71, U = 661, p = 0.0006). There was also a statistically significant negative correlation between age and the number of behavioral patterns exhibited (N = 103, Rho = −.38, Z = −3.838, p = 0.0001).

These trends were also statistically significant for the Takasakiyama data collected in 1989 (Mann-Whitney, 1- to 4-year-olds N1 = 31, 5 years and older N2 = 23, U = 159, p = 0.0005; N = 34, Rho = −0.464, p = 0.0003).

Not only did the number of behaviors exhibited per stone-handling session decrease with age, but also the types of behavioral patterns utilized changed with age. While no single individual was observed to display all of these behaviors, looking at the number of behavioral patterns exhibited by age, in both 1985 and 1991, 1- to 4-year-olds exhibited twice as many of these 17 behavioral patterns than did adults (1- to 4-year-olds in 1985: mean 14.5 per age, SD 2.38 n = 4; in 1991: mean

12.75, SD 1.5 n = 4; 5 years and older 1985: mean 5.60, SD 1.52, n = 5; 1991: mean 8.2, SD 3.29, n = 10). Again, the Takasakiyama data confirms this trend for the 16 behavioral patterns recognized there (1- to 4-year-olds in 1989: mean 12.5, SD 2.08, n = 4; 5 years and older in 1989: mean 6, SD 3.03, n = 6).

Thus, as they grew older individuals tended to become more conservative in their stone-handling behavior, and narrow their handling activities to a few fixed behaviors such as gather, pick up, grasp, rub with hands, and scatter. The more active behaviors, such as clacking, move and push, flinting, toss and walk, and rub on surface, were limited to 1- to 4-year-olds.

Most individuals had their own idiosyncratic repertoire of behaviors that remained stable over an extended period of days, weeks, and in the case of a few of the oldest stone-handling adults, years.

Firm conclusions about the ontogeny of these behaviors await the testing of future data (preferably video) collected from individuals throughout their lifetimes.

Patterns of Transmission

In June of 1984, 49% (115/236 individuals) of the troop had been seen to exhibit stone handling (Fig. 3a). As stone handling is a spontaneous behavior, there is no way to verify whether or not an individual has acquired it other than by persistent checking over time. The survey continued and by June of 1985, an additional 27 (60%, 142/236) individuals born before June 1984 were added to the list (indicated in gray on Fig. 3b). This increase in numbers between 1984 and 1985 is thought to be an effect of increased observation hours rather than an actual increase in the number of new stone handlers during this period. Eighty percent (92/115) of the individuals observed were born between 1980 and 1983, that is, after the first observed record of stone-handling behavior in this troop. The remaining 20% included 6 young adult males (between 4.5 and 8.5 years old), 11 adult females (5+ years), and 6 4-year-old young adult females.

The first female seen to exhibit stone handling, lower-middle ranking Glance-6476, was the only individual of her age group observed to acquire stone handling. Three older females, two her cousins of similar rank, Glance-6775 and Glance-6774, and lower ranking Blanche-596475 were the only monkeys older than Glance-6476 seen to exhibit the behavior. The likelihood that stone handling was first initiated in the group sometime around 1978 or 1979, if not by Glance-6476, then at least by one of the three females listed above, is strongly supported by these observations. Had stone handling begun earlier, we would expect to have found older stone handlers.

Unlike, sweet potato washing and wheat washing, stone handling was never

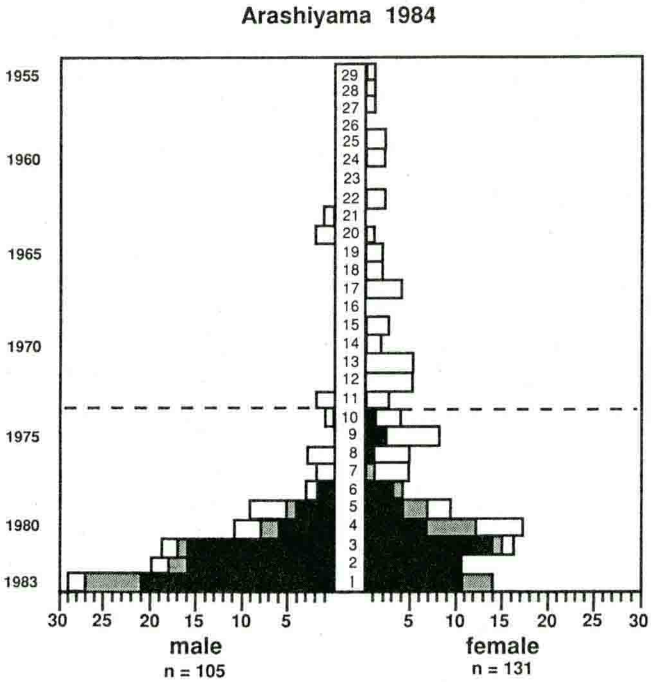


Fig. 3. Histograms of Arashiyama troops in 1984 (B troop) and 1991 (E troop). Black areas represent the number of verified stone handling individuals. Gray areas represent those additional individuals verified as stone handlers between June 1984 and June 1985 in B troop. White area represent those individuals not verified as stone handlers.

acquired by individuals after reaching the age of 5. In the July 1991 survey, no new individuals older than these three females born in 1974 and 1975 acquired the behavior. However, every individual under the age of 10 observed in E troop, was verified to be a stone handler (Fig. 3). In 1985, all offspring (n = 13) of the six mothers 10 years old or younger that exhibited stone handling (Glance-6774, Glance-6775, Blanche-596475, Glance-6476, Oppress-7078, Momo-5978), had also acquired it. It is likely that the infant is first exposed *in utero* to the "click-clacking" sounds of stones as its mother plays, and is then exposed visually to stone handling

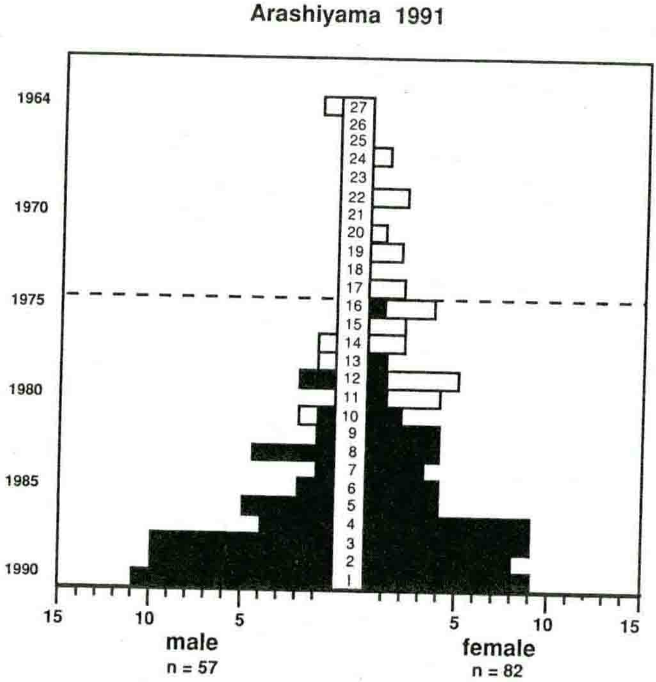


Fig. 3.—*Continued*

as one of the first activities it sees after birth, when its eyes begin to focus on objects around it (Fig. 4).

In 1985, 72% (28/39 pairs) of offspring 5 years old or younger, of nonstone-handling mothers 10 years old or older, had also been seen to handle stones. This observation clearly shows that stone handling can be acquired by a young individual even if its mother does not exhibit the behavior. For example, the infant of Glance-69 (who did not handle stones) was observed to attempt to pick up stones as early as 2 weeks after birth. The infant of Mino-636974 also began to pick up and scatter stones at about 10 weeks after birth even though its mother was not a stone handler. In both cases older siblings exhibited the behavior, suggesting that stone

Fig. 4. Momo-5978 and female infant (Momo-597885) during stone handling bout.

handling may have been acquired by watching the behavior of siblings or their sibling's playmates who spent much time with an infant after feeding and while engaged in stone handling. Observations made periodically during the fall and winter months between 1985 and 1989 strongly suggest that all infants acquired stone-handling behavior within the first 6 months after birth. The exact mechanism of transmission is not known, but social facilitation is likely to play an important role.

TRANSMISSION OF STONE HANDLING AND OTHER CULTURAL BEHAVIORS COMPARED

Figure 5 shows differences and similarities in the patterns of diffusion of stone handling and previously reported cultural behaviors in Japanese macaques. Unlike potato washing or wheat washing, which initially spread from offspring to mother (Fig. 5a), from younger to older kin and among sibs (Kawai, 1965), stone handling first spread only laterally among individuals of the same age class (Fig. 5c). Fish

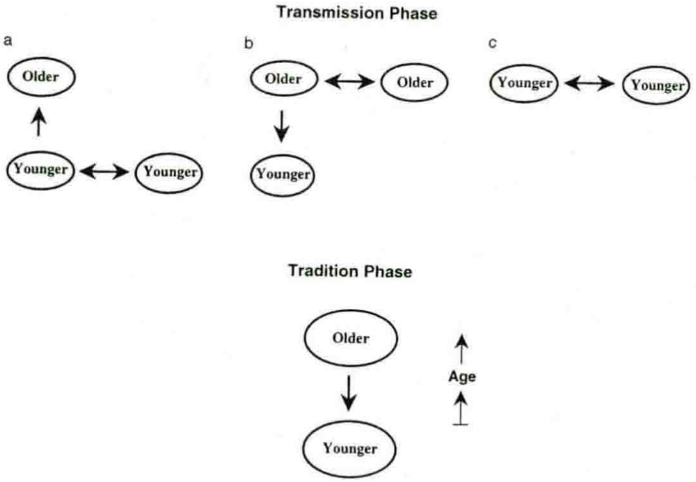


Fig. 5. Patterns of the transmission of Japanese macaque cultural behaviors. (a) Potato-washing, wheat-washing etc. (b) Fish eating and other newly acquired food sources. (c) Stone handling.

eating, on the other hand, initially spread from peripheral males to adult females within the Koshima troop (Fig. 5b). Once fish eating was acquired by adult females, it spread quickly from them to their offspring and among other members of the group (Watanabe, 1989). The pattern of the spread of fish eating is similar to other earlier reported cases of acquisition of new foods by Japanese macaques (Azuma, 1968; Kawamura, 1959, 1965; Yamada, 1958) in that the habit first spread from older to younger individuals. In all cases, this initial period of transmission is recognized as the transmission phase (Huffman, 1984). In common with all the behaviors is the fact that they were subsequently passed down from older to younger individuals in successive generations. This is called the tradition phase (Huffman, 1984, 1991b).

From the above discussion it can be seen that the route of transmission of a novel behavior or food item is in part determined by the nature of the behavior and the social networks in which it normally occurs. Those most likely to be together while engaging in behaviors of the same type should be likely to learn new variants of these behaviors from one another.

For example, while feeding, mothers, their offspring, and their close kin are more likely to feed together than nonkin, making the transmission of innovations concerning provisioned food more likely to occur within matrilines. The transmission patterns of both potato-washing or wheat-washing behavior and stone-handling behavior can be understood in these terms.

THE OCCURRENCE OF STONE HANDLING IN OTHER TROOPS

To the present, stone-handling behavior has been observed in five geographically isolated free-ranging troops of Japanese macaques besides the Arashiyama troop; Koshima (M. Kawai and S. Mito, personal communications), Takagoyama (Hiraiwa, 1975), Takasakiyama (Huffman, 1984; Matsui, 1984), Gagyuzan (F. Fukuda, personal communications) and Funekoshiyama (Itani, Huffman personal observations). See Fig. 1.

According to Kawai and Mito, during the early days of provisioning at Koshima, one individual was seen to clack stones together. However, no other monkeys were observed to replicate this behavior.

Stone handling was first observed at Takagoyama (troop 1) in 1974 by Hiraiwa (1975). However, the frequency of occurrence was much lower and the behavioral patterns less diverse; equivalent to gathering, cuddling, pick up, rubbing stones, and roll in hands as described for Arashiyama (Huffman, 1984). Diffusion of stone-handling behavior had not yet reached the tradition phase, as only individuals 3 years old or younger were observed engaged in the activity. After provisioning at Takagoyama was stopped in 1984, individuals were only occasionally observed handling stones (T. Fujita, personal communication cited in Huffman, 1984).

According to Matsui (1984), stone handling was first noticed at Takasakiyama in 1979 around the same time as it was first seen at Arashiyama. However, the behavior was not widespread enough for me to notice it while briefly observing the Takasakiyama troops (A, B, C) in December of 1979. By 1984, however when I next visited the Takasakiyama site, as at Arashiyama, stone handling had become a widespread, daily occurrence. In the survey conducted at Takasakiyama in 1989, the behaviors observed at Takasakiyama could be classified into the same patterns as those seen at Arashiyama (Huffman, 1991b). Now, at Takasakiyama, as at Arashiyama, stone handling is firmly established as a tradition, i.e., it is consistently passed from one generation to the next. All the behavioral patterns recorded at

Arashiyama (see above), except for pick up and drop, have been observed at Takasakiyama (Huffman, 1991c).

While written records do not exist, I. Narahara, a caretaker at the Funekoshiyama Monkey Park, recalls seeing stone handling at this site perhaps as early as 1966 (I. Narahara, cited in K. Kaneko, unpublished report). Stone handling does not appear to have ever spread widely among the approximately 300-member troop. The frequency of occurrence of stone handling is noticeably lower at Funekoshiyama than in either of the similar-sized Arashiyama troops, or the much larger Takasakiyama troops (A,B,C; approximately 2000 individuals total). However, the behavioral patterns displayed are similar (K. Kaneko, unpublished report, Huffman, personal observations).

FACTORS POSSIBLY RESPONSIBLE FOR THE OCCURRENCE OF INNOVATIVE BEHAVIORS AT DIFFERENT SITES

Whether a given behavior spreads and is maintained as tradition within a troop depends on any number of factors, that have yet to be defined. One reason for the variation between sites in the expression of behaviors may be environmental differences between study sties which act to enhance or suppress the transmission of certain new behaviors.

Like stone handling, potato-washing behavior has been observed in a number of troops at locations other than Koshima (Kawai, 1965). Since 1979 I have observed only two adult females, one at Arashiyama and another at Takasakiyama, wash off dirt from potatoes in a small watering pond. While the behavioral elements of brushing off dirt or sand from food items with the hand are typical of Japanese macaques, and nearly all provisioned Japanese macaques at one time or another have been given sweet potatoes, potato washing as a behavioral tradition has never been reported in any free-ranging troop in Japan other than Koshima.

Since the feeding stations of both Arashiyama and Takasakiyama are located on the steep slopes of mountains where there is little space around the limited water sources, opportunities for the behavior to be observed and practiced by many individuals are considerably less than they are at Koshima. This may partially explain why the behavior has never widely spread among monkeys in other provisioned troops in Japan.

When conditions are right, however, the behavior can and has been observed to spread in captive situations. Scheurer and Thierry (1985) report the spontaneous transmission of potato washing among Japanese macaques kept in a sandy enclosure with a pool and water spigot at the Burgers' Zoo in Arnhem, Netherlands. Also, Visalberghi and Fragaszy (1990) have artificially induced food-washing behavior in both hand-reared capuchins and crabeating monkeys by placing sandy foods and water basins in their cages. In doing so, Visalberghi and Fragaszy demonstrated that both species have an innate propensity to perform this behavior. However, while free-ranging crabeating monkeys frequently wash and rub food items in water (Wheatly, 1988), food washing in wild capuchins does not appear to be a naturally occurring habit (Visalberghi & Fragaszy, 1990). In the same light, gorillas and orangutans have not been reported to habitually use tools in the wild, but when either is raised in the presence of humans or in captivity they are quite skillful (Russon & Galdikas, 1993; see McGrew, 1992 for discussion).

The fact that we can observe a behavior in some populations, but not others, tells us that the behavior even if within the behavioral capacity of a species, is not always habitual. Environmental factors appear to be important in influencing the expression of such behaviors.

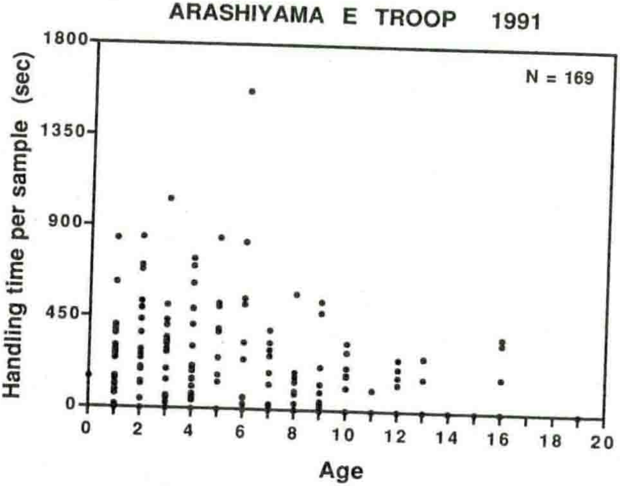
On the other hand, in places where the environmental conditions are quite similar, but behavioral patterns are different, these differences may be attributable to sociopsychological differences such as troop history or in some instances even individual personality traits. Itani and Nishimura (1973) attributed the rapid acquisition of wheat eating in the Minoo B troop to their long history of contact with humans and novel food and material objects.

LIFE HISTORY VARIABLES OF STONE HANDLING

Age and Gender

Two video surveys were conducted in the winter of 1989 at Takasakiyama and the summer of 1991 at Arashiyama. Only data from these video recordings of focal animals were used in the analyses described below. A highly significant negative correlation was found between subject age and total handling time/stone-handling session at both Takasakiyama and Arashiyama (Takasakiyama: $n = 53$, $Rho = -.488$, $p = 0.0004$; Arashiyama: $n = 167$, $Rho = -.435$, $p = 0.0001$; Fig. 6a, b). During any one stone-handling session, older monkeys spent less time stone handling than younger monkeys.

Because the Takasakiyama data set was not large enough to represent equally all age-sex classes, only the Arashiyama data set was used in the following analysis.



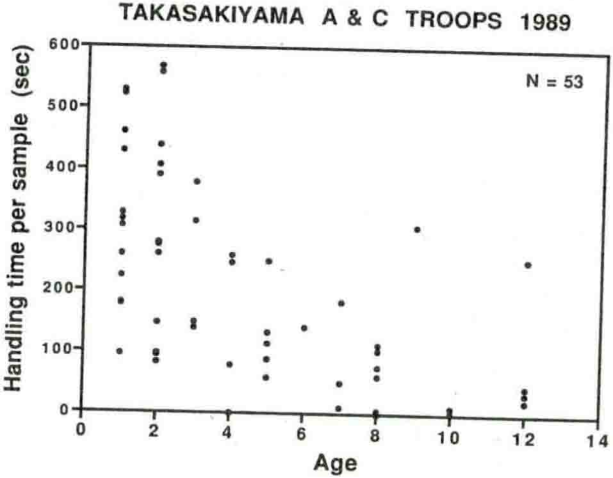


Fig. 6. Distribution of stone handling time (sec.)/bout by age of the stone handler at Arashiyama E troop in 1991 and Takasakiyama A and C troops in 1989.

Among immature males and females (1–4 years old), there was no significant difference in the amount of time spent stone handling during a given session. However, among adults (5 years and older), females spent significantly less time/stone-handling session than did males (Mann-Whitney, Males N1 = 45, Females N2 = 85, U = 1334.5, p = 0.0029).

Parity

Between 1985 and the birth season in the spring of 1986, particular attention was paid to possible changes in stone-handling behavior of females before and after giving birth. Some females were observed to engage in stone handling on the day they gave birth. For example, primiparous Oppress-7079 did not at first, appear to know what to do with her infant; she tried to shrug away from it at times and eventually forced the infant onto the third-ranking male, Deko-64, and moved away to handle stones. Multiparous females will often stone handle with their newborn infants clinging to their chests and nursing. Clearly, birth of an infant does not prevent adult females from stone handling. However, it was found that females with infants 6 months old or younger spent significantly less time/stone-handling session than did adult females without infants (Mann-Whitney with infant n1 = 54, without infant N2 = 31, U = 637, p = 0.04).

Changing Social Roles

In Japanese macaques, females become sexually mature at 3.5 years and males at 4.5 years. At about the time of sexual maturity both males and females stop exhibiting typical play behavior and start to devote more of their energies to the formation and maintenance of different social relationships both inside and outside of their immediate kin groups.

While females' lives may change drastically between the ages of 4.5 and 5.5 years with the birth of their first infants, males of the same age still spend most, if not all, their time in the periphery of the group with a few other males of similar age. This is an extension of the life males have lead since the age of 2 or 3.

Nonetheless, as demonstrated above, males too spend less and less time in stone handling as they mature. For males, the beginning of the resocialization process with adult males and females in the center of the troop, attainment of the highest rank in the periphery, or a move back into the central part of the troop appears to effect a decline in stone-handling time. Older, higher-ranking males both in the central part of the troop and in the periphery spend more time feeding or "policing" disturbances during feeding time than do younger, lower ranking counterparts.

At both Arashiyama and Takasakiyama, adult males between 8 and 13 years old engage in stone handling much less frequently than do females of the same age. Some older males have been observed to only grip briefly or scatter a few stones in passing (Huffman, 1990, unpublished observations). At Arashiyama, the high-ranking adult son of the alpha female, Mino-63697481 has not been seen stone handling since 1985. He has remained within the central part of the troop his entire life and has attained a high rank in E troop.

Unlike potato or wheat washing, in which monkeys stop exhibiting these behaviors only when they are not given potatoes or wheat to wash (Watanabe, 1994), the decline in stone handling by maturing individuals is closely correlated with social and biological life history variables.

THE ADAPTIVE VALUE OF STONE HANDLING CONSIDERED

To date, all newly acquired cultural behaviors reported in Japanese macaques have in common the fact that they are subsistence oriented and thus provide direct benefits to the user in daily feeding activities. Monkeys who wash sweet potatoes, dip them in salt, or separate sand from wheat, are benefiting from their efforts. It is possible that observations of direct benefits acquired by individuals from practice of these behaviors actually encourages their wide diffusion.

However, as the study of stone handling suggests, it is not necessary for a behavior to provide tangible benefits in order for it to be passed from one generation to the next. Stone handling can not be explained in terms of contribution to reproductive fitness or facilitation of subsistence activities. In this respect, stone handling differs from all other cultural behaviors previously reported in Japanese macaques. To the best of my knowledge, stone handling is the first documented case of object play (sic. Candland, French, & Johnson, 1978) as cultural behavior in Japanese macaques.

While stone handling, in its current state, provides no tangible benefits to the performer, it is possible that there are less direct benefits of the behavior. Reminiscent of worry beads or pocket-sized rubbing stones used by humans in some cultures, stone handling itself may be relaxing or stimulating and thus its benefits could be psychological or physiological in nature. Such benefits would go undetected by the human observer without the aid of sophisticated devices to monitor physiological variables such as pulse rate.

It has also been argued that if stone handling persists in any one of these troops material benefits may be acquired in the future if the behaviors undergo modification or are adapted to more practical applications (Huffman & Quiatt, 1986). For example, the initial experience of stone manipulation is an important precursor to the use of stones for adaptive purposes: as tools or as elements of display patterns (e.g., Eaton, 1972; Candland, 1978, 1981; Huffman & Quiatt, 1986).

While not every socially learned behavior is or has to be adaptive, the propensity to learn and adopt new behaviors surely is adaptive in most circumstances. Perhaps someday as a result of the experience gained from stone handling, a new behavior of adaptive value to the troop will arise. However, in its present state stone handling, rather than being the means to an end, appears to be rewarding in itself.

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10

Biological and ecological foundations of primate behavioral tradition

10.1 Introduction

An interest in nonhuman primate behavioral traditions has existed since the beginning of primatology, with some of the earliest details coming from the Japanese macaque (*Macaca fuscata*). When Kyoto University researchers began their investigations in 1948, under the leadership of Denzaburo Miyadi and Kinji Imanishi (Asquith, 1991), animals were considered to act on instinct and such concepts as tradition or culture were considered to be a uniquely human trait (de Waal, 2001; Kroeber and Kluckhohn, 1952). Imanishi (1952) predicted the presence of "culture" in animals even before the results of these observations had begun to be published. He emphasized that, unlike instinct, culture in animals should be viewed as the expression of developmentally labile behaviors. He reasoned that, if one defines culture as behavior transmitted to offspring from parents, differences in the way of life of members of the same species, whether they are human, monkey, or wasp, belonging to different social groups could be attributed to culture. Imanishi's general argument still holds today, albeit with greater refinements in our overall view of the phenomenon (e.g., Avital and Jablonka, 2000; de Waal, 2001; McGrew, 2001). Currently, healthy debate over whether culture or tradition in humans and animals is really the same is ongoing (e.g., Boesch and Tomasello, 1998; Galef, 1992; Tuttle, 2001; see also Ch. 6).

We use the term behavioral tradition in this chapter to denote those behaviors for which social context contributes to their acquisition by new practitioners and which are maintained within a population through social means (as defined by Fragaszy and Perry in Ch. 1; McGrew, 2001). Operationally, we define a behavioral innovation as any single (or set of) species-typical voluntary action performed in a novel context that has not previously been observed to be performed by members of that group. Thus, new behavioral traditions arise from behavioral innovations (typically made up of existing behaviors) and can diffuse within a group through any of several possible processes, including local enhancement, social facilitation, observational learning, and imitation (Galef, 1976; Whiten, 2000). Visalberghi and Fragaszy (1990) have pointed out the importance of knowing the history of a behavioral innovation to assess the contribution of any one of these possible processes in its diffusion within a group. In nature, only under the best of long-term observational conditions is it possible to know with any degree of certainty whether or not one is documenting a behavioral innovation. Likewise, the diffusion of a new behavioral innovation into a group can be a long process. Rarely have such events been observed and documented in detail. Controlled experimentation sometimes allows us to avoid such difficulties and gain a better appreciation of the situation in nature (e.g., Hirata and Morimura, 2000; Inoue-Nakamura and Matsuzawa, 1997; Matsuzawa, 1994). Laboratory studies have also provided useful insights into the details of social diffusion, providing various parsimonious interpretations of the learning processes involved (e.g., Lefebvre, 1995; Visalberghi and Fragaszy, 1990; Chs. 6 and 7). Even under the best of experimental conditions, however, it is difficult to reconstruct faithfully the complex ecological and social conditions under which innovation and its subsequent diffusion may occur in natural populations.

Innovation and diffusion of new behaviors within a troop, and the establishment of group-specific behavioral traditions, have been topics of great interest from the beginning of research on Japanese macaques (e.g., Huffman, 1984, 1996; Huffman and Quiatt, 1986; Itani, 1958; Itani and Nishimura, 1973; Kawai, 1965; Kawamura, 1959; Watanabe, 1994). By the early 1950s, at well-known sites such as Koshima, Takasakiyama, Arashiyama, and Minoo, provisioning and individual recognition of all troop members was accomplished, starting off the practice of long-term comparative research of troops across the country (see Huffman, 1991; Takahata *et al.*, 1999; Yamagiwa and Hill, 1998). Provisioning provided the first outdoor laboratory situation for recording the process of behavioral innovation and diffusion of behaviors in a novel environment. Research at these sites has contributed much to our understanding of the patterns of diffusion of innovative behavior in monkeys (see Itani and Nishimura, 1973; Nishida, 1987; Thierry, 1994). A growing number of long-term studies of chimpanzee populations have also revealed an array of behavioral variation between populations that has been attributed to social learning. Currently, a set of behavioral traditions within a group and differences in such sets of tradition between groups is given by some as evidence for chimpanzee culture (see Whiten *et al.*, 1999).

In chimpanzees, the uniqueness of a particular behavior to a given group is often highlighted (e.g., McGrew and Tutin, 1978; Nakamura *et al.*, 2000; Nishida *et al.*, 1983). As more sites have reached long-term study status, however, a number of these behaviors, shown to be practiced regularly within a group and socially transmitted to each new generation, are frequently found to occur in more than one population. In both Japanese macaques and chimpanzees, there are examples of behavioral traditions that occur in geographically isolated groups of the same species and or among different subspecies. They include foraging skills (ant dipping, leaf sponge, honey dipping), self-medication (leaf swallowing), social conventions, communicative signals (hand clasp grooming, leaf clipping) and a form of object play (stone handling) (see Boesch, 1996; Huffman, 1996, 1997).

While it is accepted that behavioral innovations can be passed to future generations via social learning, the foundations of behavioral innovations themselves, which form the basis of behavioral traditions in any species, including our own, have been little discussed. How can it be that behavioral innovations socially transmitted amongst members of one group can also occur in other groups for which social diffusion of behavior cannot possibly occur? A historical explanation would assume that such behavioral traditions are extremely old, implying that ecological, geographical, or even subspecies barriers now close previously open pathways of intergroup behavioral transmission. While plausible, in some cases this may often be difficult to demonstrate, and it does not explain cases where a particular behavioral innovation is observed to emerge simultaneously in more than one group under geographically isolated conditions. Alternatively, a biological explanation assumes that members of the same or closely related species possess common behavioral propensities, leading to a greater than random probability of a behavioral innovation based on them to arise independently in more than one group. This can happen simultaneously or at greatly different points in time. The biological explanation helps to explain why the same or similar behavioral traditions, which apparently arise from innovation, can occur in more than one group.

This strongly suggests that aspects of species-typical behavior can and do indeed shape the pattern of behavioral innovation among members of a taxonomic group. Here, both historical and biological explanations can be complimentary, and indeed important for a clear understanding of the phenomena. However, we have excluded the overly parsimonious assumption that behavioral innovations depend only upon species-wide, latent tendencies and require only the appropriate stimuli to bring them out independently in all individuals of a group or species.

This chapter addresses the various factors supporting behavioral innovation and discusses the interaction between the biological and environmental variables (both social and ecological) that influence the diffusion of such innovations in free-living populations. We synthesize research on Japanese macaque behavioral traditions to discuss the possible effects of group size and behavior type on the rate of diffusion and the pathways of transmission. New information is also presented from long-term multisite comparative studies of two behavioral traditions: stone handling in Japanese macaques (Huffman, 1984, 1996; Huffman and Quiatt, 1986) and leaf swallowing in the African great apes (Huffman, 1997; Huffman *et al.*, 1996; Huffman and Caton, 2001). This exploration of the biological and ecological foundations of animal traditions is intended to improve our understanding of fundamental aspects of social learning, and the role behavioral traditions may play in the survival of the organism.

10.2 Biological basis of behavioral innovation: behavioral predispositions

Given enough time to familiarize oneself with a particular social group of animals, it is apparent that each individual has its own unique personality. Further time spent comparing two or more groups will invariably lead one to the conclusion that different groups in different regions of the distribution of a species can differ strikingly from one another in some details of their social or feeding habits. These population differences in the overall behavioral repertoire of a species are what we most readily identify as behavioral traditions. At the same time, there are inescapable similarities between groups and the individuals within groups, which make them recognizable as members of the same species. That is, the better you get to know the behavior of individuals in one group, the easier it becomes to predict with a relatively high level of accuracy just how any individual of that species will respond in a particular social situation elsewhere. An individual's unique qualities, based on personal experience and other attributes, coexists with a relatively high species-level predictability (behavioral predisposition) (see also Mendoza and Mason, 1989). We argue that this constitutes the biological foundations of behavioral traditions in any animal species, including humans.

Keeping these factors in mind, we make six basic assumptions about the role of species-level behavioral predispositions as important biological features of behavioral innovation and discuss their possible role in the emergence of behavioral traditions arising in geographically distinct populations of the same species.

1. The basic motor units of behavior evident in a species are shared by all members of that species. These basic behavioral units are the product of adaptation to social and ecological challenges in its evolutionary past and are shared by all members of a species in the present.
2. In order to survive and reproduce, animals have to be good at reading and appropriately responding to the behavior of conspecifics and to changing environmental conditions. These behavioral units are the basic building blocks of behavioral traditions.
3. The reliability with which a behavior occurs in a species is based on the predictability of the response to stimuli in the social and ecological environment and the reliability with which a particular set of environmental conditions occurs. (See Ch. 2, for a model of the rate of environmental change.)
4. Predictable behavior across individuals of a species reflects reliable production of a finite set of behavioral units. The capacity for innovation is limited to the possible number of permutations of such behaviors an individual can produce.
5. While the possible number of behavioral permutations is influenced by biological constraints (physiological and morphological), an individual may never fully exploit the full potential of its species in any given environment. This is considered to be the source of a behavioral innovation and intergroup variability upon which behavioral traditions are based.
6. A shared repertoire of behavioral units and a shared degree of predictability in the production of particular behaviors in particular situations makes it possible for common behavioral innovations to appear and common behavioral traditions to arise among socially and geographically isolated groups.

The juxtaposed predictability and unpredictability of behavior in a species becomes more apparent the more familiar we become with that species. Behavioral predispositions make members of a species interact with their environments in a relatively predictable way. At the same time, we fully recognize the dual importance of individual differences and the novelty of social and ecological contexts in which behavioral innovations arise. An innovation is likely to arise when an individual(s) or group is faced with new social or ecological challenges for which it currently has no workable solution in its existing behavioral repertoire.

Intuitively, the more generalist a species, the greater array of behavior it is likely to exhibit and, therefore, the more flexible to environmental change it should be. As a general principle then, those species found to exist in a wide range of social, climatic, and ecologically diverse environments should be expected to exhibit the greatest array of behavioral traditions. They may also be better social learners, but this is a different issue. Reader (Ch. 3) reports a significant positive correlation between the incidence of reports of social learning, innovation, and tool use and the absolute "executive" brain volume and the ratio of "executive" brain over brainstem in nonhuman primates. If these measures are a robust indicator of adaptability and intelligence, regardless of relative phylogenetic positions, behavioral traditions will be more frequent among generalist species than among specialists. This should hold true for any animal species and behavior in which social context contributes to behavioral acquisition.

10.3 Innovative behaviors in Japanese macaques

10.3.1 Phases of behavioral diffusion

In macaques, and presumably other social animals, the diffusion of a behavioral tradition can be divided into three distinct phases: transmission, tradition, and transformation (Huffman and Quiatt, 1986). The *transmission phase* is the period of early dissemination of a behavior and is typically similar from group to group and presumably species to species, at least among primates. The first individual(s) to display a behavior may do so repeatedly and perhaps for increasingly longer periods of time. The behavior is first acquired by a network of spatial–interactional associates of the innovator. The membership of this network is directly influenced by the nature of the behavior being performed and its context (e.g., feeding, resting, traveling, mating, etc.). Laland's (1999) work on the transmission of digging behavior in rats, however, suggests that the innovator of a new behavior is not always easy to detect, and multiple individuals may exhibit the behavior almost simultaneously.

A behavioral tradition need not diffuse to all members of a social group. The more specialized the functions and context of the behavior is, the more limited will be the subgroup of individuals (age, sex, rank, etc.) that will acquire it. Diffusion rate and the distribution of the behavior across age–sex classes should, therefore, vary according to the behavior in question. For example, if the behavior were a form of sexual display, like leaf clipping in Mahale chimpanzee, then we would not expect it to be acquired by sexually immature or postreproductive individuals at any phase of the diffusion process. In such cases, the behavior would never spread to 100% of a group. If, however, the context of leaf clipping were to be altered at some point to a general solicitation of intent or to attract attention of others, for example, we could expect to see an increase in the proportion of the population exhibiting the behavior starting from that point in time.

The *tradition phase* is the period in which a behavior is passed down from mother to offspring or along other multigeneration lines. At this time, the rate of diffusion will depend upon the direction of diffusion and once again upon who the target of the behavior is in the transmission phase.

The *transformation phase* is a period in which prolonged practice and acquired familiarity with a behavioral pattern is gained. Increased behavioral variety brought about by more active manipulation occurs largely among younger age groups, which naturally tend to be more physically active and explorative. This can be a period of behavioral drift or easily changing fads. An example of this is the divergence in behavioral patterns that developed for wheat washing and potato washing in the 20 or more years following its initial spread at Koshima (Watanabe, 1994). Details on the direction of diffusion at this stage, however, are not clear. In this case too, diffusion is expected to be influenced by the innovator's network of spatial–interactional associates.

Among the reported cases of the diffusion of behavioral innovations in Japanese macaques, most are in one way or another related to food or foraging activity, including the acquisition of new foods and food-processing techniques. In general, information regarding food should be of importance to all members of a group and, therefore, foraging innovations are

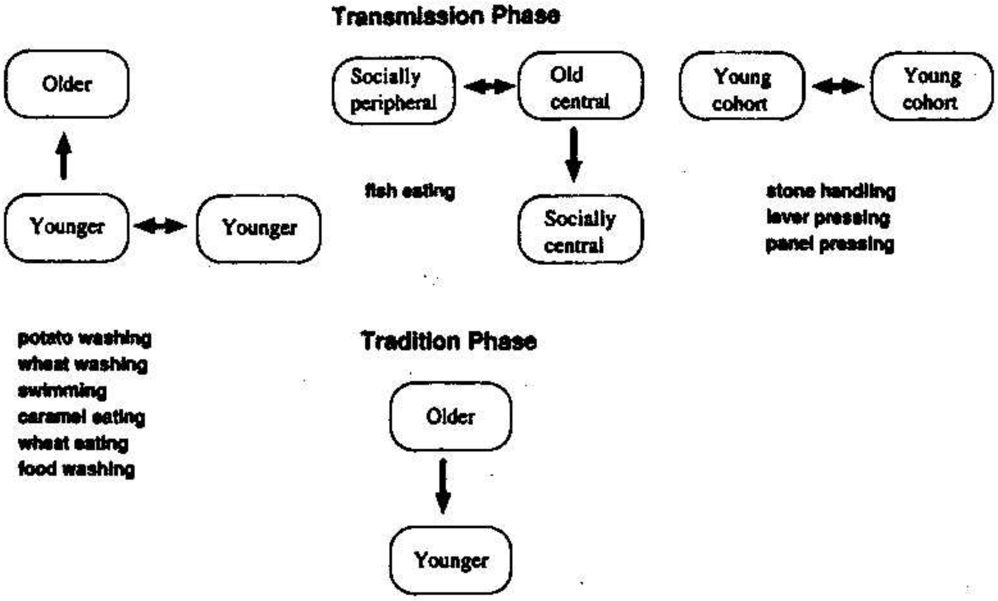

Fig. 10.1. Pathways of diffusion by behavioral type exhibited in Japanese macaques.

expected to diffuse widely. However, socio-ecological factors affecting access to novel foods or more preferred food can enhance or impede the rate and routes of diffusion (e.g., Giraldeau, 1997; Giraldeau, Caraco, and Valone, 1992; Tokida *et al.*, 1994; Watanabe, 1989).

10.3.2 Pathways of diffusion

Three basic pathways of behavioral diffusion in the transmission phase have been recorded: younger to older, peripheral to central group members, and between young of the same cohort. These pathways are shown in Fig. 10.1 along with the characteristic older to younger pathway inherent in the tradition phase. Some examples of the different behaviors associated with each pathway are also given. Other pathways are likely to exist, but to our knowledge they have yet to be reported. Pathways are dependent upon the nature of the behavior and the relationships of those individuals most likely to be in proximity with each other when the behavior is being practiced. In many, but not all, cases, this is characteristic of the transmission phase. As a general rule, behavioral type and the context of the behavioral innovation in question will strongly determine this pathway and thereby to some extent also the rate of diffusion.

Of the behaviors noted in Fig. 10.1, food-related behavioral traditions were most consistently associated with the initial lateral transmission among young, followed closely by the upwardly vertical transmission to older kin members and then across kin boundaries to other adults.

The pathway of transmission of fish eating at Koshima is different in that it first appeared in an adult male living in the troop's social periphery. An old female of the troop eventually acquired the habit next. She was reported to be the link by which the behavior then diffused to some members within the troop's social central area (Watanabe, 1989). This food habit was acquired in response to a drastic reduction in provisioned foods. Those individuals most directly affected by the food shortage, who had less access to provisioned foods, and who had social contact with the peripheral adult male were reported to be the first to acquire the behavior. Fish eating was adopted by about a third of the population and is an interesting case of a putative behavioral tradition where diffusion within the group is limited by need (Watanabe, 1989).

Stone handling was first observed being performed by a young juvenile female, Glance 6774, in December of 1979. By June 1985, stone handling was found to have diffused throughout 60% ($n = 142$) of the 236 member B troop (Huffman, 1984). Of these 142 individuals, 80% were born between 1980 and 1983; that is after stone handling was first observed in the troop. Only limited diffusion to individuals older than the first female seen stone handling occurred, suggesting the recent emergence of this behavior within the troop: at least since provisioning was first begun at this site in 1954. It also shows that the behavior did not spread to adults within the troop. Those three individuals older than Glance-6774 that acquired stone handling were two of her female cousins, Glance-6775 and Glance-6774 (sisters), and one lower-ranking non-kin-related female, Blanche-596475.

By 1985, these four females and two others (Oppress-7078, Momo-5978), all then 10 years or older, had one or more offspring of their own. All 13 of these females' offspring also acquired stone-handling behavior. In 1986, B troop divided, becoming E and F troops (Huffman, 1991). By August 1991, 12 years after the first appearance of stone handling, every individual under the age of 10 years in E troop was verified to have acquired the behavior (F troop gradually stayed away from the provisioning site and observations on them were stopped). Stone handling had spread to the young of every kin group in the troop. Unlike potato washing or wheat washing, however, no individual 5 years of age or older in 1979 (when the behavior first appeared at Arashiyama) ever acquired stone handling later on.

Long-term observations made on stone handling have revealed that the social network of diffusion has varied over time as a function of the age of individuals exhibiting the behavior and the social context of the behavior itself. In the initial transmission phase of stone handling, this network included a very small group of cousins, sisters and non-kin playmates. Very shortly thereafter, however, the behavior began to spread more widely between play groups composed of kin and non-kin as it diffused downward to younger individuals from mother to offspring, older to younger siblings, etc. in the tradition phase (Fig. 10.1).

Consequently, in the first few years, infants of stone-handling mothers were exposed to the behavior earlier than other infants. However, according to the 1985 census, even those infants whose mothers had not acquired stone-handling behavior began to pick up or scatter stones on the ground as early as 10 weeks. In all these infants, the behavior was exhibited by older siblings indicating that stone handling can also be acquired via older siblings. However, since then and up to the time of writing this paper, all infants acquire the behavior within the first 6 months of life. Multiple modes are suspected to have played a role at different stages of the behavior's history, with some form of social facilitation no doubt playing a central role.

From this, we would predict that no one particular age, sex, or rank class had a monopoly on innovation skill. Rather, the type of innovation is likely to be influenced by the unique position of each individual within its social and ecological environment.

10.3.3 Behavior type, group size, and rates of diffusion

Earlier evolutionary and population-level models of cultural transmission assumed rapid and, as discussed by Laland and Kendal (Ch. 2), temporally accelerating rates of behavioral diffusion within a group, producing a sigmoid curve (Boyd and Richardson, 1985; Cavalli-Sforza and Feldman, 1981; Pulliam, 1983). Most of these models assume that, as each new individual acquires the behavior, the rate of diffusion will increase as a function of an increase in the number of demonstrators who can influence the remaining naïve individuals. Laland and Kendal (Ch. 2) disagree and suggest that the shape of the curve of diffusion is not always consistent with the pattern of learning (social versus asocial). They conclude that the shape of the diffusion curve may not allow us to identify the learning process. Lefebvre

(1995) found supporting evidence for an increase in the rate of diffusion with the increase in number of demonstrators in an analysis of the rates of acquisition of innovative behaviors reported in the primate literature, including potato washing, wheat washing and fish eating in the Japanese macaque. He found accelerating rates of diffusion as the number of practitioners of a behavior increased in some but not all behaviors. Conversely, Lefebvre and Giraldeau (1994) also found that large group size could have a negative effect; many naïve bystanders could slow down diffusion. However, we must not assume that a behavioral innovation will be of relevance to every individual in the group. In social learning models, we cannot assume *a priori* that all behaviors will reach 100% diffusion within a group. As seen from fish eating, not even food-related innovations are totally free from such considerations.

Behavior type and group size are not typically included in models of cultural transmission. The question we ask here is, "What effect do these variables have on the rate of diffusion?" From our discussions above, we know that the pathway of diffusion is affected by behavior type and that the function of the behavior determines the type of individual and, therefore, the total number of individuals within a group that will acquire it. Based on this evidence, we predict that group size alone does not have an over-riding effect on the rate of diffusion. To test this, we calculated the theoretical rate of increase in the number of individuals performing 12 novel behaviors reported in Japanese macaques to estimate the time it would have taken each behavior to spread to 50% of the group. Here we assume a constant rate of increase. The number of days necessary to diffuse to 50% of the population in these 12 behaviors was not found to be significantly related to group size alone (Spearman rank correlation coefficient $(r_s) = 0.38$; $n = 12$; not significant). This pattern remained constant even when we excluded experimentally induced behaviors (caramel eating and lever and panel pressing; $r_s = 0.49$; $n = 7$; not significant). No consistent pattern was found with regards to troop size (Fig. 10.2). However, we did find a significant difference in the number of days to diffuse to 50% of the population when these 12 new behaviors were grouped into four behavioral types (Kruskal–Wallis ANOVA: $H_{(3,12)} = 8.1$; $p < 0.05$) (Fig. 10.3). Food processing and play were much slower to diffuse (over 1400 days) than accepting a new food and experimental tasks (less than 200 days). As predicted, behavioral type does have an important effect on the rate of diffusion and the effect of group size is inconsistent, even when using a linear model (see also Ch. 2).

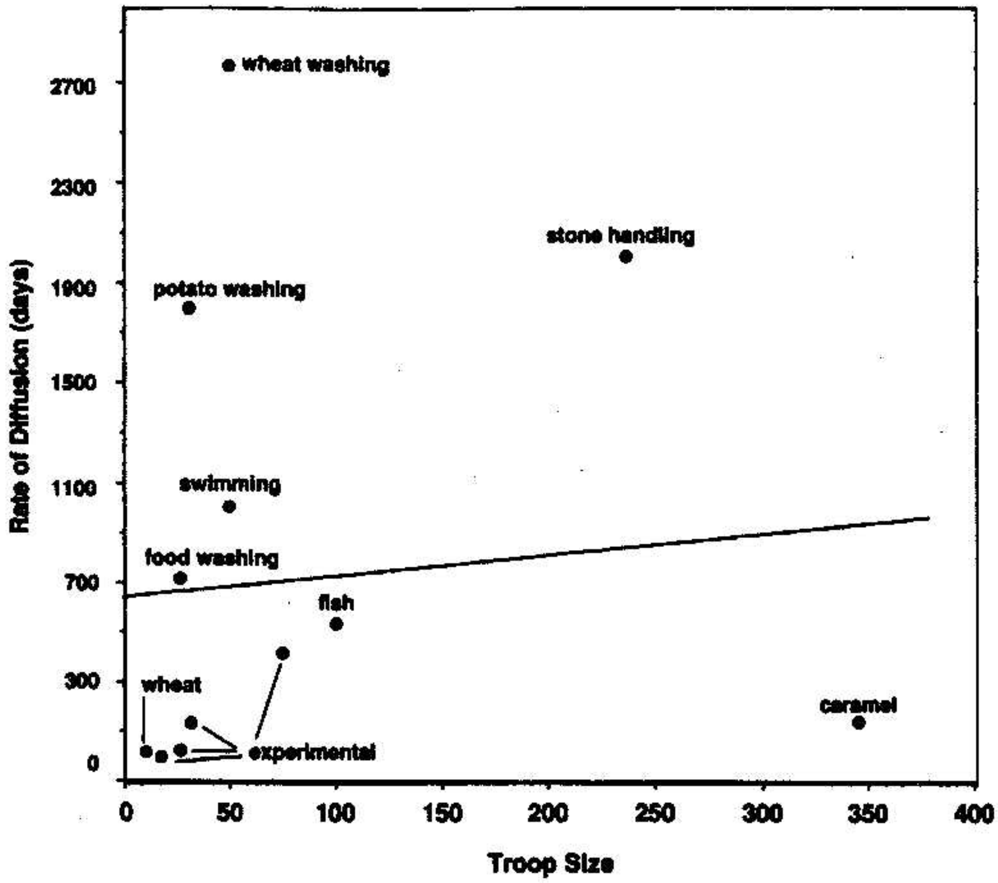

Fig. 10.2. Correlation between troop size and estimated rate of diffusion among 50% of the population for 12 behavioral traditions observed in Japanese macaques.

This difference in rates of diffusion can be explained by the fact that accepting a new food item or manipulating an experimental device for immediate food reward does not compete with an existing way of handling a problem (e.g., already available food). In the case of play, the new behavior is likely to be acquired only by a specific subset of the population, constraining the rate and defining the level of diffusion into the group.

Previously, a slow rate of diffusion has been considered an argument in favor of the more parsimonious mechanism of individual learning supporting the acquisition of some behaviors in Japanese macaques (Galef, 1991, 1992). However, in light of our empirical analysis discussed above and supported by the theoretical discussion of Laland and Kendal (Ch. 2), we conclude that variations in the rate of diffusion do not necessarily reflect more or less reliance on social context in learning.

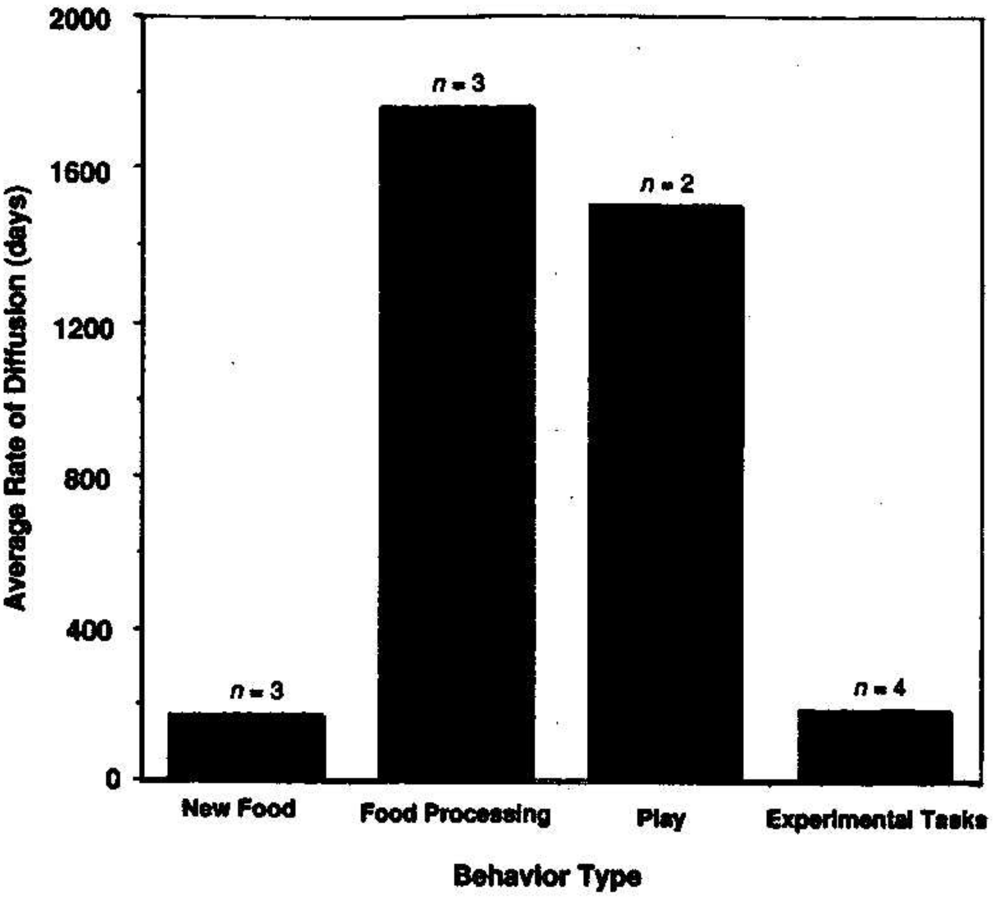

Fig. 10.3. Average rate of diffusion to 50% of the population by behavior type. New Food, acquisition and consumption of food; food processing, new way to process food; play, play-related behavior, such as stone handling and swimming; experimental tasks, new behavior induced by the introduction of a novel experimental setting.

10.4 Factors influencing the innovation, diffusion, and maintenance of primate behavioral traditions

10.4.1 Appearance and disappearance of behavioral traditions

Behavioral traditions can appear, disappear, and even reappear sometimes in slight variation within the same group over time (see Ch. 14). Very few studies have been able to document such change given the long time investment required. Some behaviors, while practiced by a few individuals in any population, may not endure very long. For example, stone handling was observed at Arashiyama and Takasakiyama for the first time in late 1979, after over 30 years of close observation at both sites by a number of researchers and park employees (Huffman, 1984, 1996). Interestingly, before provisioning was started at Arashiyama in 1954, young macaques were sometimes seen to play with inedible hard-covered citrus fruits in a fashion resembling some of the current stone-handling patterns (see Huffman, 1984). The initial circumstances bringing about the practice of stone handling and other new behaviors at these sites are unknown. Site differences in the frequency of provisioning and the size of the feeding area may have some influence on the relative daily frequency of occurrence as well as the overall opportunities for others to observe and take up the practice of the behavior habitually. Although not completely understood, some of the possible factors are discussed below.

10.4.2 Provisioning

Early research on Japanese macaques used provisioning as a way of speeding up the process of habituation and to lure them out into the open for better observation. This brought about a change in the life habits of the monkeys, providing them with access to new foods and environments previously not encountered. These types of change preceded such innovations as potato washing, wheat washing, and altered swimming behavior at Koshima (Kawai, 1965).

With provisioning comes a tendency for a more sedentary lifestyle. More time is spent around the feeding area and that too can have profound effects on behavioral and dietary innovation (see Fa and Lindburg, 1996). At Arashiyama, Huffman (1984) found, on the one hand, that the natural diet of the troop decreased from its early provisioning period (1954–1958) level of approximately 192 species of plants (Murata and Hazama, 1968) to as few as 67 species between 1979 and 1980. On the other hand, while the diversity of their natural diet decreased and dependence on provisioned foods increased, at least 17 new natural and introduced plant foods were acquired in the process of adjusting to life in the newly exploited 1 km radius of the feeding site.

Provisioning can also bring about other changes in behavior. With less time spent actively searching for food, more time is left for other activities such as play and socializing. Provisioning improves reproductive potential in females and causes a shortening of the interbirth interval. This, in turn, can have an effect on a number of behaviors, ranging from infant care practices to modification of matrilineal dominance-rank systems (Hill, 1999; Itani, 1959; Kutsukake, 2000). Little attention has yet been paid to the possible relationship of behavioral innovations and changes in population structure. This should be a fruitful area of future investigation.

In a restricted sense, provisioning can be considered to be synonymous with dramatic changes in a more natural habitat. That is to say, changes in the distribution, defensibility, and abundance of food or other sought-after resources in nature are also expected to trigger changes in social organization, group behaviors, and diet.

10.4.3 Competition

As shown in this chapter, the rate of diffusion of innovative behaviors and their longevity is a complex issue. The relative abundance of resources associated with the innovation also affects which individuals will acquire a new behavior that another practices. The type of behavior under consideration is very important. This will directly influence who is most likely to acquire the behavior, and in the end how widely a behavior will spread among members of a group. If, for example, a behavior allows an individual to obtain a resource previously denied because of sex, age, or rank, the behavior is not likely to spread widely, passing only very slowly to others in the same social situation who are tolerated by the innovator. An example of this is tool manufacture by a chimpanzee to rouse a squirrel out of its hiding place in the hole of a tree (Huffman and Kalunde, 1993). Meat is a highly prized food resource by chimpanzees, with access controlled by a few adult males of the group based upon social and sexual status of the potential recipient (Nishida *et al.*, 1992; Stanford, 1999). The manufacture and use of tools to drive a squirrel out of hiding is an extremely rare behavior at Mahale. The orphan adolescent female observed performing this behavior would normally have no chance to obtain meat from others or to hunt larger prey on her own. Hunting in the presence of others increases the likelihood of the catch being taken away from a subordinate, and, therfore, such activities tend to be done in secret (Huffman and Kalunde, 1993). Here, the lack of social tolerance (see Ch. 11) indirectly encourages efforts to obtain a meat source not highly open to competition. At the same time, this suite of characteristics of the individual and the behavior inhibits the diffusion of the behavior to more powerful individuals in the group. Consequently, although the behavior is potentially important to all, it is not likely to diffuse widely or be observed frequently, because of both limited opportunities for observation by others and the intolerance of subordinate individuals to competitors for a limited resource. This is in contrast to ant fishing, where resources are more widely distributed and abundant, resulting in less competition. By comparison, behaviors with a clear benefit to all members are more likely to spread throughout an entire group and be maintained indefinitely if the resources required for its performance are widely available (e.g., potato washing).

10.4.4 Maintenance of "neutral" behaviors

In some cases, traditions emerge that seem to have no (or even mildly negative) immediate adaptive consequences (e.g., capuchin hand sniffing, Ch. 14). Presumably these behaviors are maintained because of some internal consequences that we cannot as yet measure. Stone handling is a case in point (Huffman, 1996). Unlike the leaf-swallowing behavior exhibited by chimpanzees in the wild, the significance of stone-handling behavior to a Japanese macaque is difficult to interpret. Individually, motivation to perform the behavior simply may be the social value placed on these items by others in the group (Huffman, 1984). The immediate motivation to act as others do and the long-term motivation to continue performing a behavior may be different at both the individual and group levels. This is an especially important area for theorists to consider, because assumptions about motivation and performance should be approached from both short- and long-term perspectives. For example, during the tradition phase (Fig. 10.1) of behavioral transmission, when behaviors are acquired by the very young from their mothers or older siblings, the motivation to perform a behavior is likely to be quite different from that which induced the innovator(s), and perhaps subsequent early initiates in the propagation phase, to acquire the behavior. Furthermore, once a behavioral habit is acquired, individuals may continue to perform it even after the original conditions for promoting its adoption are no longer present if there is no cost to performing it. They are continued merely out of habit.

10.5 A behavioral tradition in multiple troops of the same species: stone handling among Japanese macaques

10.5.1 Behavioral description

Classified as a form of object manipulation or play (Candland, French, and Johnson, 1978), stone handling has so far never been observed in a nonprovisioned troop (Huffman, 1984, 1996). However, there are also several provisioned troops where stone handling has never been recorded (Fig. 10.4). In provisioned and nonprovisioned troops where stone handling has never been seen, prolonged physical contact with stones is absent. At sites where it does occur, stone handling is habitual and occurs most predictably just after feeding time. In this situation, individuals have gathered all the food (often grains of wheat or soy beans) they can

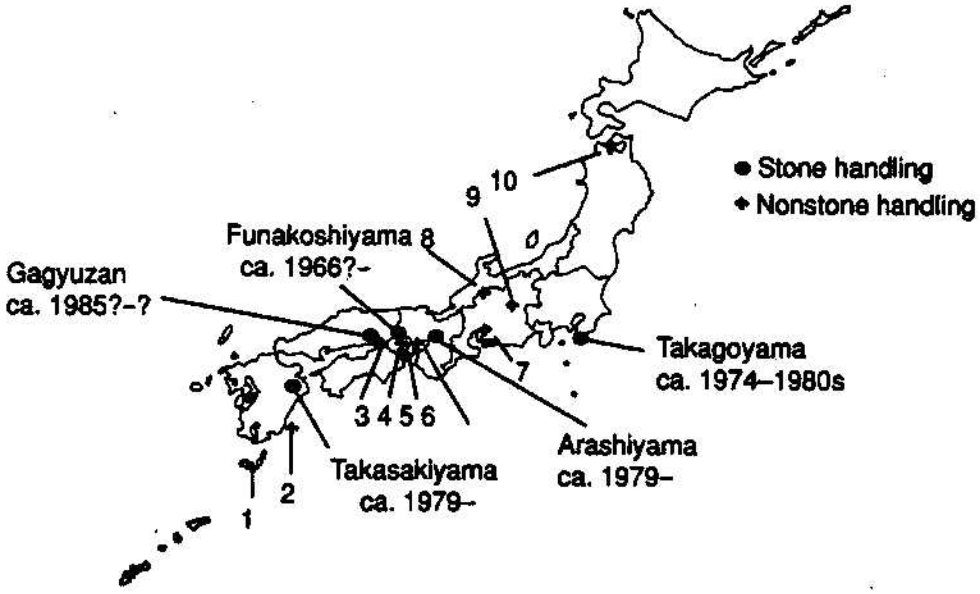

Fig. 10.4. Distribution of study sites where stone handling has been observed in free-ranging, provisioned populations of Japanese macaques. Sites denoted by numbers are provisioned sites where stone handling has not been observed; 1, Yakushima; 2, Koshima; 3, Katsuyama; 4, Shodoshima; 5, Awajishima; 6, Minoo; 7, Hanyama; 8, Hakusan; 9, Jigokudani; 10, Shimokita.

at one time and are slowly pushing the items from the cheek pouch back into the mouth to be chewed before swallowing. Stone handling can be interspersed with bouts of feeding but begins to taper off in most individuals when the food has been completely consumed. The general mood of individuals is relaxed with an intense concentration directed toward the activity, sometimes ignoring or refusing the solicitations for play or mating. There is nothing to stop them from feeding on provisioned food or from moving into the forest to feed on natural vegetation, yet they choose to manipulate stones first.

Some individuals will continue to carry stones around for several minutes after feeding time has finished, depositing the stones in piles at the feeding site, at the base of trees on slopes in the forest, or even sometimes in the fork of a tree. Based on the analyses of video surveys conducted in the winter of 1989 at Takasakiyama and the summer of 1991 at Arashiyama, a highly significant negative correlation was found between age and total handling time per stone-handling session at both sites (Arashiyama: $n = 167$; $r_s = -0.435$; $p = 0.0001$; Takasakiyama: $n = 53$, $r_s = -0.488$; $p = 0.0004$; Huffman, 1996). For both males and females, the decline in stone-handling activity with age appears to be closely correlated with social and biological life-history variables (Huffman, 1996).

Stone handling replaces other activities that normally follow or are interspersed with foraging. In a nonprovisioned troop, and indeed among individuals that do not handle stones in provisioned troops, this is a time for social grooming and play. Only the most dominant individuals are likely to continue feeding until the last bit of provisioned food has disappeared. Mothers can be seen grooming the backs of their offspring who are handling stones, while they themselves are processing the food they have stored in their own cheek pouches.

Macaques in general may have an intrinsic propensity towards manipulatory activity concurrent with foraging. If so, stone-handling activity fits nicely into that time slot. In nonprovisioned groups, forging activity is likely to take longer because food resources are less abundant in any one location and are more spread out, making it necessary to feed for a longer time to obtain the same amount of food. Interspersed with traveling between food patches, this would leave little time for such leisure activities as stone handling.

10.5.2 Intergroup and interspecies behavioral comparison of stone handling

Stone handling has been observed to occur independently in at least five free-living provisioned populations across Japan (Fig. 10.4) and in two captive groups kept at the Kyoto University Primate Research Institute (Huffman, 1984, 1996; Huffman and Quiatt, 1986).

The spatial and temporal distribution of known stone-handling sites demonstrates the behavioral tradition's independent origin in each group. There is no geographical or temporal pattern of emergence to suggest that the behavior spread between provisioned troops within a region (Fig. 10.4). The behavior does not reliably occur in neighboring populations within the same regions where it does occur. An interesting example from this perspective is that stone handling appeared in both the Arashiyama and Takasakiyama populations at around the same time in 1979, while it is thought to have started much earlier at the intermediate location of Funakoshiyama, around 1966. Separated by an ocean barrier and several hundred kilometers of land, it is implausible that the behavior was transmitted between these different populations on Kyushu and Honshu islands.

Only sketchy details are known about most of the other sites where stone handling has been observed. Hiraiwa (1975) made the first brief report of stone handling in Japanese macaques from her observations of the Takagoyama troop. The frequency of occurrence was low and only subadults, younger than 3 years of age, exhibited the behavior. Later on in 1984 when provisioning was stopped, the practice of stone handling gradually ceased (T. Fujita, personal communication). On the island of Koshima in the early 1980s, a 15–16-year-old male named Ira was frequently observed carrying and clacking stones together along the rocky shoreline, but the behavior never spread to other group members (K. Watanabe, M. Kawai, and S. Mito, personal communications). Written records do not exist for the first occurrence of stone handling at the Funakoshiyama Monkey Park, but the caretaker in charge of provisioning this free-ranging troop remembers seeing the behavior as early as 1966 (I. Narahara, personal communication). Stone handling has not spread widely within this troop with approximately 300 members. Details of stone handling at Gagyuzan are even scarcer. The behavior apparently underwent a couple of periods in which its visibility rose and subsequently dropped again in frequency (F. Fukuda, personal communication).

At Arashiyama, where the most detailed studies of stone handling have been conducted, 17 basic behavioral types have been classified (see Table 10.1 for these and the abbreviations). The first five behaviors (GA, PU, SC, RIH, and RT) are commonly exhibited by macaques in general when manipulating objects in their environment such as twigs and acorns or novel human-introduced objects with which they come into contact. The last three behaviors (TW, MP, and GW), connected with moving, are considered to reflect a growing familiarity with stones and are a product of human habitats where hard-packed ground, roofing, or concrete is available.

With the exception of one behavior (PUD), all of the Arashiyama behavioral types have been observed at Takasakiyama (Huffman, 1996), and at relatively similar frequencies (Fig. 10.5). The most common behavioral patterns observed at both Arashiyama and Takasakiyama were SC, RWH, GW, and GH. At Takagoyama, the relative frequency of occurrence was low and the behavioral patterns limited to GA, CD, PU, RT, and RIH (Hiraiwa, 1975), five of the same eight basic behaviors first observed at Arashiyama (Huffman, 1984). The general visibility of stone handling at Funakoshiyama, as observed in the mid-1990s, was much lower than at either Arashiyama or Takasakiyama, despite the troop's large size. The behavioral patterns observed (GA, RWH, RT, RIH, GH, etc.) were identical to those recorded in the other groups (K. Kaneko,

Table 10.1. *The 17 basic behavioral patterns of stone handling observed at Arashiyama*

Behavioral pattern	Characteristics
Gathering (GA)	Gathering stones into a pile in front of oneself
Pick up (PU)	Picking up and placing stones into one hand
Scatter about (SC)	Scattering stones about on the ground in front of oneself
Roll in hands (RIH)	Rolling stones in the hands
Rubbing stones together (RT)	Rubbing stones together
Clacking (CL)	Clacking two stones together
Carrying (CA)	Carrying stones from one place to another
Cuddling (CD)	Holding or cradling stones
Pick up and drop (PUD)	Pick up repeated over and over
Rub on surface (ROS)	Rubbing stones on tin roofing, cement surfaces, etc.
Flinting (FL)	Striking one stone against another held stationary
Pick up small stones (PUs)	Resembling the picking up of wheat grains or soy beans
Rub with hands (RWH)	Similar to potato-washing behavior
Grasp with hands (GH)	Clutching a pile of stones gathered and placed in front of oneself
Toss walk (TW)	Repeated tossing ahead and picking up of a stone(s) while walking
Move and push (MP)	Pushing a stone with both hands while walking forward
Grasp walk (GW)	Walking with one or more stones in the palm of one or both hands

unpublished report; J. Itani, M. A. Huffman, unpublished observations). These comparisons demonstrate that the behaviors that make up stone handling are based on the wide behavioral repertoire of the species.

The behaviors exhibited in stone handling appear to be a predisposition shared by macaques in general. Two sites where stone handling is seen in semiprovisioned troops of long-tailed macaques (*Macaca fascicularis*) in Indonesia and Thailand have recently been brought to the authors' attention. Stone handling occurs in a free-ranging, potato- and fruit-provisioned troop of long-tailed macaques inhabiting the sacred monkey forest of Padangtegal, Ubud Bali. Here, CL, SC, PUD, RWH, ROS, and RIH are the behaviors observed most often (A. Fuentes, personal communication). These macaques have also been observed to exhibit food-washing behavior similar to that on Koshima (Wheatly, 1988) and other forms of object-rubbing behavior (Fuentes, 1992). Another troop living along the coast in Prachuap Province, Thailand are opportunistically

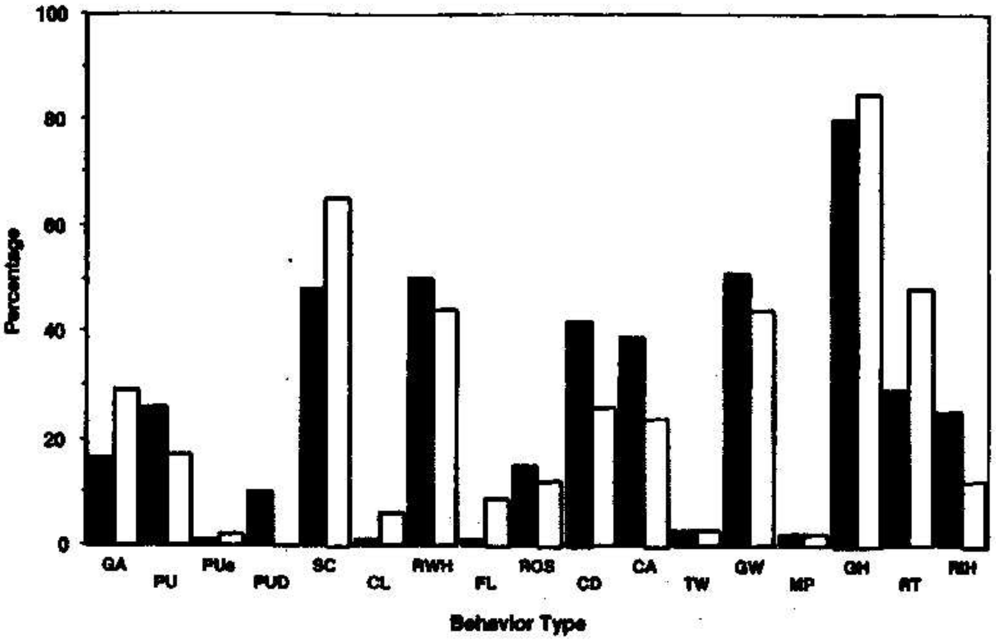

Fig. 10.5. Comparison of the frequency of behavioral patterns of stone-handling displayed by Arashiyama (■) and Takasakiyama (□) Japanese macaques. See Table 10.1 for the behavior types for these abbreviations.

fed bananas and peanuts, which are sold to tourists. At this site, the stone-handling patterns exhibited are ROS, CA, POD, TW, and MP (K. Bauers, personal communication).

In the late 1980s, at the Primate Research Institute, Inuyama Japan, the habit of clacking hard food pellets together was seen to spread from one to other individually caged rhesus macaques (A. Mikami, personal communications). Stone handling or its proximate behavior with other objects appears to be a genus level behavioral propensity associated with provisioning and a sedentary lifestyle.

10.5.3 Factors influencing the rate of diffusion of stone handling

The rate of diffusion of stone handling in Arashiyama was estimated at two time points from surveys conducted in 1983 (B troop) and 1991 (E troop) (Fig. 10.6). The natural logarithm of the yearly total number of individuals for which stone handling was observed was plotted against time to compare the slopes of the linear regression equations (Sokal and Rohlf, 1994). The rate of diffusion was significantly higher in B troop ($y = -0.9 + 0.6x$) than in E troop ($y = 2.8 + 0.2x$) ($p < 0.001$).

In 1986, B troop divided, producing E and F troops (Huffman, 1991). Regardless of the smaller size of E troop, the age–sex class structure of stone

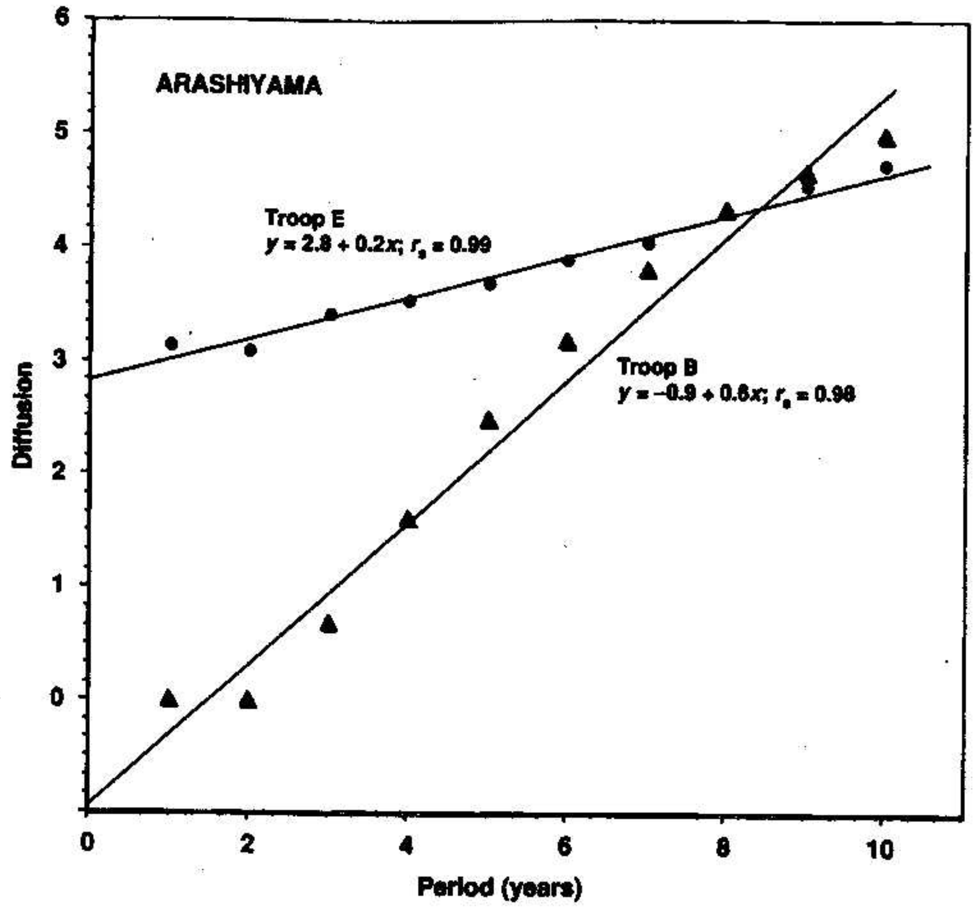

Fig. 10.6. Diffusion of stone handling in two Arashiyama troops of different sizes (troop E with 139 and troop B with 236 members). Each time period on the *x* axis represents one year. The number of individuals performing stone handling for each period was estimated on the basis of two surveys conducted in 1983 (B troop) and 1991 (E troop). The natural logarithm of the yearly number of individuals performing stone handling (diffusion) was calculated; the significance of the difference in slope between the two linear regression equations was $p < 0.001$.

handlers remained basically the same. Rather than the rate of diffusion being a function of group size, these estimated differences in the rate of diffusion are the result of the current phase of transmission. At this phase, acquisition of stone handling was only occurring among infants, because all individuals acquired the behavior within their first 6 months of life. Therefore, the increase in new stone handlers after this point in time is purely a function of new births.

If the period of innovation of stone-handling behavior had not been observed in the detail achieved at Arashiyama, an investigator seeing the behavior for the first time today would find it difficult to conclude that stone handling is a behavioral innovation. Although phylogenetic and group-history factors are difficult to establish in field research, it is important to keep in mind the importance of both these factors when interpreting the origin of a behavior.

10.6 Behavioral tradition in multiple groups and among subspecies: leaf swallowing, a self-medicative behavior in African great apes

10.6.1 Behavioral description and its context of performance in the wild

Attention was first brought to leaf-swallowing behavior by Wrangham and Nishida (1983). They pointed out that leaf swallowing was unlikely to provide any nutritional value as they noticed a pattern of folded, undigested leaves of *Aspilia* spp. in the dung of chimpanzees at both Gombe and Mahale.

Leaves are most commonly swallowed early in the morning or shortly after climbing out of the night nest, often by visibly ill individuals, as one of the first items ingested after waking (Huffman and Caton, 2001; Huffman *et al.*, 1996; Wrangham and Goodall, 1989; Wrangham and Nishida, 1983). Leaf swallowing is a form of animal self-medication (Huffman, 1997) and has been documented in the greatest detail in chimpanzees at four study sites in East Africa (Mahale, Gombe, Kibale and Budongo see Fig. 10.7). At these sites, the behavior is strongly associated with the expulsion of adult intestinal nematodes and or cestode proglottids (Huffman and Caton, 2001; Huffman *et al.*, 1996; Wrangham, 1995). The gastrointestinal tract responds to the swallowed leaves by rapidly expelling the undigested leaves approximately 6 hours after swallowing. Repeated periodically throughout peak periods of infection, leaf swallowing was projected to have a significant impact on the level of *Oesophagostomum* sp. infection (Huffman and Caton, 2001).

10.6.2 Species comparison and geographical distribution of leaf swallowing

The evidence that great apes practice leaf-swallowing behavior as a form of self-medication has stimulated researchers to look for this anomalous feeding habit among apes across Africa. At the writing of this paper, leaf-swallowing behavior involving the use of more than 34 different plant species has been noted in at least 22 social groups at 13 great ape study sites in Africa (Fig. 10.7). Represented by these observations are

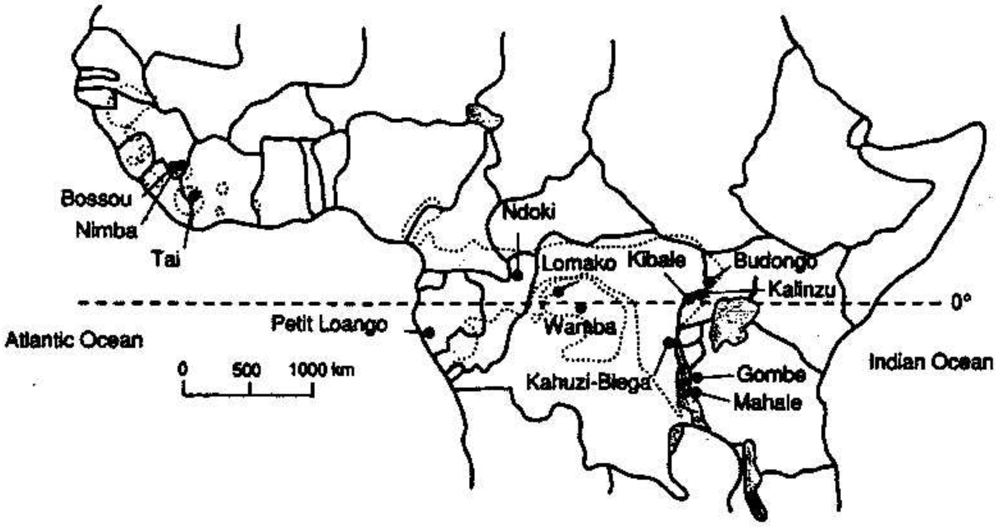

Fig. 10.7. African great ape study sites where whole leaf swallowing has been observed (Based on Huffman, 1997 and M. A. Huffman unpublished data). Species represented by each study site are as follows; bonobo (Lomako, Wamba), chimpanzee (Bossou, Nimba, Tai, Petit Loango, Ndoki, Mahale, Gombe, Kahuzi-Biega, Kalinzu Forest, Kibale, Budongo Forest), eastern and western lowland gorillas (Kahuzi-Biega, Lope).

three subspecies of chimpanzee, the bonobo, and both western and eastern lowland gorilla species. The behavioral details described above are basically the same at other sites, where leaf swallowing has been directly observed (Tai: Boesch, 1995; Bossou and Mt. Nimba: Matsuzawa and Yamakoshi, 1996; Sugiyama and Kohman, 1992; Mahale and Gombe: Huffman, 1997; Takasaki and Hunt, 1987; Wrangham and Nishida, 1983; Lomako: Dupain *et al.*, 2002).

Self-medication is most likely a very old behavior and, therefore, widespread throughout the distribution of the species that practice it. One source of behavioral variation in leaf swallowing among sites is the species of plant selected for leaf swallowing (Huffman, 1997; Huffman and Wrangham, 1994). Local variation may not be manifest in the behavioral pattern itself, but in the materials used; the species selected for use in the wild appear to be transmitted among individuals within a group. The local, regional and pan-African patterns of plant species selected for leaf swallowing suggest that transmission of information about which particular plant species are used also occurs between neighboring groups. Local and regional level similarities, not explainable by plant distribution alone, suggest that social learning and intergroup diffusion of the behavioral tradition exists for leaf swallowing (Huffman, 2001).

10.7 Future prospects and directions

To-date, the majority of behavioral traditions described in the literature have been related to food or foraging activity. While a good case for adaptive value can be made for such foraging-related behavioral traditions, it need not be an absolute criterion for the emergence or the continued existence of a behavioral tradition, as long as the behavior is not maladaptive. Pleasure seeking, stress release, even addictions are the motivation behind widespread human behavioral traditions, such as using worry beads, smoking, alcohol consumption, bungee jumping, or automobile racing. Versions of these traditions exist in practically every human culture. These behaviors are, in part, based on common propensities rooted in the evolutionary past of our species. Other species also have a great range of possibilities for traditions. New examples from emerging long-term studies on capuchin species are presented for the first time by Perry *et al.* (Ch. 14). Boinski *et al.* (Ch. 13) provide interesting new examples of social interactions, foraging techniques, and object manipulation that are suggestive of behavioral traditions.

One of our tasks for the future is to evaluate the potential impact of behavioral traditions on the survival of the individual and the group. At the same time, it will be productive to identify the ecological variability and biological foundations upon which these behaviors may be based and to look for similarities and differences among taxonomically related species. The knowledge gained from such research, when integrated into the current theoretical models used to explain the dynamics of behavioral transmission, should provide a broader understanding of the role of animal traditions in the survival of the species.

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ORIGINAL ARTICLE

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An experimental study of leaf swallowing in captive chimpanzees: insights into the origin of a self-medicative behavior and the role of social learning

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Abstract Chimpanzees in the wild swallow the rough hispid leaves of certain plant species as a means of physically expelling intestinal parasites. A plant with such a leaf texture was introduced in 36 trial sessions to a captive group of 11 healthy adult chimpanzees to investigate the possible origin and acquisition of leaf swallowing behavior. One male (housed separately from the group during testing) and one female, both captive born, spontaneously exhibited the behavior on their first trial without prior opportunity to observe others with this plant. Six other chimpanzees on their first trial displayed a phobic response to these leaves and rejected them entirely, while another two chewed and swallowed the leaves in a normal way. Four individuals eventually exhibited the behavior, after having approached and closely observed the leaf swallowing of the first female to exhibit the behavior in the group. Four of the six individuals that initially avoided the leaves never overcame their phobia toward this plant and were not in proximity to a chimpanzee performing leaf swallowing during test sessions. Individuals born to wild chimpanzee mothers were no more likely to perform the behavior than captive-reared group mates. These results suggest that the acquisition of this behavior is based in part on a propensity to fold and swallow rough, hispid leaves, but that the acquisition and spread of leaf swallowing within a group is likely to be socially influenced. This study provides support for the hypothesis that leaf swallowing originated in the wild from opportunistic feeding behavior and was later passed down in the form of a self-medicative behavioral tradition.

Keywords Feeding · Social tolerance · Behavioral tradition · Self-medication

Introduction

Attention was first brought to leaf swallowing behavior by Wrangham and Nishida (1983) when they pointed out the significance of this ingestive behavior as unlikely to be that of providing any nutritional value. They noticed a pattern for the occurrence of folded, undigested leaves of *Aspilia* species in the dung of chimpanzees at both Gombe and Mahale. Currently, leaf swallowing is documented in the greatest detail in chimpanzees at four study sites in East Africa (Mahale, Gombe, Kibale, and Budongo), where its use is associated with the expulsion of adult intestinal nematodes and or cestode proglottids (Wrangham 1995; Huffman et al. 1996; Huffman and Caton 2001). Leaf swallowing has since been noted to occur in at least 22 social groups of chimpanzees, bonobos, and lowland gorillas at 13 study sites across Africa (Huffman 2001). The 34 different plant species selected at these sites vary in life form (herb, vine, shrub, and tree), but they all share the common property of being rough and hispid (Huffman 1997).

The widespread occurrence of leaf swallowing and this universal criterion for selecting rough, bristly leaves suggests a behavioral predisposition for leaf swallowing in all African great apes. There is also evidence to suggest that transmission within the group occurs at least in part by some form of social learning (Huffman and Hirata 2003). Observations from the wild suggest that individuals' first exposure to leaf swallowing and other forms of self-medicative behavior occurs at an early age, not when ill themselves, but by observing the behavior of close family members or associates that are ill.

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Chimpanzees as young as 1 year of age closely watch this behavior and have been seen to attempt immediately thereafter to perform it on their own with varied success, regardless of health condition (Huffman and Seifu 1989; Huffman and Wrangham 1994). At this stage, it is most likely treated as one more element of the mother's foraging repertoire that engages the infant's interest.

We do not expect that the behavior is first acquired because of any understanding of its self-medicative function, rather, that the self-medicative aspects of use are likely to be learned over time if the appropriate selective forces (e.g. parasite infection) are present in the habitat in question. A combination of learning the context of use from watching others and positive feedback from any perceived personal relief from physical discomfort that leaf swallowing may assist in providing the ingestor is predicted to occur. Presently, the details of this underlying mechanism and how long it takes to acquire the behavior in its self-medicative context is unclear. It is extremely difficult to collect such evidence from the field given that these traditions appear to be already well established in all groups where leaf swallowing is known to occur (Huffman 2001). Furthermore, as the behavior itself occurs at low frequencies in the wild due to strong seasonality linked with periods of parasite reinfection (Huffman et al. 1996; Huffman 1997), the acquisition process of the behavior by new individuals is difficult to follow precisely under natural conditions.

There is a range of possibilities for how leaf swallowing behavior started and how individuals come to swallow leaves instead of simply chewing them. At one extreme, animals may have an innate tendency to select appropriate properties in plants when ill, so that the role of social context is local enhancement. That is, naive individuals may have their attention drawn to areas with plant species used by others (Huffman and Wrangham 1994). At the other extreme, animals may have a propensity to swallow certain items without chewing, but due to unfamiliarity with rough bristly leaves in their daily diet, must somehow learn that such leaves can be ingested before they are able to learn about any possible benefit from doing so. Thus, initial acquisition by young or naive individuals, like the proposed origin of this behavior itself, may occur in the context of opportunistic feeding behavior that is later molded over time through further individual experience and association of its practice with illness in other group members. To elucidate some of these important questions regarding the intrinsic nature and acquisition process of leaf swallowing behavior, we conducted a study on a socially living group of captive chimpanzees.

Methods

The study was conducted between 9 October and 11 November 1997 on a group of 11 (3 males, 8 females) adult chimpanzees used in cognitive studies at Kyoto University's Primate Research Institute in Inuyama, Japan (Table 1). Among the 6 individuals born in Africa, all but 2 of the oldest (Gon, Puchi) were brought into captivity and reared from the age of 1 year. The remaining 5 individuals were captive born and or human reared in Japan or Europe. The veterinary staff routinely examines the chimpanzees. None of the subjects displayed symptoms of parasite infection during the study period.

From 1996 up to the time this study was conducted in 1997, the chimpanzees had daily access to an environmentally enriched outdoor enclosure containing 63 species (390 individual plants) of trees and shrubs, a flowing stream, and an 8-m-high multi-tiered tower (Ochiai and Matsuzawa 1998, 1999). Prior to the experiments described below, their exposure to plants in the outdoor compound was limited to these 63 known species and a few local grass species that spontaneously took root. None of the plants in the compound resembled the texture of plants used for leaf swallowing by chimpanzees in the wild.

The test plant species used in this study, *Helianthus tuberosus* (Compositae), was selected because the leaves are virtually identical in texture to species such as *Aspilia mossambicensis, Lippia plicata,* and *Ficus exasperata* used by chimpanzees at Mahale, Gombe, and elsewhere. No member of the study group had been exposed to this or other species resembling it in leaf texture prior to testing. *H. tuberosus* grows semi-wild between June and November along roadsides, in open lots, and in some gardens in the neighborhood of the Institute. Fresh branches were collected within 20 min prior to testing and placed in water to maintain their freshness. Native to North America, *H. tuberosus* is a nontoxic plant whose leaf and stem are often used as cattle fodder. Introduced to Japan over 100 years ago, the tubers are a delicacy consumed by people in some rural areas of the country. The plant is known as "kiku imo" in Japanese and "earth apple" in English.

In total, 36 trial sessions were conducted on the chimpanzee colony, with a minimum of 3 sessions per individual. A branch of 29–40 cm in length with 18–40 leaves and occasionally 1–8 flowers was given to an individual, selected randomly over the study period. It was possible to call an individual chimpanzee to the wall of the enclosure and drop a branch down to it from the observation

Table 1 Leaf swallowing test subjects at the Primate Research Institute (*PRI*)

Name	Sex	Age[a]	Arrived at PRI (age at arrival)	Origin (date of birth)
Gon	M	31	30.1.79 (12)	West Africa, pet in Japan (1966, month unknown)
Puchi	F	31	30.1.79 (12)	West Africa, pet in Japan (1966, month unknown)
Reiko	F	31	3.7.68 (1.6)	West Africa (December 1966)
Mari	F	21	30.1.78 (1.5)	West Africa (June 1976)
Akira	M	21	30.1.78 (1.5)	West Africa (June 1976)
Ai	F	21	10.11.77 (1)	West Africa (October 1976)
Pendesa	F	20	12.11.79 (2.7)	Japan Monkey Centre (2 February 1977)
Chloe	F	16	28.1.85 (5)	Paris Zoo (13 December 1980)
Popo	F	15		PRI[b] (7 March 1982) daughter of Puchi–Gon
Reo	M	15		PRI[b] (18 May 1982) son of Reiko–Gon
Pan	F	13		PRI[b] (7 December 1983) daughter of Puchi–Gon

[a] Age at the time of experiments in October 1997

[b] Artificial insemination, hand reared

point. Normally tests were conducted on individuals in a social group setting in the outdoor enclosure ($n = 28$) with all or most members present. Three test sessions, however, were conducted with a sub-group of 3 individuals in a smaller holding room; one plant was introduced and the 3 interacted consecutively with the same plant. During the entire study period, adult male Reo was kept in a separate enclosure from the main group during the day, with occasional access to his mother or other female companions. During testing Reo was always alone in all 3 of his trial sessions. Due to the physical separation of his enclosure from the main outdoor enclosure, Reo had no opportunity to see other individuals during their sessions and vice versa. The old adult male Gon and adult female Pan were also tested alone on one occasion each. None of the subjects had access to the test plant species outside of these trial sessions.

Observations were recorded by the authors using 8-mm video and by handwritten notes. All feeding behaviors and behavioral interactions between the focal animal and others in the group were recorded. To obtain complete behavioral sequences of a subject's response to the plant material and interactions with others, observations were continued for 5 min after the focal individual no longer possessed test plant material. There was no stealing or disruption by others while the plant was in the possession of the focal subject. Because it was impossible to retrieve a plant from the enclosure if it was abandoned or retrieved by another, the behavior of the new possessor and interactions with all others was recorded as a new trial session. In eight cases, an onlooker picked up all of the remaining plant material after the original focal subject freely discarded it. Because of this, no plant material was left in the enclosure after the end of the final trial session of any given day.

To independently verify our assessment of leaf swallowing in the trial sessions, individuals were separated from the rest of the group when they were brought inside for the night and put singly into a night sleeping room when day-to-day management and ongoing research protocol allowed. The following morning, after these individuals were rejoined with the group, feces in their sleeping rooms were inspected.

Results

Verification of leaf swallowing behavior

Folding and swallowing of leaves became the major mode of ingestion for 6 of the 11 individuals at some point during the study (Fig. 1). The behavior was similar to that observed for chimpanzees in the wild (LS-Wild ESM1, LS-Chloe ESM2), supporting the notion of a species-wide propensity to perform this behavior in chimpanzees. Leaves were deliberately folded, using a combination of lips, palate, and tongue, while a leaf still attached to the stalk was slowly drawn into the mouth. The behavior was distinct from normal feeding as chewing action was overtly absent and the leaves were deliberately put into the mouth one at a time. Of those 6 individuals that leaf swallowed, there was no significant difference in the number of African born (3/6) versus captive born (3/5) subjects (Fisher's exact test, two-tailed, $P = 1.000$, NS) to exhibit this behavior.

Results of the 11 next-morning follow-up dung inspections are presented in Table 2. All individuals selected for the follow-up inspections were observed

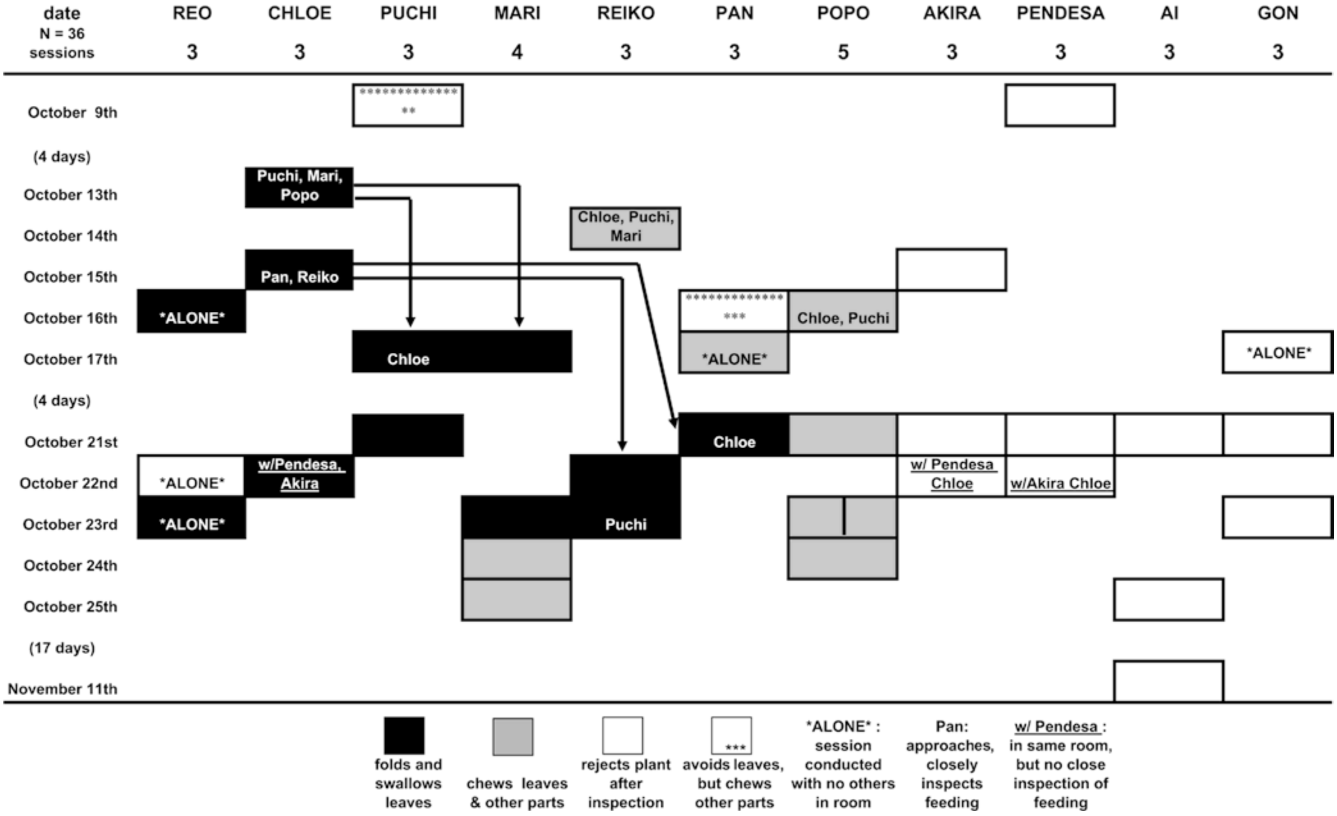

Fig. 1 Observed responses of chimpanzees in trial sessions with novel plant stimuli (*Helianthus tuberoses* L.). *Solid lines* connecting boxes denote putative social learning network between Chloe (leaf swallowing "demonstrator") and individuals that first displayed leaf swallowing behavior in subsequent trial sessions

Table 2 Results of dung inspection the day after individual observation sessions. *Underlined subjects* were observed to swallow leaves during the trial session

Date	Subject	Parts ingested the previous day	Contents of dung
10 October	Puchi	Stalk, flowers	No leaf trace
14 October	Chloe	Leaves, flowers	3 folded leaves
15 October	Reiko	Leaves, flowers	No leaf trace
16 October	Chloe	Leaves, flowers	10 leaves
18 October	Puchi	Stalk, leaves, flowers	2 leaf fragments
18 October	Mari	Flowers, leaves	No trace
22 October	Pan	Stalk, leaves	1 leaf
22 October	Puchi	Stalk bark, leaves, flowers	No leaf trace
23 October	Reiko	Stalk bark, leaves, flowers	6 leaves
24 October	Mari	Stalk, leaves	No leaf trace
24 October	Reiko	Stalk, leaves	6 leaves

to have ingested some or all parts of the plant during the test session in question. Eight of these cases were of individuals directly observed to exhibit leaf-swallowing-like behavior during the session. The following morning, in 6 of these 8 cases, dung was found to contain one to six folded, nondigested *H. tuberosus* leaves. No whole or partial undigested leaves were found in the 3 cases in which individuals were only observed to chew leaves and or other plant parts.

Individuals' first response to rough hispid leaves

The first response to the leaves varied from individual to individual. Chloe and Reo, two captive-born individuals, spontaneously displayed leaf-swallowing-like behavior in their first session without the benefit of observing it in other group members. Chloe consistently displayed this pattern as her major mode of ingestion during all three of her test sessions. Mari also folded and swallowed a portion of the leaves on the branch given to her on her first (and second) session. She did so after having closely observed Chloe fold and swallow leaves 4 days earlier (Fig. 1).

The typical first response to the plant for six other individuals was an almost phobic rejection of the rough hispid leaves (Akira, Pendesa, Ai, Gon, Puchi, and Pan). Four of these individuals consistently rejected the entire plant throughout the study, while the other two discarded all of the leaves but ate other plant parts (Pan, Puchi). In contrast, two other individuals, (Reiko and Popo) chewed and ate the leaves in their first trial session. Popo continued to chew and eat leaves in all of her subsequent sessions. She displayed no aversion whatsoever, rapidly consuming everything (Fig. 1).

Leaf swallowing and social interactions among individuals during the trial session

Leaf swallowing was observed in 10 of the 31 trial sessions conducted in a group setting. Individuals in possession of *H. tuberosus* attracted the attention of others in 5 of these sessions (Fig. 1). Puchi, Mari, Reiko, Pan, and Popo approached within close proximity (< 1 m) to, and intently inspected, Chloe while she exhibited leaf swallowing during her 1st and 2nd trial sessions. This group of females also approached and closely inspected one another when leaves and other parts were being eaten (Fig. 1), showing their mutually tolerant social relationships. With the exception of Popo, these females all subsequently exhibited leaf swallowing behavior themselves for the first time 2–9 days after having observed Chloe perform leaf swallowing behavior. During this study, Chloe was the first and only possible model of leaf swallowing for these four females (Fig. 1). Chloe approached closely and intently watched the first instance of leaf swallowing exhibited by Reiko and Pan.

Due to other ongoing research Ai and Pendesa were frequently absent when group-setting test sessions were conducted in the outdoor enclosures. During ten sessions outdoors in which leaf swallowing was observed, Ai was absent during seven and Pendesa during six sessions. Akira, Gon, Ai, and Pendesa were never observed to approach and inspect the feeding behavior of others in the possession of *H. tuberosus*, whether they were leaf swallowing or chewing leaves or other parts of the plant. These four individuals consistently rejected *H. tuberosus* in all of their test sessions.

Discussion

Possible modes of acquisition and the origin of leaf swallowing

This is the first ever attempt to investigate leaf swallowing under semi-controlled conditions. Bearing in mind the limited sample size and management restraints on observational procedure, some basic aspects of the nature of leaf swallowing and insights into the possible modes of acquisition of this behavior by chimpanzees can be considered. The spontaneous performance of leaf swallowing by two individuals during their first trial, in the absence of a leaf swallowing "demonstrator," shows that chimpanzees may have a propensity to fold and swallow rough hispid leaves. This supports evidence from the wild that the behavior can emerge without inter-group social contact in geographically isolated populations or subspecies (sec. Huffman and Hirata 2003). However, unlike their counterparts in the wild that often exhibit this behavior when ill and/or infected with parasites (Wrangham 1995; Huffman et al. 1996), these captive individuals were parasite free and showed no visible signs of ill health when they performed the behavior. From this we conclude that folding and swallowing of leaves is not an innate response to parasite infection. Indeed, the initial response for more than half of the subjects was a phobic avoidance of these leaves or the entire plant. Our results support the current hypothesis regarding the origin of leaf swallowing behavior (Huffman and Wrangham 1994), which proposes it may have originated in the feeding context of a novel plant item. It is suggested here that the leaf's rough hispid texture encourages the peculiar mode of ingestion, that is, folding and swallowing leaves whole.

Our results also support observations in the wild that the acquisition and spread of leaf swallowing within a group is at least in part socially influenced, rather than being solely the product of individual trial-and-error learning. It is clear that the behavior was not acquired by every individual in this study via the same mode of learning. Excluding Chloe and Reo, who seemingly acquired leaf swallowing behavior spontaneously, the other individuals that later exhibited the behavior may indeed have used multiple modes of learning over the period of acquisition (sec. Visalberghi and Fragaszy 1990). Among the individuals that eventually exhibited the behavior during our study, social tolerance among them in the feeding context (sec. van Schaik et al. 1999) is considered to have been an important facilitator of exposure to leaf swallowing, and thus opportunities for social learning. As suggested for object manipulation in Japanese macaques (Huffman and Quiatt 1986) and foraging-related tool-use acquisition in orangutans (van Schaik 2003), here too, interpersonal social networks and social tolerance could be important factors in the transmission of leaf swallowing behavior. This is further supported by the fact that those individuals that never approached and observed another chimpanzee leaf swallowing never overcame their phobia of the plant's rough, hispid leaves. All individuals that eventually exhibited leaf swallowing behavior did so only after having seen the behavior being exhibited by Chloe, the first individual in the social group observed to display folding and swallowing of *H. tuberosus* leaves spontaneously.

Future studies

Controlled studies of self-medicative behavior in parasitized organisms are rare and limited to mice (Vitazkova et al. 2001) and invertebrates (Karban and English-Loeb 1997). There are obvious ethical reasons why we chose not to conduct a controlled study on chimpanzees in the context of parasite infection. We have shown here that there are important things to be learned without such invasive methods. Given the fact that bonobos and lowland gorillas too are known to habitually exhibit leaf swallowing behavior in the wild (Huffman 1997), the propensity for folding and swallowing of rough hispid leaves is expected to be a shared trait of all African great apes. It follows then that the self-medicative function of leaf swallowing behavior must be a secondary adaptation of a feeding response brought about by leaf texture, raising the question as to how the self-medicative context of leaf swallowing emerged independently across Africa.

Further refined, noninvasive testing of captive chimpanzee groups naive to rough hispid leaves is being planned. Similar controlled and noninvasive studies regarding the acquisition process of leaf swallowing and other self-medication in the African great apes and other primates is strongly encouraged. Greater attention should be paid to the social networks of group individuals to grasp greater detail of the possible mode(s) of social learning involved in the transmission of such behaviors within the group (e.g. White and Burgman 1990; Ginsberg and Young 1992; Coussi-Korbel and Fragaszy 1995; Whitehead 1997). Such studies are expected to increase our understanding of the possible origins of self-medicative behaviors and the role social learning may play in their maintenance in nature.

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BRIEF REPORT

A New Case of Fish-Eating in Japanese Macaques: Implications for Social Constraints on the Diffusion of Feeding Innovation

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This is the first detailed report of social factors affecting fish-eating in Japanese macaques under natural circumstances. We video-recorded a complete event of fish eating, involving a new fish food species for the monkeys on Koshima island. Following the discovery of a large beached sea bass by a peripheral male, we observed a total of 16 individuals feeding on the fish in turns, and interacting around it. The rank order of access to the fish was mainly explained by the spatial position of group members, whereas dominance determined how long the fish was monopolized. Although limited, the tolerated presence of close-bystanders while feeding was affected by kinship and affiliation. Genealogic data suggested that fish-eating behavior was well maintained in terms of maternal lineages. This report should contribute to a better understanding of how social features may constrain the long-term diffusion of feeding innovations in free-ranging primate groups. Am. J. Primatol. 69:821–828, 2007. © 2007 Wiley-Liss, Inc.

Key words: fish-eating; feeding tradition; behavioral diffusion; *Macaca fuscata*

INTRODUCTION

On Koshima island, the first case of fish-eating by a Japanese macaque was recorded in 1979. By 1986, this new feeding habit had spread to 75% of the group, seemingly from older to younger individuals [Watanabe, 1989]. On the basis of a relatively small data set (six sample points over a 7-year period), mathematical models suggested that fish-eating at Koshima island was a socially transmitted behavioral tradition [Lefebvre, 1995]. It is critical to know the history of a

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behavioral innovation to assess how social learning processes may contribute to its diffusion within a group [Visalberghi & Fragaszy, 1990]. However, cases of behavioral innovation and diffusion have rarely been observed and specifically documented in free-ranging primate populations [Huffman & Hirata, 2003]. In several decades of regular observations on Koshima island, fish-eating by Japanese macaques was only observed six times. The first two observations were made by chance during routine work, and therefore were not described in detail [Watanabe, 1989]. The next four records of fish-eating did not occur under natural conditions. Most macaques observed feeding on small fish (sardines) were actually given this food by humans once a year [Watanabe, 1989]. Moreover, little is known about the influence of sociodemographic variables (such as kinship, dominance, and affiliative relationships) on the likelihood of learning and adopting innovative behaviors [Huffman & Hirata, 2003]. More quantitative data, taking into account the social context of diffusion of feeding innovations, are needed to obtain a deeper understanding of the cultural transmission processes [Lefebvre, 1995].

The goal of this report is threefold: (1) to provide a detailed descriptive account (in terms of social status and relationships of the individuals involved) of a seldom observed event of fish-eating at Koshima island, under natural conditions; (2) to examine the social conditions, at least partially reconstructed, under which feeding innovation and its subsequent propagation may occur in Japanese macaques; and (3) to assess the generalization, long-term diffusion, and maintenance of the fish-eating habit in Koshima monkeys by providing a genealogy [after Watanabe, 1989] of lineages of fish eaters recorded on the island to date.

METHODS

The observations took place at Koshima island, Japan. Figure 1 shows genealogic information about the two groups of Japanese macaques living on the island (main and Maki branch groups). Although the habitat of the island provides them with various kinds of natural foods (including leaves, fruit, and small invertebrates), the monkeys are provisioned twice a week with 4 kg of wheat grains by the staff technicians of the Koshima Field Station, Kyoto University. In January and February 2004, two observers (JBL and NG) used video-recorded focal-animal sampling and ad libitum recording of avoidance and aggressive interactions [Altmann, 1974]. On the day of the fish-eating event, the observation procedure was altered to collect specific information about the identity and behaviors of the individuals present around the fish. The first observer used focal-place sampling, with continuous video recording focused on the fish and the close vicinity (within 3 m). The entire sequence of events was filmed from start (when the first monkey discovered the fish) to finish (when the last monkey discarded the remains of the eaten fish). The second observer used a tape recorder to collect all occurrences of changes in position and aggressive interactions involving all individuals present within a radius of 1, 3, 5, and 10 m around the fish. Visibility was excellent. The observers could stand on the beach within 3–10 m of the sampled monkeys.

We defined a foraging bout as the period of time during which an individual exhibited an investigative or processing behavior directed to the fish (including sniff, touch, probe into the fish, and remove scales with hand). We distinguished the durations of the activities of foraging and feeding (bite into and ingest) on the fish. A monkey sitting within 10 m around the fish for at least 0.5 min, and

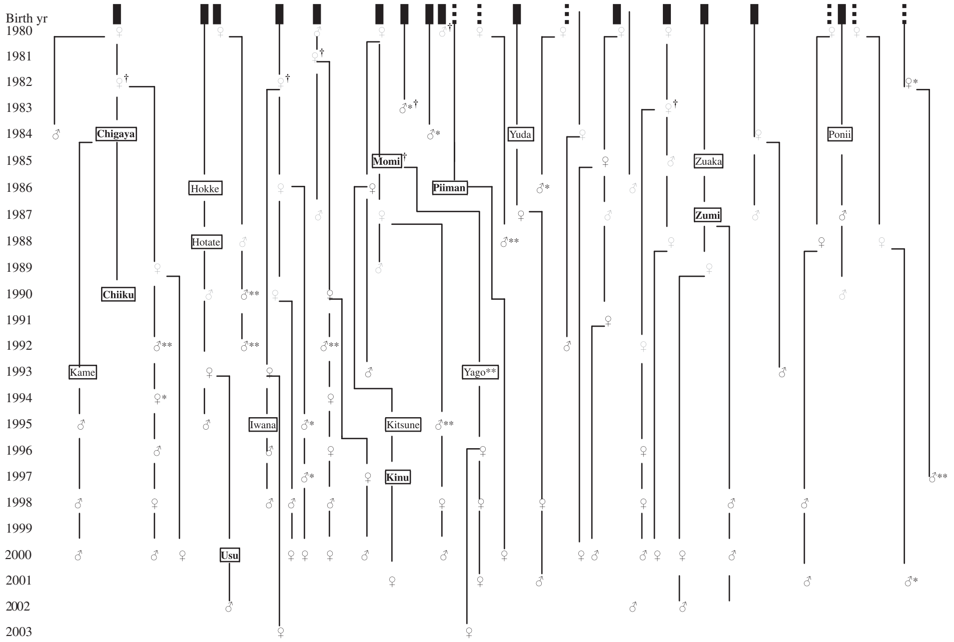

Fig. 1. Distribution of the individuals observed feeding on the sea bass according to age, sex, matrilineages, and group membership. Fish eaters in 2004 (framed) are labeled by their names. †, Individuals observed to eat fish between 1980 and 1985; bold line, matrilineage of fish eaters before 1980; and dotted line: matrilineage of non-fish eaters before 1980 [after Watanabe, 1989]. Males: regular font; females: bold font;. dead individual are engraved. **Solitary individual; *member of the Maki branch group; no asterisk: member of the main group.

intermittently watching the feeding animal was referred to as a bystander. During the 2-month observation period, we recorded 704 avoidances and unidirectional aggressions. We ranked individuals in a dominance hierarchy and verified the linearity of the hierarchy (Matman, $h' = 0.23$, $P < 0.001$). We categorized individuals into three classes according to dominance rank (high, middle, and low-ranking; $N = 18$ for each dominance class) and two age classes (mature: over 5 year-old and immature: between 1 and 5 years).

RESULTS

On January 24, 2004 at 9:23 h, an adult male moving alone in the foremost periphery of the main group, first arrived at Odomari beach, and discovered a large dead fish (approximately 90 cm) recently beached on the sand. The fish was an Asian temperate sea bass, *Lateolabrax japonicus* (Kanchi, personal communication). This species had never been recorded in the diet of Koshima monkeys before. After inspecting the fish for a minute, the discoverer foraged and fed on it for about 17 min, while being particularly vigilant toward possible newcomers. At 9:41 h the first-third of the main group, including the alpha male, arrived on the beach. The discoverer left the beach, avoiding higher-ranking group members. Most newly arrived individuals were already involved in an intense conflict and did not notice the fish immediately. This allowed two females to forage and feed on the fish successively for the next 4 min, before being supplanted by the alpha male. For the next 3.5 hours, several individuals processed and/or ate the fish in turns, surrounded by many bystanders. At 13:15 h, the last individual present on the beach discarded the head of the fish and moved back to the forest. Except for small pieces of fins and scales scattered on the sand, every other part of the fish was consumed by the monkeys. We recorded a total of 16 individuals processing and eating the fish.

Each of the 16 individuals performed investigative foraging patterns (such as sniff, touch, manipulate, and probe into) before starting to feed on the fish. Such patterns were significantly more frequent toward the fish than earthworms, a natural familiar food found in the habitat (sign test, $n = 16$, 14 positive signs, $P = 0.002$).

SocioDemographic Features of the Individuals Involved in the Event

We report the group membership, age, sex, dominance class, and rank of the fish eaters (Table I). We also report for each individual the rank order of first access to the fish and the total durations of foraging and feeding activities. Among the 16 individuals observed processing and eating the fish, 15 were members of the main group and one was a solitary individual (the last eater in chronological order). Fifteen individuals were mature and only one was an immature (with very restricted access to the fish). Males spent significantly more time feeding on the fish than females (Mann–Whitney U-test: $n_1 = 9$, $n_2 = 7$, medians = 11.6 and 1.2 min, respectively; $U = 6.0$, $P = 0.005$).

We tested the effect of dominance on the capability to monopolize the fish. We found a significant difference in the duration of foraging bouts among the high, middle, and low-ranking individuals present on the beach (Kruskal–Wallis H-test: $n_{\mathrm{high}} = 16$, $n_{\mathrm{middle}} = n_{\mathrm{low}} = 17$, mean ± SD = 13.3 ± 17.3, 0.4 ± 1.6, and 0.2 ± 0.7 min, respectively, $H = 18.2$, $P < 0.001$). Multiple paired comparisons among mean ranks showed that high-ranking individuals spent much more time foraging on the fish than individuals belonging to the two other dominance classes ($P < 0.05$). We found a significant positive correlation between the duration of foraging bouts and the dominance rank of the fish eaters (Spearman rank correlation coefficient test: $N = 16$, $R = 0.815$, $P < 0.001$). However, there was no significant correlation between the hierarchical rank of the feeding animals and their rank order of access to the fish (Spearman rank correlation coefficient test: $N = 16$, $R = 0.238$, $P = 0.374$).

Among the 64 monkeys observed on the beach at the time of the event, we recorded the presence of 42 bystanders (including 14 of the 16 fish eaters). This means that 34% of the individuals present on the beach were not bystanders. Out of the 42 bystanders, 41 individuals were members of the main group, and one individual was a solitary adult male. Among these 41 bystanders, there were fewer immature than mature individuals (14 and 27 monkeys, respectively), but when considering close bystanders (within 3 m), we found that immatures sat and watched much longer than mature individuals (mean ± SD = 15.8 ± 16.2 and 4.9 ± 9.3 min, $n_{\mathrm{immat.}} = 13$, $n_{\mathrm{mat.}} = 18$, Student's t-test: $t = 2.190$, $\mathrm{df} = 29$, $P < 0.025$). On average, there were two times fewer bystanders within 3 m than within 5–10 m of the feeding animal (mean number of bystanders per minute = 2.2 ± 3.0 and 4.4 ± 4.3, respectively, Student's t-test: $t = -1.709$, $\mathrm{df} = 30$, $P < 0.05$), but contrasting differences appeared according to the identity of particular fish eaters (Table I). We never recorded the presence of a bystander ranking higher than the current fish eater.

Out of the 42 bystanders, only three immature individuals were observed sitting in body contact with the feeding animal and touching the fish for short

TABLE I. Socio-Demographic Information about the Fish Eaters Ranked in Chronological Order of Access to the Fish, Total Duration of Foraging and Feeding Activities, and Mean Number of Bystanders per minute According to the Distance from the Feeding Animal

Individual name	Group	Age (yr)	Sex	Dominance class (rank)	Access	Total foraging order[a]	Total feeding duration (min)	Mean no. bystanders duration (min) within 3 m/min	Mean no. bystanders within 5–10 m/min
Iwana	Main	8	Male	High ranking (12)	1	41.2	29.9	0.4±0.5	0.3±0.6
Kinu	Main	6	Female	Low ranking (51)	2	3.4	2.3	0.0±0.0	0.0±0.0
Chiiku	Main	13	Female	High ranking (14)	3	0.2	0.2	0.0±–	1.0±–
Hotate	Main	15	Male	High ranking (1)	4	50.9	50.4	0.9±1.2	7.9±2.9
Yuda	Main	19	Male	High ranking (3)	5	14.2	13.9	7.0±2.4	5.8±1.5
Usu	Main	3	Female	Low ranking (44)	6	0.2	0.2	0.0±–	0.0±–
Hokke	Main	17	Male	High ranking (2)	7	47.7	34.8	1.7±1.1	6.6±5.0
Zuaka	Main	18	Male	High ranking (5)	8	11.4	10.5	6.0±1.3	5.7±3.8
Chigaya	Main	19	Female	High ranking (11)	9	17.3	16.5	9.4±1.6	6.6±0.5
Kame	Main	10	Male	High ranking (8)	10	8.0	8.0	1.0±0.0	0.0±0.0
Ponii	Main	19	Male	High ranking (4)	11	11.1	11.6	0.8±0.6	2.9±0.5
Momi	Main	18	Female	High ranking (13)	12	2.5	2.0	5.0±0.0	0.0±0.0
Kitsune	Main	8	Male	Middle ranking (29)	13	6.6	6.5	0.0±0.0	0.0±0.0
Zumi	Main	16	Female	Low ranking (46)	14	0.1	1.0	1.0±–	0.0±–
Piiman	Main	17	Female	Middle ranking (25)	15	1.2	1.2	0.0±–	0.0±–
Yago	Solitary	10	Male	High ranking (15)	16	10.9	10.6	0.0±0.0	0.0±0.0
Total						226.8	199.4	2.2±3.0	4.4±4.3

[a] For the first foraging bout only.

periods of time. The alpha female was contacted by her offspring for 3.8 min. The third-ranked male was contacted by two young siblings (for 1.9 and 0.5 min, respectively) with whom he spent 71.1% of his social activity budget (127.7 min interacting positively with the two siblings out of 179.6 min of total positive social interactions). We never observed two or more individuals feeding together on the fish. We recorded one single event of food theft: a 16-year-old female grabbed a bit of fin from her 18-year-old sibling. We recorded a total of 69 aggressive interactions occurring within 10 m of the fish (17.9 aggressive interactions/hr). As a comparison, we found a rate of aggression six times less (3.2 aggressive interactions/hr) during our daily observations in other feeding and non-feeding baseline contexts. Out of the 69 aggressions, 44 involved bystanders only.

Maintenance of Fish-Eating Behavior by Lineage

The 16 fish eaters belonged to eight separate lineages. To trace the maintenance of fish-eating behavior in Koshima monkeys, we added the current observations to Watanabe's [1989] genealogy of fish-eating individuals (Fig. 1). We found that 15 out of 16 monkeys confirmed to eat fish in 2004 belonged to matrilineages of fish eaters recorded before 1986. Out of the six matrilineages of non-fish eaters before 1980, five lineages still had no fish eaters in 2004.

DISCUSSION

To some extent, our observations allowed us to reconstruct some elements of the social contexts underlying the appearance, diffusion, and maintenance of the fish-eating tradition in Japanese macaques living on Koshima island. We showed that the monkeys treated the fish like a novel food rather than like a familiar food. The investigative behaviors performed are reminiscent of food neophobia found in macaques [Johnson, 2000]. The social status of the discoverer of the fish (a young adult male traveling in the periphery of the group) was consistent with early observations of fish-eating at Koshima [Watanabe, 1989]. In some primate species, peripheral individuals were more frequent innovators than central group members [Kummer & Goodall, 1985]. Living on the outskirts of the group is likely to make novel food sources more accessible to individuals whose social status would not allow access if they were in a more central position [Di Bitetti & Janson, 2001]. This could account for the lack of correlation we found between the rank order of access to the fish and dominance rank of the fish eaters. When food location is unpredictable and group cohesion is relatively low [Mori, 1977], food discovery may be better explained by the spatial position of group members than by their social ranks.

After most group members arrived on the beach, we found that the capability to monopolize and feed on the fish, as well as the presence and interactions around the fish were mainly explained by social factors. First, group membership appeared to be a major factor accounting for the presence of bystanders around the fish. We found that 94% of the fish eaters and 98% of the bystanders were members of the main group. Living in a social group allows individuals to gain valuable information from observing others' exploitation of novel foods [Di Bitetti & Janson, 2001]. Second, the fact that only a relatively small proportion (25%) of the individuals present could get access to, monopolize, and feed on the fish was mainly explained in terms of dominance. By limiting access to the fish, dominance is likely to limit individual opportunities to learn from this novel food. In dominance-structured groups, social status may constrain feeding innovation and its subsequent propagation. Dominance style in Japanese macaques is stricter than in other macaque species [Thierry, 2000]. In macaques and capuchins, once a novel food or a familiar clumped food source is encountered by several group members, social rank is likely to significantly affect food competition and foraging success [Belisle & Chapais, 2001; Di Bitetti & Janson, 2001].

Third, we found that feeding competition around a highly prized clumped food source can significantly increase the rate of aggression compared with the baseline situation. The high risk of aggression and possible injury related to food competition may be the reason why there were more far-bystanders than close-bystanders and a third of the individuals present on the beach did not even approach within 10 m of the fish. Compared with food sources involved in other newly acquired feeding habits in Japanese macaques (wheat eating, potato-washing: e.g., Itani & Nishimura, 1973), the fish had a unique feature as a novel food (one large food item). Higher competition around the fish may affect the social conditions under which the fish-eating habit is maintained within the group. Fourth, although limited, the tolerated presence of body contact while feeding seemed to be affected by kinship, and to some extent, affiliation. Close and peaceful proximity to a feeding individual, namely co-feeding [King, 1994], has been proposed as a major factor in the transmission of feeding innovations because it is assumed to enhance opportunities for social learning [Coussi-Korbel & Fragaszy, 1995]. Young primates tend to feed at the same time and on the same food items as their mothers, and such synchronous feeding may influence the development of food selection or feeding habits [e.g., Ueno, 2005]. Belisle and Chapais [2001] found that rates of tolerated co-feeding increased significantly with degree of kinship in Japanese macaques. Since Japanese macaques show a high degree of kin bias or favoritism in most behaviors and interactions, compared with other macaque species [Chapais et al., 1997], it is not surprising that many innovative foraging behaviors were shown to diffuse widely within kin lineages.

From our anecdotal observation, we could not reliably estimate the rate of diffusion of the fish-eating behavior. The difference in the proportion of fish eaters recorded in 1986 [75%: Watanabe, 1989] and during this event (25%) may depend on the conditions of fish-eating in the two studies (several little fish artificially given to the monkeys vs. one single big fish discovered under natural circumstances). However, we provided valuable information about the maintenance of the fish-eating habit in Koshima monkeys. The addition of a new fish species to the diet of Koshima macaques can be regarded as a generalization of this feeding tradition. The continuation of the genealogy of fish eaters suggested that this behavior was well preserved in terms of maternal lineages. When practiced only occasionally and by very few group members, some traditional behaviors may tend to disappear [Huffman & Hirata, 2003]. Although the prevalence and strictness of dominance in Japanese macaques may constrain the spread of the fish-eating habit to all age, sex, and dominance classes, the rare occurrence of beached fish may be sufficient to maintain the behavior in the study group.

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Japanese macaque cultures: Inter- and intra-troop behavioural variability of stone handling patterns across 10 troops

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Summary

Stone handling (SH), a form of solitary object play, consists of an individual manipulating stones by performing various behavioural patterns. Previous findings from the Arashiyama population of Japanese macaques suggested that SH is socially transmitted across generations as a behavioural tradition. To further test the hypothesis that SH is a traditional behaviour in this species, we present the most systematic inter-troop comparison of this behaviour from an investigation of nine troops of *Macaca fuscata fuscata* and one troop of *M. f. yakui* living at six sites in Japan. We analyzed a total 1280 video-recorded SH bouts and charted the relative frequency of occurrence of 45 SH behavioural patterns across age classes. Many SH patterns showed geographically patchy distributions and were referred to as local variants or SH traditions. In terms of behavioural complexity, we found three levels of SH culture, each level being defined by troop-dependent clusters of SH traditions. We found a positive correlation between geographic proximity and cultural similarity in SH between troops. To explain similarities in the SH repertoires between the free-ranging troops living at the same site, we discussed the phenomenon of cultural zones. We interpreted intra-group variability in the performance of SH patterns from the viewpoint of developmental factors. We found no major difference between the two subspecies in the occurrence and form of SH.

Keywords: stone handling, local variants, behavioural tradition, behavioural predispositions, *Macaca fuscata*.

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Introduction

Charting intra- and inter-group behavioural diversity in non-human primates provides valuable empirical information to test predictions and fit models generated from theories about the role of cultural processes in human evolution (van Schaik et al., 1999; Whiten et al., 2001). Most evidence for behavioural variability between and within wild primate populations comes from four genera: *Cebus* (capuchins), *Macaca* (macaques), *Pongo* (orang-utans) and *Pan* (chimpanzees). Long-term collaborative field studies focusing on various types of behaviour or variants of the same behaviour, including interspecific interactions, communicatory, courtship, display, grooming, object play and social play behaviours, feeding habits, food processing techniques, medicinal plant use and tool use, have documented troop-specific behavioural patterns and substantial inter-troop behavioural variability at different field sites in Costa Rica (Curu, Lomas Barbudal, Palo Verde, Santa Rosa: white-faced capuchins; Chapman & Fedigan, 1990; Panger et al., 2002; Perry et al., 2003a,b; Rose et al., 2003; O'Malley & Fedigan, 2005), Japan (Arashiyama, Katsuyama, Koshima, Takasakiyama, Yakushima: Japanese macaques; Itani, 1958; Kawai, 1965; Itani & Nishimura, 1973; Huffman, 1984, 1996; Huffman & Quiatt, 1986; Watanabe, 1989; Suzuki et al., 1990; Kawai et al., 1992; Nakamichi et al., 1998; Huffman & Hirata, 2003), Indonesia (Gunung Palung, Kutai, Ketambe, Suaq Balimbing, Lower Kinabatangan, Muara Singgersing, Tanjung Putting: orang-utans; van Schaik & Knott, 2001; van Schaik, 2003; van Schaik et al., 2003; Fox et al., 2004) and different African countries (Assirik, Senegal, Bossou, Diécké and Seringbara, Guinea, Budongo and Kibale, Uganda, Campo, Cameroon, Gombe and Mahale, Tanzania, Lopé, Gabon, and Taï and Yealé, Côte d'Ivoire: chimpanzees; Boesch et al., 1994; Huffman & Wrangham, 1994; Wrangham et al., 1994; Matsuzawa & Yamakoshi, 1996; Sugiyama, 1998; Whiten et al., 1999, 2001; Humle & Matsuzawa, 2001, 2002; McGrew et al., 2001, 2003; Yamakoshi, 2001; Nakamura & Nishida, 2006).

Within the same species, a given behaviour can be customary in some populations and rare or even absent in others although it is ecologically possible. When enduring across generations and largely dependent on social means for their diffusion and maintenance, such behavioural differences are referred to as cultural or traditional (McGrew, 1998; Fragaszy & Perry, 2003). Following Whiten (2005), we define a 'tradition' as a local behavioural variant, showing different frequencies of occurrence across the study sites, i.e., being customary or habitual in at least one site, but absent elsewhere. We define a 'culture' as a package of multiple related traditions, and 'cultures' as distinctive arrays of clustered traditions.

By defining culture more broadly ('the way we do things'), McGrew (2003) pointed out the need for a systematic examination of the similarities and differences in the behavioural patterns between wild populations of primates. The first step to study cultural variation in a species is to do comparative analyses focusing on the motor patterns of spontaneous behaviours (McGrew, 1998). Like ethnography in human social sciences, the ethnographic approach to cultural primatology consists of documenting patterns of geographic variation in primate behaviour (Wrangham et al., 1994). In chimpanzees and Japanese macaques, various sets of (sub)species-typical behaviours were found to occur in several geographically isolated populations, but with some minor alterations in the form of the actions performed. When such local variants are demonstrated to be long-lasting and transmitted over generations via social means, a cultural phenomenon can be inferred (Huffman & Hirata, 2003).

The ethnographic approach to primate traditions emphasizes the product (which differences are observed in the form of behaviours) rather than the mechanisms (which specific processes are involved in producing such differences). Since little is known about the factors affecting the maintenance of socially learned behaviours in the wild, a controversy arose about the validity of animal traditions (Galef, 1996). However, like the powerful comparative method used in ethology, the advantage of the ethnographic approach is to be deeply rooted in what the animals actually do or do not do in the wild. Patterns in the presence or absence of behavioural variants in particular populations have been largely considered as defining features of primate traditions. Although still debatable, there is now a general consensus on the occurrence of traditions in monkeys and apes (Whiten et al., 1999; Fragaszy & Perry, 2003; Huffman & Hirata, 2003; Perry & Manson, 2003; McGrew, 2004).

Although behavioural diversity is a possible starting point in demonstrating the occurrence of culture, it is neither a necessary nor sufficient condition (McGrew, 2003). The 'method of elimination' is a multi-step decision procedure that may be used to assess whether a geographically variable behaviour is or is not a tradition (van Schaik, 2003; see also Boesch, 1996). First a geographic distribution of clear troop-dependent clusters of behavioural variants must be demonstrated. Second, simple alternative explanations should be ruled out. Although there is evidence for inter-site behavioural differences among different subspecies of chimpanzees (Boesch et al., 1994; Whiten et al., 1999) and different macaque species (Huffman, 2005; C. Nahallage, pers. comm.; A. Zeller, pers. comm.), it is acknowledged that the effects of genetic and ecological factors should be minimal for such behavioural variability to be regarded as cultural. Third, the behaviour should meet a set of criteria, such as being customary or habitual within one age class of one troop, being socially transmitted within age structures or along matrilineages and persistent over a number of years. As more elements congruent with the concept of tradition are provided, the likelihood of alternative interpretations decreases (van Schaik, 2003). Accordingly, socially-mediated behavioural diversity at the group, population, or subspecies level could be cultural (McGrew, 2003).

Japanese macaques (*Macaca fuscata*) are renowned for their behavioural innovations. In this species, the diffusion of various types of newly acquired behaviours has been investigated, such as the consumption of novel foods (caramel-eating: Itani, 1958; Itani & Nishimura, 1973; wheat-eating: Kawai, 1965; fish-eating: Watanabe, 1989; Leca et al., in press), food-processing techniques (potato- and wheat-washing: Kawai, 1965; Itani & Nishimura, 1973; Kawai et al., 1992; grass root-washing: Nakamichi et al., 1998) and play behaviour (stone handling: Huffman, 1984, 1996; Huffman & Hirata, 2003; swimming: Kawai, 1965). Most reported behavioural innovations in primates occur in the context of foraging, probably because information about food is critical to every individual (Reader & Laland, 2001).

However, the best-documented case of a non-subsistence traditional activity in monkeys is stone handling (SH), a form of solitary object play consisting of the manipulation of stones by performing various behavioural patterns, such as gathering stones into a pile, clacking stones together, or repeatedly pounding a stone on a substrate (Huffman, 1984). Previous findings from two populations of Japanese macaques at Arashiyama and Takasakiyama, Japan suggest that SH is a traditional behaviour for these groups (Huffman, 1984, 1996; Huffman & Quiatt, 1986; Huffman & Hirata, 2003). The appearance, initial and long-term diffusion, context of occurrence and behavioural diversity of SH have been documented at several points in time for over two decades at Arashiyama. This behaviour appears to be socially transmitted across generations (Huffman, 1984, 1996; Huffman & Quiatt, 1986).

A survey conducted at Takasakiyama in 1989 has revealed striking similarities in the SH repertoire and the frequency of occurrence of SH behavioural patterns of the two troops. Out of the 17 behavioural patterns recorded at Arashiyama, 16 were also observed at Takasakiyama, and at similar frequencies (Huffman, 1996; Huffman & Hirata, 2003). These first comparative data showed no evidence for SH local variants (defined as SH patterns that show geographically patchy distribution) and were not consistent with inter-troop variability in the form of SH. The SH patterns shared by both troops included collecting, rubbing and percussive actions with stones. This suggests that such behaviours are Japanese macaque universals, i.e., they are part and parcel of the common behavioural repertoire of the species (Huffman & Hirata, 2003). In both troops, age appeared to affect the diversity and type of SH patterns displayed. As they grew older, individuals tended to perform less varied and more simple patterns, such as gather, scatter, or pick up stones (Huffman & Quiatt, 1986).

A recent study conducted on the captive Takahama troop (Primate Research Institute, Kyoto University), using similar observation methods, has revealed a remarkably greater diversity in SH behaviours, with 45 distinct patterns recorded (Nahallage & Huffman, 2007). Age-related differences in the form of SH were also found. SH patterns involving vigorous motor actions were mainly performed by young individuals whereas complex patterns were almost exclusively observed in adults. Overall, immatures displayed a greater number of patterns than mature individuals (Nahallage & Huffman, 2007). In addition to these three studied troops, SH activity has been reported in at least nine other geographically isolated troops of Japanese macaques, but no quantitative data were recorded (Huffman & Hirata, 2003; Nahallage & Huffman, 2007). Until now, SH in Japanese macaques was only observed in the *Macaca fuscata fuscata* subspecies widely distributed in the Japanese archipelago. Despite long-term studies including behavioural records, SH has never been observed in *M. f. yakui* (G. Hanya, pers. comm.), the subspecies endemic to Yakushima, a small island at the southern limit of distribution of the species (cf. Fooden & Aimi, 2005). The lack of detailed documentation of SH from an ethnographic perspective and the above mentioned differences in the repertoire and form of SH at the group and individual levels highlights the need for a more systematic investigation of inter- and intra-troop variability in SH patterns.

We present what may be the most extensive and systematic survey focused on the variability of a single type of behaviour between and within troops of Japanese macaques to date. Through a detailed report of the occurrence of various SH patterns across age classes in nine troops of *M. f. fuscata* and one troop of *M. f. yakui* living at six geographically isolated sites in Japan, our main goal is to test the hypothesis that SH is a traditional behaviour in Japanese macaques. Our specific objectives are: 1) to establish the comprehensive repertoire of SH local variants in Japanese macaques; 2) to provide a broader inter-group comparison of the form of SH and intra-group diffusion patterns of SH variants according to age; 3) to test the association between geographic proximity and cultural similarity; 4) to present the first survey of SH patterns exhibited by *M. f. yakui* and compare them with those exhibited by *M. f. fuscata*; 5) to explore the complexity and diversity in the form of SH from the perspective of stone-tool use in non-human primates. We will discuss our results from the perspective of behavioural predispositions (cf. Huffman & Hirata, 2003) and socially transmitted behaviours.

Material and methods

Study conditions

A total of ten troops of Japanese macaques, four captive (PRI Arashiyama = Ara.A, Wakasa = Wak.A, Takahama = Takh. and Japan Monkey Center Yakushima macaques = JMC) and six free-ranging troops (Koshima = Kosh., Arashiyama E = Ara.E, Shodoshima = Sho.A and Sho.B, Takasakiyama = Tak.B and Tak.C), were observed at six geographically isolated sites in Japan (Figure 1). Nine troops belonged to the *M. f. fuscata* subspecies and one troop was *M. f. yakui*. In Table 1, we present the study conditions at each site. Captive troops were housed in large outdoor enclosures at the Kyoto University Primate Research Institute and at the Japan Monkey Centre, and 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 technicians of the Koshima Field Station, Kyoto University or by the staff of monkey parks. Although provisioning schedules were different, free-ranging troops living at the same site (Sho.A/Sho.B and Tak.B/Tak.C) had overlapping home ranges and came into occasional contact.

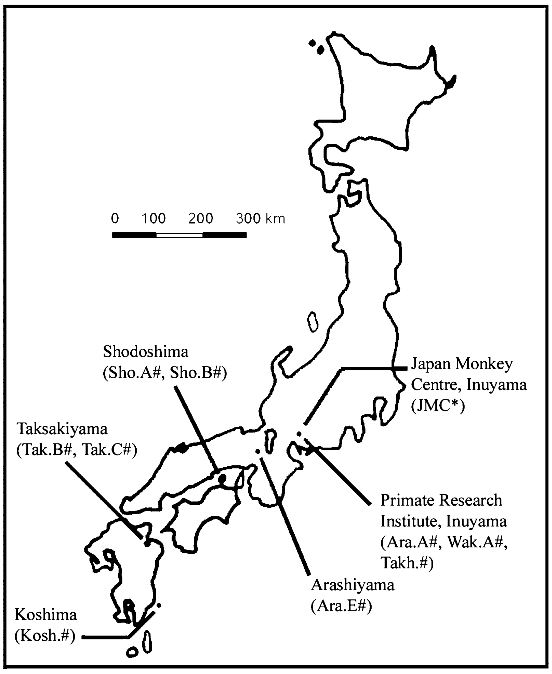

Figure 1. Map of study sites in Japan; In parentheses: abbreviation of studied troops; Sharp indicates the subspecies *Macaca fuscata fuscata*; Asterisk indicates the subspecies *Macaca fuscata yakui*.

For each troop, basic demographic information was known (Table 2). The ten study troops varied both in size and demography: two small-sized captive troops (Ara.A and Wak.A), two medium-sized captive troops (Takh. and JMC), two medium-sized free-ranging troops (Kosh. and Ara.E) and four large-sized free-ranging troops (Sho.A, Sho.B, Tak.B and Tak.C). The proportion of individuals belonging to the different age/sex classes also varied. Individual identification was possible for only some of the study troops (Ara.A, Wak.A, Takh., Kosh. and Ara.E), and for them the exact age in years of each individual and their matrilineages were known. For the other troops (JMC, Sho.A, Sho.B, Tak.B and Tak.C), every sampled subject was labelled according to its age and sex classes. Age classes were defined after Fedigan et al. (1983). The daily observation period was between 7:00 am and 6:00 pm. Visibility was excellent. We sampled captive troop members from observation platforms overhanging the enclosures. Free-ranging troop members could be approached and sampled within 3-5 m.

Table 1. Inter-troop comparison of study conditions and total data sets. In parentheses: abbreviation of troop name; $^{\#}$: *Macaca fuscata fuscata*, *: *Macaca fuscata yakui*; CP: captive troop, FR: free-ranging troop; The first two authors were the main observers (†: occasionally assisted by M.A.H. and Charmalie A. D. Nahallage); T.O.T.: Total observation time; NS: Number of scan sessions.

Troop name, subspecies and ranging conditions	Study site	Study period	Observers	T.O.T.	NS
Arashiyama A (Ara.A$^{\#}$), CP	Primate Research Institute, Inuyama, Aichi prefecture	Sep-Dec 2003	NG	179.9	644
Wakasa A (Wak.A$^{\#}$), CP	Primate Research Institute, Inuyama, Aichi prefecture	Aug-Nov 2003	NG	224.6	809
Takahama (Takh.$^{\#}$), CP	Primate Research Institute, Inuyama, Aichi prefecture	Sep-Dec 2003	JBL	449.2	1593
Japan Monkey Centre (JMC*), CP	Japan Monkey Centre, Inuyama, Aichi prefecture	Aug-Dec 2003, Mar-Apr 2004	JBL, NG	99.1	275
Koshima (Kosh.$^{\#}$), FR	Koshima Islet, Miyazaki prefecture	Jan-Feb 2004	JBL, NG	339.7	252
Arashiyama E (Ara.E$^{\#}$), FR	Iwatayama Monkey Park, Arashiyama, Kyoto pref.	May-Aug 2004	JBL, MAH†, CN†	431.3	1010
Shodoshima A (Sho.A$^{\#}$), FR	Wild Monkey Park, Shodoshima island, Kagawa pref.	Feb 2005	JBL, NG, CN	77.6	66
Shodoshima B (Sho.B$^{\#}$), FR	Wild Monkey Park, Shodoshima island, Kagawa pref.	Feb 2005	JBL, NG, CN	51.5	42
Takasakiyama B (Tak.B$^{\#}$), FR	Takasakiyama Natural Zoo, Takasakiyama, Oita pref.	Dec 2003-Jan 2004	JBL, NG	22.8	58
Takasakiyama C (Tak.C$^{\#}$), FR	Takasakiyama Natural Zoo, Takasakiyama, Oita pref.	Dec 2003-Jan 2004	JBL, NG	73.8	72

Table 2. Distribution of individuals according to age and sex classes in each studied troop. *N* total: Total number of individuals aged at least one year; Asterisk: In large-sized troops, figures were approximately assessed during yearly surveys (Sho.A and Sho.B: after K. Watanabe, pers. comm.; Tak.B and Tak.C: after H. Kurita, pers. comm.); In parentheses: number of sampled individuals.

Troop	Age class (years)												*N* total
	Yearling (1)		Juvenile (2-3)		Subadult (4-6)		Young adult (7-10)		Middle-aged adult (11-15)		Old Adult (16-)		
	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	
Ara.A	1 (1)	2 (2)	1 (1)	2 (2)	0 (0)	0 (0)	0 (0)	0 (0)	4 (4)	0 (0)	5 (5)	3 (3)	18 (18)
Wak.A	0 (0)	1 (1)	2 (2)	2 (2)	4 (4)	3 (3)	3 (3)	0 (0)	2 (2)	0 (0)	2 (2)	0 (0)	19 (19)
Takh.	3 (3)	6 (6)	4 (4)	2 (2)	1 (1)	4 (4)	7 (7)	2 (2)	4 (4)	0 (0)	10 (10)	3 (3)	46 (46)
JMC	3 (3)	1 (1)	9 (9)	12 (9)	8 (8)	14 (11)	15 (12)	5 (5)	11 (7)	9 (4)	11 (5)	4 (2)	102 (76)
Kosh.	2 (2)	3 (1)	11 (5)	10 (6)	7 (4)	8 (6)	7 (4)	12 (9)	4 (4)	7 (6)	8 (7)	9 (7)	88 (61)
Ara.E	7 (7)	5 (5)	10 (10)	5 (5)	15 (14)	4 (3)	20 (20)	5 (4)	30 (26)	2 (2)	31 (29)	7 (7)	141 (132)
Sho.A*	20 (4)	20 (11)	80 (6)	80 (5)	60 (10)	50 (5)	30 (2)	10 (2)	40 (6)	10 (1)	40 (3)	10 (0)	450 (55)
Sho.B*	10 (4)	10 (6)	60 (11)	60 (10)	50 (7)	40 (6)	30 (3)	20 (2)	30 (3)	10 (1)	20 (1)	10 (0)	350 (54)
Tak.B*	30 (13)	35 (9)	60 (5)	60 (8)	50 (6)	20 (6)	37 (3)	10 (7)	60 (7)	16 (6)	50 (4)	10 (0)	438 (74)
Tak.C*	68 (17)	69 (17)	96 (31)	95 (26)	80 (16)	20 (12)	70 (17)	10 (8)	86 (17)	20 (3)	50 (8)	12 (0)	676 (172)

Data collection

We used the same observation procedure in all troops studied (except for Tak.B and Tak.C troops, see below for details). Two observational sampling methods were used: continuous focal-animal sampling interspersed with instantaneous group scan sampling (Altmann, 1974). Behavioural data collection was occasionally supplemented with ad libitum sampling.

Focal sampling

We video-recorded every focal session with Sony digital video cameras (DCR-TRV22 and DCR-TRV33). Whenever possible, the focal individual was filmed from the front and about one-meter square in-frame. We focused on all the behaviours and interactions of the focal individual. Since the field observation conditions did not allow us to perform totally random focal sampling, we selected individual focal targets using a semi-random procedure. The daily observation period was divided into one-hour blocks. We selected the focal individual, independent of its activity, in an ordered list of temporarily under-sampled individuals or members of each age and sex class (when focal subjects were not individually identified).

We recorded the starting time of each focal session. As previously done by Huffman (1996), the typical duration of a focal session was 15 minutes. If the focal individual performed SH activity during the last two minutes of this period of time, the observation was extended for 5 minutes and ended thereafter unless SH was still in progress.

Scan and ad libitum sampling

Before and after each focal session, the troop was scanned for evidence of any SH activity. For each scan sampled stone handler, we recorded the identity (or age and sex classes) and whenever possible the SH patterns observed (Table 3). The observer recorded scans on data sheets, visually (for captive troops) or physically (for free-ranging troops) moving from one side of the troop to the other, in a set direction, so that each individual was sampled only once in a given scan session.

To supplement SH data sets, we devoted an average of 38.8 ± 31.8% of total observation time to collect ad libitum data on individuals performing SH patterns. Whenever possible, ad libitum sessions were video-recorded,

Table 3. Forty five SH patterns performed by Japanese macaques and categorized according to general activity patterns (after Nahallage & Huffman, in press).

Category	Name (code)	Definition
Investigative activities (Inv.)		
	Bite (B)	Bite a stone
	Hold (H)	Pick up a stone in one's hand and hold on to it, away from the body
	Lick (L)	Lick a stone
	Move inside mouth (MIM)	Make a stone move inside one's mouth with tongue or hands
	Pick (P)	Pick up a stone
	Put in mouth (PIM)	Put a stone in one's mouth and keep it sometime
	Sniff (SN)	Sniff a stone
Locomotion activities (Loc.)		
	Carry (CA)	Carry a stone cuddled in hand from one place to another
	Carry in mouth (CIM)	Carry a stone in mouth while locomoting
	Grasp walk (GW)	Walk with one or more stones in the palm of one or both hands
	Move and push/pull (MP)	Push/pull a stone with one or both hands while walking forward/backward
	Toss walk (TW)	Toss a stone ahead (repeatedly) and pick it up while walking
Collection or gathering activities (Coll.)		
	Cuddle (CD)	Take hold of, grab or cradle a stone against the chest
	Gather (GA)	Gather stones into a pile in front of oneself
	Grasp with hands (GH)	Clutch a stone or a pile of stones gathered and placed in front of oneself
	Pick up (PU)	Pick up a stone and place it into one's hand
	Pick and drop (PUD)	Pick up a stone and drop it repeatedly
	Pick up small stones (PUS)	Pick up small stones and hold them between fingertips (like the picking up of wheat grains)

or otherwise collected on a notepad. For Tak.B and Tak.C, we did not collect focal sessions, but only video-recorded ad libitum sessions during post-feeding periods, when SH is most likely to occur (Huffman, 1996). When the sampled individual was filmed through the entire sequence of SH, from start (a few minutes after provisioning time, when it just left the feeding site and began contacting stones) to finish (five minutes after it last discarded stones), this ad libitum session was defined as complete. When a SH episode

Table 3. (Continued).

Category	Name (code)	Definition
Percussive or rubbing sound producing activities (Perc.)		
	Clack (CL)	Clack stones together (both hands moving in a clapping gesture)
	Combine with object (COO)	Combine (rub or strike) a stone with an object different from a stone (food item, piece of wood, metal, etc.)
	Flint (FL)	Strike a stone against another held stationary
	Flint in mouth (FLM)	Strike a stone against another held in mouth
	Pound on surface (POS)	Pound a stone on a substrate
	Rub in mouth (RIM)	Rub a stone against another held in mouth
	Rub/roll on surface (ROS)	Rub or roll a stone on a substrate
	Rub stones together (RT)	Rub stones together
	Rub with mouth (RWM)	Rub a surface with a stone held in mouth
	Scatter (SC)	Scatter stones about, on a substrate, in front of oneself
	Shake in hands (SIH)	Take stones in one's open palm hand and shake the stones with the hand moving back and forth
	Slap (SL)	Slap, tap or pound a stone with one's fingertips or palm of hand
	Swipe (SW)	Swipe stones together (both hands moving in a sweeping gesture)
	Tap in mouth (TIM)	Tap a stone held in mouth with fingertips or palm of hand
Other complex manipulative activities (Comp.)		
	Flip (FP)	Turn a stone over with both hands
	Put in water (PIW)	Put a stone in water
	Roll in hands (RIH)	Roll a stone in one's hands
	Rub/put on fur (ROF)	Rub or put a stone on one's fur while self-grooming
	Rub with hands (RWH)	Hold a stone in one hand and rub it with the other (like potato-washing)
	Spin (SP)	Spin a stone around on the ground using two fingers of one hand or both hands (one moving forward and the other backward)
	Stone-groom (SGR)	Allo-groom with a stone
	Throw (TH)	Throw a stone without jumping or running
	Throw and jump (TJ)	Throw a stone and jump (or vice versa)
	Throw and run (TR)	Throw a stone and run (or vice versa)
	Throw and sway (TS)	Throw a stone and sway (or vice versa)
	Wash (W)	Put a stone in water or pick up a stone from water and rub it with hands
	Wrap in leaf (WIL)	Wrap a stone in a leaf (or wrap a leaf around a stone)

was recorded on notepad or when the sampled individual was not filmed through the entire sequence of SH, we referred to the ad libitum session as incomplete.

Data analysis

Based on video-records, J.-B.L. transcribed each focal session onto a data sheet and measured the duration of all activities (feeding, foraging, locomoting, resting, socializing, SH, non-stone object exploring, and other) and every SH pattern in seconds. We defined the troop total observation time as the total time in hours spent observing each troop, including focal time, scan time and time spent collecting ad libitum data, and summed the times of all observers, when several were present. We verified inter-observer reliability using the kappa coefficient of Cohen (1960). Based on individual identities, activities and interactions, we found $\kappa = 0.92$. In Table 4, we present the total data sets per troop and age class. Individuals less than one year old were not taken into account in the analyses.

We distinguished two types of SH records: SH bouts (collected from focal sessions or complete ad libitum video-recorded sessions) and SH notes (collected from scan sessions or incomplete ad libitum sessions). We defined a SH bout as the display of SH activity with possible pauses of no longer than 120 seconds. If the individual resumed SH within 120 seconds after pausing, then the two SH episodes were considered as a single SH bout. If SH was resumed more than 120 seconds after pausing, this would mark the start of a new SH bout.

For the analyses of SH patterns, we grouped all observed SH patterns into five categories according to general activity patterns (Table 3). Based on the definitions by Whiten et al. (1999, 2001), we assessed the level of occurrence of each SH pattern in each troop by distinguishing among five frequencies of occurrence: customary, habitual, present, absent and unknown (Table 5). We drew on all SH bouts and SH notes available for analyses regarding the frequency of occurrence of SH patterns and the percentage of sampled individuals exhibiting each SH pattern in each troop. For analyses about the mean percentage of SH patterns performed in each troop, we drew on all SH bouts. From the frequency value of each SH pattern recorded per SH bout, we calculated the percentage of each pattern per bout and the mean percentage for all SH bouts.

Table 4. Data sets collected according to age classes in each studied troop. Tot: All age classes pooled; FT: Focal time (total duration in hours of focal sessions); SH Bt (F, CAL): Number of SH bouts collected during focal sessions (F) and during complete ad libitum sessions (CAL); SH Nt (IAL): Number of SH notes collected during incomplete ad libitum sessions (IAL) (see methods for detail); n/a: Age class not available; –: Data not available.

Troop	Age class						Tot
	Yng	Juv	SuAd	YgAd	MdAd	OlAd	
Ara.A							
FT	23.3	23.3	n/a	n/a	31.5	62.0	140.1
SH Bt (F, CAL)	12, 0	1, 0	n/a	n/a	0, 1	1, 0	14, 1
SH Nt (IAL)	10	15	n/a	n/a	2	1	28
Wak.A							
FT	10.0	39.3	59.8	27.8	19.8	18.0	174.7
SH Bt (F, CAL)	2, 4	16, 14	35, 36	0, 4	4, 1	2, 3	59, 62
SH Nt (IAL)	18	45	140	3	5	13	224
Takh.							
FT	70.2	42.7	39.9	73.1	31.1	96.6	353.6
SH Bt (F, CAL)	108, 6	68, 5	38, 4	56, 6	17, 3	22, 4	309, 28
SH Nt (IAL)	267	254	206	190	72	210	1199
JMC							
FT	4.3	7.5	12.3	10.5	13.8	6.3	54.7
SH Bt (F, CAL)	2, 6	6, 38	10, 27	1, 24	3, 4	0, 0	22, 99
SH Nt (IAL)	4	33	24	27	3	0	91
Kosh.							
FT	13.3	38.0	30.3	42.5	38.0	53.3	215.4
SH Bt (F, CAL)	5, 8	4, 6	0, 0	0, 0	0, 0	0, 0	9, 14
SH Nt (IAL)	2	5	0	0	0	0	7
Ara.E							
FT	14.2	14.9	19.6	21.1	38.4	52.4	160.6
SH Bt (F, CAL)	39, 8	57, 8	39, 3	56, 7	50, 2	76, 7	317, 35
SH Nt (IAL)	57	97	75	106	106	138	579
Sho.A							
FT	5.0	3.9	3.8	0.5	3.1	0.5	16.8
SH Bt (F, CAL)	13, 4	8, 3	6, 3	0, 0	3, 0	0, 0	30, 10
SH Nt (IAL)	3	4	8	4	4	4	27
Sho.B							
FT	0.0	0.5	0.5	0.0	0.3	0.0	1.3
SH Bt (F, CAL)	0, 1	3, 10	1, 8	0, 4	0, 2	0, 1	4, 26
SH Nt (IAL)	10	32	16	4	4	1	67

Table 4. (Continued).

Troop	Age class						Tot
	Yng	Juv	SuAd	YgAd	MdAd	OlAd	
Tak.B							
FT	–	–	–	–	–	–	–
SH Bt (F, CAL)	0, 9	0, 11	0, 17	0, 9	0, 11	0, 2	0, 59
SH Nt (IAL)	17	14	14	15	13	2	75
Tak.C							
FT	–	–	–	–	–	–	–
SH Bt (F, CAL)	0, 14	0, 67	0, 44	0, 32	0, 18	0, 7	0, 182
SH Nt (IAL)	64	163	70	51	41	2	391

Table 5. Frequency of occurrence of SH patterns ranked in descending order in a given troop (after Whiten et al., 1999, 2001); Asterisk: in large-sized troops (Sho.A, Sho.B, Tak.B and Tak.C), the number of sampled individuals was substantially different from the number of group members (see Table 2).

Frequency of occurrence	Definition
Customary	Exhibited by at least 90% of the sampled* individuals in at least one age class, or at least 70% of the sampled* individuals in at least two age classes
Habitual	Not customary but observed at least three times in several individuals, consistent with some degree of social transmission
Present	Not customary or habitual, but observed at least once
Absent	Not observed despite sufficient observation time (at least 90 hours of total observation time)
Unknown	Not observed but absence uncertain because of insufficient observation time (less than 90 hours of total observation time)

To test the association between geographic proximity and cultural similarity, we used a matrix correlation (Matman program, Noldus). In a first matrix, we assessed inter-troop geographic proximity by distinguishing between the troops living at the same site and having occasional encounters (Sho.A/Sho.B and Tak.B/Tak.C, with a ‘1’ proximity value) and all the other troops (with a ‘0’ proximity value). In a second matrix, we entered the cultural similarity, defined as the number of SH patterns showing the same frequencies of occurrence across troops. We set the number of permutations of matrices at 10 000 and used the Pearson’s correlation coefficient. To test the effect of age on the complexity of SH patterns, we used a mixed-model

ANOVA, with age classes as between factor and two degrees of complexity as repeated measures (simple patterns: investigative, locomotion and collection activities and complex patterns: percussive/rubbing and other complex manipulative activities). We used SPSS 12.0 for statistical analyses and set significance level at $\alpha = 0.05$.

Results

SH traditions (local variants) and levels of SH cultures

We found considerable differences in the occurrence of SH patterns among the studied troops (Table 6). Out of the 45 patterns defined in Table 3, Takh. exhibited a total of 44, whereas Ara.A and Kosh. displayed 17 and 16 SH patterns, respectively. The other troops exhibited between 22 and 32 different patterns. It should be noted that most of the patterns found in Ara.A and Kosh. were simple ones, corresponding to investigative and collection activities. These two troops also showed extremely low SH occurrences compared to most other troops, with 0.2 and 0.1 SH bouts and notes per hour, respectively (Table 6). Accordingly, we will consider the interaction with stones in the Ara.A and Kosh. troops as the baseline level of interest in stones by Japanese macaques.

Overall, Table 6 showed that the frequency of occurrence of SH patterns was highly variable according to the pattern and troop in question. Even though most simple SH patterns (corresponding to investigative, locomotion and collection activities) could be observed in most study troops, their frequency of occurrence varied from present to customary. For example, the pattern consisting of licking a stone (L) was not observed in Sho.A and Sho.B, merely present in Ara.A, JMC, Kosh., Ara.E, Tak.B and Tak.C, habitual in Wak.A and customary in Takh. Although close in form, the pattern consisting of biting a stone (B) showed a different distribution: it was observed in all troops, but only present in Ara.A, JMC, Sho.B and Tak.B, habitual in Ara.E, Sho.A and Tak.C, and customary in Wak.A, Takh. and Kosh. Likewise, CA was absent in Ara.A, present in Kosh., habitual in Takh., JMC, Sho.A, Sho.B, Tak.B and Tak.C, and customary in Wak.A and Ara.E.

The frequent occurrence of more complex SH patterns, corresponding to percussive, rubbing and other complex manipulative activities was even more restricted to particular troops, but again highly variable depending on the

Table 6. Frequency of occurrence of the 45 SH patterns observed in Japanese macaques according to studied troop; C: Customary, H: Habitual, P: Present, –: Absent, (–): Unknown; Tot. pattern occurrence: Total number of SH patterns scoring at least the Present status; SH occurrence per hr: Level of occurrence of SH obtained by dividing the total number of SH bouts and notes scored by the total observation time.

SH pattern	Ara.A	Wak.A	Takh.	JMC	Kosh.	Ara.E	Sho.A	Sho.B	Tak.B	Tak.C
Investigative activities										
Bite	P	C	C	P	C	H	H	P	P	H
Hold	P	H	P	P	P	H	H	P	H	H
Lick	P	H	C	P	P	P	(–)	(–)	P	P
Move inside mouth	–	H	H	P	–	P	(–)	(–)	P	P
Pick	C	P	P	P	P	P	P	(–)	(–)	P
Put in mouth	P	H	H	P	–	P	H	P	P	P
Sniff	C	C	C	H	P	H	P	P	H	H
Locomotion activities										
Carry	–	C	H	H	P	C	H	H	H	H
Carry in mouth	–	H	C	P	–	P	P	P	P	P
Grasp walk	P	C	C	H	P	C	H	P	H	H
Move and push/pull	–	C	H	P	P	H	P	P	P	P
Toss walk	P	P	C	P	–	H	(–)	(–)	P	P
Collection (gathering) activities										
Cuddle	C	C	C	H	C	C	H	H	H	H
Gather	P	C	C	P	P	C	H	H	H	H
Grasp with hands	P	C	C	H	P	C	H	H	H	H
Pick up	C	P	C	P	P	H	H	P	H	H
Pick and drop	–	–	P	–	–	P	P	(–)	P	H
Pick up small stones	–	–	H	–	–	H	(–)	(–)	P	P
Percussive or rubbing sound producing activities										
Clack	P	P	H	H	–	–	P	P	P	P
Combine with object	–	P	C	P	–	H	(–)	P	(–)	P
Flint	–	H	C	P	–	P	P	P	P	H
Flint in mouth	–	P	P	–	–	–	(–)	(–)	(–)	P
Pound on surface	–	P	H	H	–	P	P	(–)	(–)	H
Rub in mouth	–	P	P	–	–	–	(–)	(–)	(–)	P
Rub/roll on surface	C	C	C	H	P	H	H	H	H	H
Rub stones together	–	H	C	P	–	C	P	P	H	H
Rub with mouth	–	P	P	–	–	–	(–)	(–)	(–)	(–)
Scatter	P	H	C	P	P	C	H	P	H	H
Shake in hands	–	–	P	P	–	P	(–)	P	P	P
Slap	–	–	H	P	–	–	(–)	(–)	(–)	(–)
Swipe	–	P	P	–	–	P	(–)	(–)	P	H
Tap in mouth	–	–	P	–	–	–	(–)	(–)	(–)	(–)

Table 6. (Continued).

SH pattern	Ara.A	Wak.A	Takh.	JMC	Kosh.	Ara.E	Sho.A	Sho.B	Tak.B	Tak.C
Other complex manipulative activities										
Flip	–	P	H	–	–	P	(–)	(–)	P	(–)
Put in water	–	–	P	–	–	P	(–)	(–)	(–)	(–)
Roll in hands	P	H	C	P	P	H	P	P	H	H
Rub/put on fur	–	H	P	P	–	P	(–)	P	(–)	(–)
Rub with hands	P	H	C	H	P	H	H	P	P	P
Spin	–	–	P	–	–	–	(–)	(–)	(–)	(–)
Stone groom	–	–	–	–	–	–	P	(–)	(–)	(–)
Throw	–	P	P	P	–	–	(–)	(–)	(–)	(–)
Throw and jump	–	–	H	–	–	–	(–)	(–)	(–)	(–)
Throw and run	–	–	P	P	–	–	(–)	(–)	(–)	(–)
Throw and sway	–	–	P	–	–	–	(–)	(–)	(–)	(–)
Wash	–	–	P	P	–	H	(–)	(–)	(–)	(–)
Wrap in leaf	–	–	H	–	–	–	(–)	(–)	(–)	(–)
Tot. pattern occurrence	17	32	44	31	16	32	23	22	27	31
SH occurrence per hr	0.2	1.5	3.4	2.1	0.1	2.2	0.9	1.9	5.9	7.8

pattern. For example, COO was absent in Ara.A and Kosh., not observed in Sho.A and Tak.B, only present in Wak.A, JMC, Sho.B and Tak.C, but habitual in Ara.E and customary in Takh. The pattern consisting of flinting stones (FL) was absent in Ara.A and Kosh., present in JMC, Ara.E, Sho.A, Sho.B and Tak.B, habitual in Wak.A and Tak.C, and customary in Takh. Some complex SH patterns occurred in a few troops only, such as SW in Wak.A, Takh. and Ara.E, W in Takh., JMC and Ara.E, RWM in Wak.A and Takh., and SL in Takh. and JMC. Finally, a few complex SH patterns were specific to one troop, such as TIM, SP and WIL in Takh., and SGR in Sho.A.

To further explore inter-troop cultural differences in terms of behavioural complexity, we used a three-step procedure for the purpose of evaluating whether some troops have a more complex set of SH patterns than others. First, we pooled together complex SH patterns (i.e., percussive/rubbing and other complex manipulative activities). Second, we only considered the SH patterns that were scored as having a cultural occurrence in a given troop (i.e., habitual and customary). Third, we distinguished among three categories of troops: 1) when a troop was scored as having none or only one complex SH pattern, this troop was referred to as having a complexity level-1 SH culture, based on simple behavioural patterns (N_{CBP} = number of complex behavioural patterns, Kosh.: $N_{\mathrm{CBP}} = 0$, Ara.A and Sho.B: $N_{\mathrm{CBP}} = 1$);

2) when a troop was scored as having from two to ten complex SH patterns, this troop was referred to as having a complexity level-2 SH culture, based on medium complexity behavioural patterns (Sho.A: $N_{\mathrm{CBP}} = 3$, JMC and Tak.B: $N_{\mathrm{CBP}} = 4$, Wak.A, Ara.E and Tak.C: $N_{\mathrm{CBP}} = 7$); 3) when a troop was scored as having more than ten complex SH patterns, this troop was referred to as having a complexity level-3 SH culture, based on high complexity behavioural patterns (Takh.: $N_{\mathrm{CBP}} = 13$).

Two out of the three troops showing a complexity level-1 SH culture (Ara.A and Kosh.) were considered ‘control groups’ with only a baseline level interest in stones. Only Takh. showed a complexity level-3 SH culture. This troop also exhibited the most numerous SH patterns (44 out of a total of 45) and showed the highest frequencies of occurrence in SH patterns (28 habitual or customary patterns) among all troops. Most study troops (six out of ten) showed an intermediate level of complexity in their SH practice (level-2 SH culture).

Almost all SH patterns showed geographically patchy distributions, i.e., had different profiles of frequency of occurrence across the study sites, and were referred to as local variants or SH traditions. In terms of behavioural complexity, we found three levels of SH culture, each level being defined by troop-dependent clusters of SH traditions. Each troop presented a unique profile in terms of mean percentages of SH patterns performed, which further supported the geographic distribution of clear troop-dependent clusters of SH variants. For example, GH represented 2.8% of the total patterns performed in Takh., 4.8% in Ara.A, 7.1% in Wak.A, 7.2% in JMC, 15.0% in Sho.B, 15.6% in Sho.A, 16.5% in Kosh., 18.3% in Tak.C, 21.2% in Tak.B and 30.8% in Ara.E.

We found a significantly positive correlation between geographic proximity and cultural similarity in SH between troops ($r = 0.333$, $p = 0.008$). There were significantly greater similarities in SH patterns in the troops living at the same site, compared to other troops. Neighbouring troops (Sho.A/Sho.B and Tak.B/Tak.C), had similar sets of SH patterns and their total numbers of patterns observed were close (23 and 22 at Shodoshima, and 27 and 31 at Takasakiyama). In the two free-ranging troops where SH was previously studied by using similar methods of data collection and analysis (Ara.E and Tak.C: Huffman, 1996; Huffman & Hirata, 2003), we found that the size of the SH repertoire almost doubled. We recorded a total 32 SH patterns in Ara.E (as opposed to 17 patterns in 1991) and 31 patterns in Tak.C (as opposed to 16 patterns in 1989). The SH patterns that were not recorded before were FP, PIW, ROF and W in Ara.E, PUD, FLM and RIM in Tak.C, and B, H, L, MIM, P, PIM, SN, CIM, COO, POS, SIH and SW in Ara.E and Tak.C.

Intra-group variability and age effect

The frequency of performance of the main SH patterns (representing at least 4% of all SH patterns performed) varied significantly according to the age class of the stone handler (goodness-of-fit tests, df = 5, all $\chi^2 > 25.0$, $p < 0.001$). After excluding the most common patterns (i.e., GA, GH and ROS), we found in several troops a significant interaction effect between age and the degree of complexity of SH patterns (Ara.A: $F_{1,12} = 18.8, p = 0.001$; Wak.A: $F_{2,97} = 5.1, p = 0.008$; Takh.: $F_{2,315} = 3.1, p = 0.048$; JMC: $F_{2,103} = 7.9, p = 0.001$; Ara.E: $F_{2,292} = 4.3, p = 0.015$; Tak.C: $F_{2,175} = 3.8, p = 0.024$). Post-hoc comparisons showed that on average, young individuals (yearlings and juveniles) performed more simple patterns than complex patterns, whereas the opposite held true for older individuals (Figure 2). In Figure 3, we present several examples of age-related variability in the mean percentage of simple versus complex SH patterns.

In several troops, the percentage of young individuals exhibiting simple SH patterns was significantly higher than the percentage of older individuals (goodness-of-fit tests, df = 5, $\chi^2 = 237.5, 232.5, 431.4, 88.6, 250.8$ and 197.7 in Ara.A, Wak.A, Takh., JMC, Kosh. and Ara.E, respectively, $p < 0.001$). Within a given troop, certain complex SH patterns were only performed by a small proportion of individuals belonging to only one age class. For example, in Takh., SP was only score in 8% of old adults, in JMC, PIM was only displayed by 5% of subadults, and in Sho.B, CL was only exhibited by 10% of the juveniles.

Similarities and differences at the subspecies level

This is the first study to document the occurrence and form of SH activity in the *M. f. yakui* subspecies. The total number of patterns and SH occurrence in JMC (*M. f. yakui*) was almost the same as those found in Ara.E (31 and 32 patterns, 2.1 and 2.2 SH bouts and notes per hour, respectively (Table 6). The SH repertoire of JMC was more comprehensive than that of *M. f. fuscata*

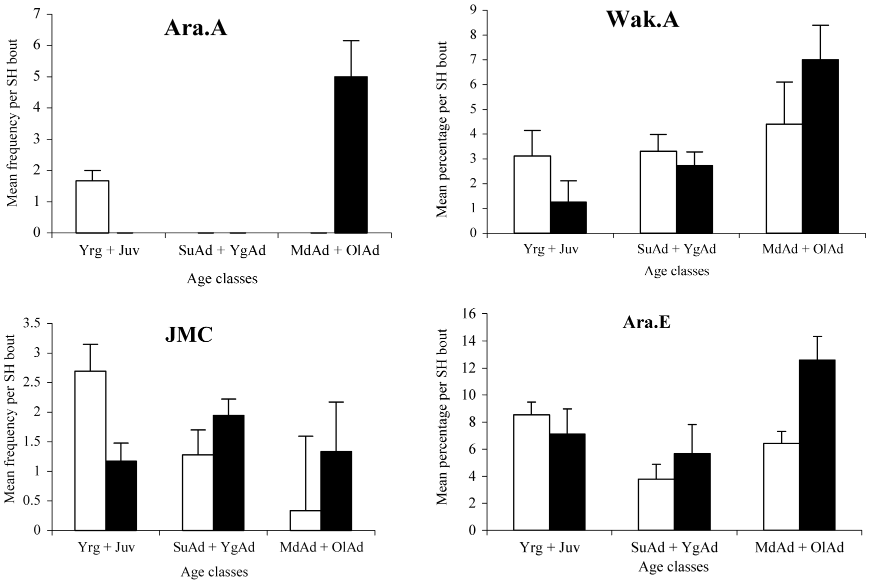

Figure 2. Effect of age on the degree of complexity of SH pattern performed in four study troops. Bars represent the mean frequency of SH patterns performed per bout ± standard error. White bars: simple SH patterns (Inv., Loc. and Coll.); black bars: complex SH patterns (Perc. and Comp.).

troops Ara.A and Kosh., that showed only a baseline level of interest in stones.

The SH repertoire of JMC did not notably differ from the SH repertoire of *M. f. fuscata* troops. Like most *M. f. fuscata* troops, JMC exhibited almost all the simple SH patterns (investigative, locomotion and collection activities) and various more complex patterns, such as CL, COO, POS, ROS, RT and RIH. The JMC troop even exhibited rare SH patterns, such as TH and W that were only observed in two *M. f. fuscata* troops (Wak.A, Takh. and Takh., Ara.E, respectively), as well as SL and TR that was observed in a single *M. f. fuscata* troop (Takh.). However, we found no SH pattern that was unique to JMC.

The effect of age on the mean percentage of most SH patterns was also found in JMC. Yearlings and juveniles performed more frequently certain simple patterns (e.g., SN and CA), whereas young and middle-aged adults performed more frequently certain complex patterns (e.g., POS) (Figure 3). In JMC, like most *M. f. fuscata* troops, the proportions of individuals exhibiting simple patterns were higher in young than in older troop members

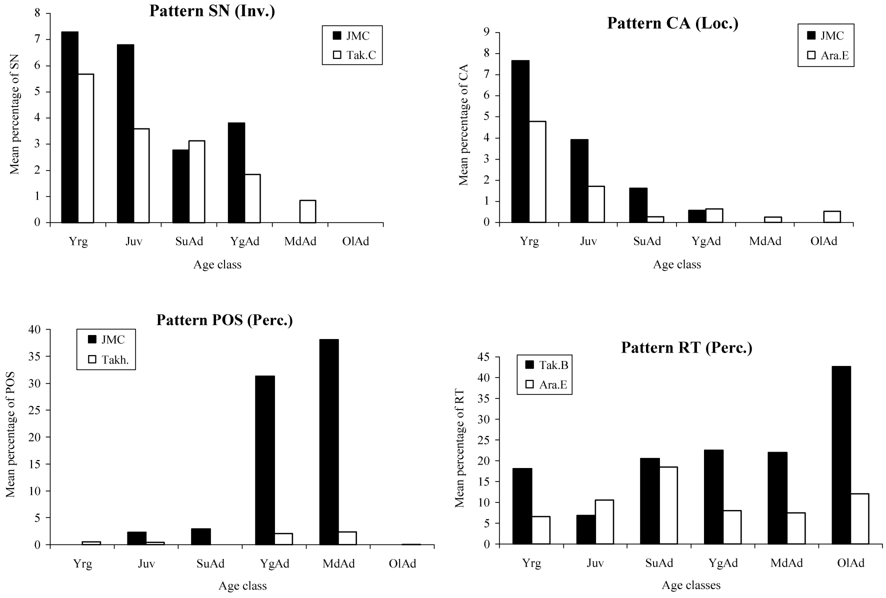

Figure 3. Examples of age-related variability in the mean percentage of several SH patterns performed (two simple patterns: SN and CA, and two more complex patterns: POS and RT).

(df = 5, $\chi^2 = 88.6$, $p < 0.001$). Overall, our comparative study revealed no major difference between *M. f. fuscata* and *M. f. yakui* in the occurrence, form and intra-group variability of SH.

Discussion

We found that Japanese macaques have SH cultures in the sense that the study troops showed distinctive levels of clustered SH traditions. Our detailed examination of the overall SH profiles showed major inter-troop differences in the occurrence and form of the behaviour. Contrary to the first comparative analysis based on data collected at Arashiyama and Takasakiyama, we found substantial qualitative and quantitative evidence for local SH variants among most of the ten troops studied here. Each troop had a distinctive set of 16-44 discrete SH patterns. Very few patterns were unique to certain troops, most others were shared between two or more troops. Although the SH profiles of each troop were distinctively different in nature and degree, the clusters of SH variants found in each troop were not mutually exclusive. However, our results revealed a significant inter-troop variability in the form of SH, consistent with the extensive and multiple inter-site behavioural differences recorded in chimpanzees, and interpreted as cultural variation (cf. Whiten et al., 1999, 2001).

In explaining the overall inter-troop variability in the form of SH, and the similarities in the SH repertoires between the free-ranging troops living at the same site, we can reasonably consider the possibility of ecological factors to be minimal. First, environmental conditions directly connected to SH activity did not differ dramatically among the study sites. All the troops were dependent to some extent upon artificial food provisioning by humans. Although stone availability was variable according to the study site, stones were available at all sites. Comparative analyses showed that site-specific stone availability was not significantly associated with inter-troop differences in the occurrence of SH (Leca, unpub. data). This suggests that the performance of SH is more diverse and more complex than the direct link to the number of stones locally available. Natural substrates (big rocks, tree trunks, outcropping roots or water holes) and artificial surfaces (metallic roofing, climbing structures, concrete walls or floors) to combine with stones (e.g., *rub/roll on surface*, *pound on surface*, *wash*) were available at all sites.

Second, SH is not considered to be a subsistence activity (Huffman, 1984, 1996). Out of the 45 different SH patterns, none of them is directly adaptive. Despite the rare occurrence of complex patterns such as *stone-groom* or *throw*, the stones handled by Japanese macaques were never used as tools to achieve an overt goal. Therefore, there is no local survival advantage in performing a particular SH pattern rather than another. As long as the basic materials (stones and substrates) are available and since the capacity for social learning in Japanese macaques has been proven in controlled studies (e.g., Kumashiro et al., 2003), we suggest that a wide range of alterations in the form of the same behaviour is likely to appear and diffuse. From a functional viewpoint, all SH variants should have similar expected frequencies of occurrence at the group level. SH is a behaviour particularly well-suited for the ethnographic approach. Its apparent lack of direct adaptative consequences and the arbitrariness of its behavioural variants make it easier to rule out ecological factors as potential causes of intergroup variation.

We found a positive correlation between geographic proximity and cultural similarity in SH between troops. The similarities in SH repertoires between free-ranging troops living at the same site may reflect the possibility of inter-troop observation when monkeys come into occasional contact around the feeding sites where most SH activity occurs (Leca, pers. obs.). Another possibility is that some SH may be transferred by males migrating from one troop to the other. Inter-troop cultural transmission in wild chimpanzees has been inferred from the geographical distribution of certain tool-using behaviours and social conventions (Boesch et al., 1994; McGrew et al., 1997, 2001), and suggested from field experiments (Biro et al., 2003). Thus we suspect a phenomenon of 'cultural zones' (cf. Biro et al., 2003) to be at work here, based on immigration or inter-troop observational learning of SH patterns, since any alternative explanation is hard to imagine.

We consider that genetic determinants may not account for the observed inter-troop variability in the form of SH. First, we showed that SH patterns varied as much between sites associated with the same subspecies (*M. f. fuscata* at seven sites) as between subspecies themselves (*M. f. fuscata* versus *M. f. yakui*). Second, we can assume that most SH patterns are Japanese macaque 'universals'. All the basic motor actions involved in every SH pattern are behavioural predispositions, i.e., they are already present in the repertoire of *Macaca fuscata* species (Huffman & Hirata, 2003). Third, it is acknowledged that genes determine the occurrence of general behavioural categories within a given species, such as the ability to handle stones or use tools. For example, gene flow between the three chimpanzee subspecies is prevented by zoogeographical barriers across Africa. Far western chimpanzees (*Pan troglodytes verus*) differ genetically from the others far more than central and eastern subspecies (*P. t. troglodytes* and *P. t. schweinfurthii*) differ themselves (Morin et al., 1994). Interestingly, the former uses percussive techniques to crack open nuts, while the latter are non-crackers (McGrew et al., 1997; but see Whiten et al., 1999 for a cultural rather than a genetic explanation). Fooden & Aimi (2005) provided information about the geographic distribution of extant populations of Japanese macaques, including continuities and discontinuities, migration, and genetic variability. Although there is evidence for geographic variation in mitochondrial DNA of Japanese macaques (Hayasaka et al., 1991), we suggest that intraspecific genetic differences are negligible in terms of possible implications for local behavioural variants, such as the manual dexterity to clack rather than rub stones together.

Our results showing high intra-group variability in most SH patterns are consistent with those drawn from a longitudinal study of SH in the Takh. troop (Nahallage & Huffman, 2007). Such variation can be interpreted from the viewpoint of developmental factors and age-related behavioural differences. As suggested by Nahallage & Huffman (2007), higher proportions of immatures exhibiting preferentially simple patterns, involving investigative, locomotion and collection activities, may reflect the development of perceptual and motor abilities in young monkeys. By contrast, the more frequent performance of complex manipulative patterns by older individuals could contribute to slow down the impairment of cognitive functions associated with advanced age (Nahallage & Huffman, 2007).

The ubiquity of certain SH patterns, such as *cuddle*, *gather* and *grasp with hand*, reemphasizes the general behavioural predispositions for Japanese macaques to manipulate stones, regardless of age. Other SH patterns, such as *swipe*, *rub in mouth*, or *wrap in leaf*, can be considered idiosyncratic or anecdotal. This finding supports the view that certain group members may 'specialize' or at least be responsible for the occurrence of particular patterns at the group level (Huffman & Quiatt, 1986). The occurrence of group member 'specialists' in particular patterns emphasizes the role of individuality in group-level phenomena in primates. It has been suggested that the occasional and restricted practice of a given behavioural pattern by very few group members may not be sufficient to maintain these patterns in a troop in the long-term (Huffman & Hirata, 2003; Leca et al., in press). When the only practitioner of a particular behavioural pattern dies, this pattern is also bound to disappear at the group level.

Our results allow to further discuss the maintenance of SH as a traditional behaviour in two previously studied troops at Arashiyama and Takasakiyama (Huffman, 1996; Huffman & Hirata, 2003). The transformation phase of SH innovation is defined as the late period in which long-enduring practice and acquired familiarity with the behaviour is gained through the integration of SH with other daily activities (Huffman & Quiatt, 1986; Huffman & Hirata, 2003). Our data showed that within about 15 years of continued observation at Arashiyama and Takasakiyama, the monkeys have largely extended and diversified their SH repertoire. The appearance of patterns combining the use of hands and mouth (e.g., *carry in mouth*, *move inside mouth*, *bite* and *lick*) suggests that SH has become more integrated with foraging and feeding activities. Newly appeared patterns such as *combine with object*, *rub/put on fur* and *wash* reveals an increased diversity in the combination of stones with other objects or substrates. Our results were not consistent with previous findings suggesting that with age, individuals tend to become more conservative in their SH patterns, limiting their performance to simple activity patterns (Huffman & Quiatt, 1986; Huffman, 1996). The more frequent and diversified practice of SH in all age classes associated with the transformation phase of SH could account for this discrepancy. Another explanation could be that the young individuals growing up with SH 15 years ago are now at an advanced age, and they carry on with more complex patterns than they showed when they were young, compared to the earliest generation of stone handlers. This would also be consistent with the transformation phase and a generational 'ratchet effect' of increased complexity of SH behavioural patterns. This could lead in future to stone-tool use, as stone behaviour becomes more deeply ingrained into the behavioural landscape of these monkeys at the population level.

Although stone tool-using has been reported in Japanese macaques under experimental conditions (Tokida et al., 1994), we found no direct evidence for an adaptive transformation in SH practice. Even complex combinatorial SH patterns did not meet the descriptive criteria of Beck's (1980) definition of tool use. The combination of stones with other objects, including food items, did not 'efficiently alter the form, position, or condition' (Beck, 1980, p. 10) of these objects. Patterns such as *rub/put on fur* and *stone-groom* may actually be cases of self- or allo-grooming while holding a stone (Weinberg & Candland, 1981). However, when practised on a daily basis and by most members of a group, the non-instrumental manipulation of stones could be considered as a behavioural precursor to the possible use of stones as tools (Huffman & Quiatt, 1986; Huffman, 1996).

Although widely used by field primatologists as a way to identify traditions, the ethnographic approach has been recently questioned for having two flaws (Fragaszy & Perry, 2003). The first flaw is conceptual. This approach does not necessarily consider an essential characteristic of traditions: their dependence on social context for individual acquisition of the behaviour under study. Many authors suggest that demonstrating the social transmission and durability of a behaviour within a group is sufficient evidence in itself of a behavioural tradition (Fragaszy & Perry, 2003; Perry et al., 2003b; Visalberghi & Adessi, 2003). Developmental, experimental and long-term studies could then compensate for this shortcoming. The second flaw is logical. When considered alone, the ethnographic approach can result in 'false negatives' and more problematic 'false positives' (Fragaszy & Perry, 2003).

When combining the ethnographic approach, evidence for social transmission and durability of SH, and the view of behavioural predispositions in phylogenetically close taxa, several findings supported the hypothesis that SH is a traditional behaviour: 1) we showed a geographic distribution of clear troop-dependent clusters of SH variants suggestive of the notion of cultural zones; 2) we provided arguments to eliminate simple alternative explanations for such behavioural variability, such as genetic or ecological differences; 3) although SH is a primarily solitary activity, non-SH individuals have plenty of opportunities to observe performances of SH by other group members and often show close interest in others' stones (Leca, Huffman, pers. obs.); 4) after SH appeared at Arashiyama, developmental data showed that the behaviour first spread laterally among young individuals and was then acquired vertically from mother to offspring through observational learning (Huffman, 1984, 1996); 5) SH is enduring in most troops, where it occurs on a regular basis; at Arashiyama and Takasakiyama, we found that this traditional behaviour has at least a 27-year history and provided evidence that it has reached its transformation phase.

Along with a lack of evidence for an instrumental use of stones, these arguments further support the notion of SH as being a non adaptive traditional behaviour (but see Nahallage & Huffman, 2007 for a possible ultimate function of SH). We drew an overall picture of rich cultural diversity in a particular type of object play behaviour in Japanese macaques. Amongst the rare non-adaptive proposed traditional behaviours (see also 'leaf-pile pulling' in chimpanzees: Nishida & Wallauer, 2003), SH is the most thoroughly documented. Additional evidence for inter-troop variability and long-term maintenance of stone-related behaviours in non-human primates may provide new insights into the emergence of hominid material culture through stone-tool technology.

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Age-related differences in the performance, diffusion, and maintenance of stone handling, a behavioral tradition in Japanese macaques

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Abstract

Identifying the sources of behavioral diversity in non-human primates is vital to understanding the evolution of human behavior. Stone handling (SH, hereafter) is a form of object play consisting of the manipulation of stones by performing various behavioral patterns. This behavior is socially transmitted from generation to generation in Japanese macaques (*Macaca fuscata*), as a behavioral tradition. SH behavior in particular may reflect on the origin and evolution of stone-tool material culture. The objective of this study was to assess how group size, age structure, and age- and sex-related differences may account for the substantial intra- and inter-troop variations in SH reported in ten troops of Japanese macaques. Our results supported the hypothesis that patterns of variation in SH across troops reflected variability in group size and composition in age classes. We found that troop size was correlated with the proportion of troop members exhibiting SH simultaneously. The effect of troop size on the synchronized performance of SH may reveal the contagious nature of play. Our results suggest that the age structure of the group may affect the diffusion of SH. As predicted by the surplus energy hypothesis, a major functional hypothesis about play, intra-group variation in SH reflected more age- than sex-related differences. SH mainly occurred and was more frequent in younger than in older individuals, whereas no significant sex differences were found. SH episodes were shorter, more vigorous, and SH patterns were more diverse and less complex in immature than in mature individuals. The present findings reveal that age-related factors and group size may constrain the performance, diffusion, and maintenance of SH within a troop. Contrary to most other socially transmitted stone-tool using behaviors in non-human primates and early hominids, there is no optimal SH pattern. Provided some form of social learning, the non-adaptive nature of SH may allow particular SH pattern preferences to emerge at the group level. Our findings urge the use of an inter-populational comparative approach based on multivariate analyses when addressing the question of the evolution of behavioral traditions in primate and human populations.

Keywords: Cultural play behaviors; Demographic constraints; Inter-troop variation; *Macaca fuscata*

Introduction

Identifying the sources of behavioral diversity in non-human primates is vital to better understand the evolution of human behavior (Wrangham et al., 1994). Recently, many researchers have sought explanations for behavioral differences within and between populations of various primate species (Wrangham et al., 1994; Perry et al., 2003; Fox et al., 2004; Ganas and Robbins, 2004). Patterns of behavioral variation are typically attributed to genetic, environmental, or cultural factors (Goldberg and Wrangham, 1997; Whiten et al., 1999; Yamakoshi, 2001). By contrast, the demographic context is seldom invoked to account for differences in behavior. Overall, group size and composition have long been disregarded as possible major factors contributing to our

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understanding of the expression of behavior. The pioneering research by Altmann and Altmann (1979) has brought us closer to understanding how group size and age/sex structure can both affect and be affected by behavior. We now understand that the demographic structure of primate social groups can play an important role in various behavioral domains such as dispersal patterns (Clutton-Brock, 1989), infanticide (Watts, 1989), mating strategies (Goldizen, 1988), hunting, territoriality, and male social relationships (Mitani and Watts, 1999; Mitani, 2006).

The potential influence of demographic settings in the occurrence and diffusion of behavioral traditions, however, has received relatively little attention. There is reason to suspect that group size and age- and sex-related differences could be major constraints shaping behavioral traditions, given that traditional behaviors are long-enduring behavioral practices shared among members of a population, which are largely dependent on social means for their appearance, propagation, and maintenance (Fragaszy and Perry, 2003). Like social parameters, the demographic structure, such as group size, or distribution of age and sex classes, is likely to affect the possible range of behavioral options available for individuals to acquire. Group size and composition also influence the likelihood of individual innovations on others, therefore influencing the probability of subsequent diffusion of a behavior (Huffman and Hirata, 2003).

When considering the influence of demographic factors on cultural transmission, mathematical models have yielded controversial results with respect to group size. Most mathematical models assume temporally accelerating rates of diffusion within a population, with more and more potential demonstrators available to the remaining naïve individuals (Cavalli-Sforza and Feldman, 1981). Under such circumstances, the expected proportion of individuals performing the novel behavior will increase as group size increases (Lefebvre, 1995). However, it seems that group size is a positive factor only below a certain threshold. Large-sized groups consist of many uninformed bystanders who could also act in ways which could slow down the diffusion (Lefebvre and Giraldeau, 1994). While group size might be an important factor involved in cultural transmission, it is not typically included in these studies of transmission, probably because a large variety of demographic settings is desirable for comparative analyses. It should be noted that when considered alone, group size had no significant effect on the diffusion rate of various novel behaviors in Japanese macaques (Huffman and Hirata, 2003).

Depending on the nature of the newly acquired behavior (e.g., a novel foraging technique which requires manual dexterity or physical strength, or a new form of play), the innovation may be restricted to a particular subset of the group (e.g., adult males or juveniles). With regards to the demographic structure of the group, it is acknowledged that new habits spread through "pivotal" individuals and follow certain set transmission paths determined by the age and sex classes to which the innovators belong (Cambefort, 1981; Huffman and Quiatt, 1986; de Waal and Seres, 1997). Regarding adaptive food-related behaviors with a potential survival value, age and sex differences in behavioral innovations and socially-learned behaviors have been extensively described in many primate species, including humans (see Choleris and Kavaliers, 1999; Reader and Laland, 2001, for reviews). In chimpanzees, gender affects the development and mastery of various cultural tool-using behaviors. Young females acquire the "termite-fishing" skill earlier than young males (Lonsdorf, 2005). As adults, females devote more time to the termite-fishing and nut-cracking activities, and are more proficient at these tasks than males (McGrew, 1979; Boesch and Boesch, 1984). In Japanese macaques, novel food-processing techniques, such as "potato-washing" and "wheat-washing," were first invented by a young female and then acquired by other group members except subadult and adult males (Kawai, 1965).

In *Homo sapiens*, a sex-based difference in innovation and skill learning also exists. Males display more risk-taking behaviors than females do (Daly and Wilson, 1983), which may result in more technological and behavioral innovation (Rogers, 1995). Age influences food production activities, such as hunting or gathering, in traditional societies (Walker et al., 2002). The influence of age and sex on the emergence and propagation of behavioral traditions is likely to date back at least to the last common ancestor of chimpanzees and humans, and probably even before (Lonsdorf et al., 2004). Thus, by both facilitating and limiting the manifestation of adaptive behaviors, demographic factors, and particularly group size and age/sex composition, can be regarded as major constraints to the emergence, transmission, and long-term diffusion of traditional behaviors.

When considering non-adaptive behaviors, such as object play, age is also likely to be a key factor, whereas no consistent effect of sex is expected. The surplus energy hypothesis, a major functional hypothesis about play, proposes that play enables the adaptive expenditure of excess metabolic energy (Barber, 1991). Since young mammals are often not limited in energy, Barber (1991) argues that play should be more frequent, more vigorous, but shorter in young than in older individuals, regardless of sex. Most studies conducted on various taxa, including rodents, carnivores, marsupials, and non-human primates, showed major age-related differences, with youngsters playing considerably more often than older individuals, but no significant sex differences (see Glickman and Sroges, 1966; Fagen, 1981, for a review). In chimpanzees, the traditional play behavior called "leaf-pile pulling" is mainly performed by young individuals with no differences between males and females (Nishida and Wallauer, 2003). In humans, not only young children, but also boys play more with objects than older individuals and girls (Pellegrini and Gustafson, 2005).

Categorized as a form of solitary object play, stone handling (SH) consists of manipulating stones in combination with various behavioral patterns (Huffman, 1984). For example, individuals may be observed putting a stone in their mouth and making it move inside their mouth with their tongue, clacking or rubbing stones together, or repeatedly pounding a stone on a substrate. Initially transmitted among young cohorts of playmates, then acquired from mother to offspring through observational learning, and socially passed from generation to generation in a long-term studied troop of Japanese macaques (*Macaca fuscata*), SH is regarded as a behavioral tradition (Huffman, 1984; Huffman and Quiatt, 1986; Huffman, 1996; Huffman and Hirata, 2003). By taking an ethnographic approach to chart inter- and intra-group diversity in SH, Leca et al. (2007a) revealed substantial variability in the frequency of occurrence and form of SH between ten troops. Investigating the effect of age and sex on the patterns of variation of SH in non-human primates may offer new insights into the origin of object play in hominids. Findings from two free-ranging and one captive troop of Japanese macaques suggest that age-related differences are involved in the performance of SH. Although individuals of all ages could handle stones, analyses showed that the young stone handled far more often and displayed more various behavioral patterns than adults (Huffman, 1996; Huffman and Hirata, 2003; Nahallage and Huffman, 2007). Like in most studies on object play in animals, no consistent sex differences were found among immatures and adults (Huffman, 1996; Nahallage and Huffman, 2007).

A long-term study on SH in a captive troop has examined the possible biological functions of this activity in Japanese macaques with special reference to hypotheses proposed for adaptive value of object play in animals (Nahallage and Huffman, 2007). These authors have attributed age-related differences in the performance of SH to possible age-specific benefits of this activity. Nahallage and Huffman (2007) showed that youngsters exhibited frequent and short SH bouts including locomotion and vigorous behavioral patterns, whereas adults engaged in fewer but longer SH episodes involving more stationary and complex body actions. These results were consistent with the motor-training hypothesis developed to explain how play behaviors may contribute to the neuro-motor development of critical behavioral patterns in young individuals (see Byers and Walker, 1995). As a psychologically relaxing activity, SH in adults was hypothesized to have long-term beneficial neurophysiological effects, such as helping to maintain neural systems and prevent the deterioration of cognitive abilities in older monkeys (Nahallage and Huffman, 2007).

Regarding a possible effect of group size, an analysis conducted over a 10-year time period at Arashiyama, Japan showed that the diffusion rate of SH (defined as the yearly total number of individuals for which SH was observed) was considerably higher in a large-sized troop of Japanese macaques prior to a natural troop fission (with 236 troop members) than after the troop's division into two smaller troops, consisting of 139 and 97 members, respectively (Huffman and Hirata, 2003). SH at Arashiyama was not acquired by adult individuals. Instead, only young monkeys continued to practice this activity into adulthood (Huffman, 1984; Huffman and Quiatt, 1986). Huffman and Hirata (2003) demonstrated that the increase in the number of new stone handlers resulted from the addition of infants born as the initial spread of this novel behavior occurred horizontally through young troop members, and diffused vertically from mother to offspring thereafter (Huffman, 1984). These findings on two troops suggest that the performance and diffusion of SH may be affected by group size and age, but not by sex. The question arises as to whether this tendency reflects a generalization of these effects at the species level.

The goal of this paper is to assess how group size, age structure, and age- and sex-related differences may account for the substantial intra- and inter-troop variations in SH reported in ten troops of Japanese macaques (cf. Leca et al., 2007a). First, due to the evidence from a previous study on effect of group size on SH diffusion rate (Huffman and Hirata, 2003), and based on our knowledge of the pathways of SH diffusion according to age classes (Huffman, 1984; Huffman and Quiatt, 1986), we hypothesized that patterns of variation in SH across troops reflected variability in group size and composition in age classes. We will test the two following predictions derived from this hypothesis: Prediction #1: Considering that the sight of conspecifics engaged in SH may strengthen an individual's assessment that the current environmental conditions are sufficiently safe to start playing, and given the contagious nature of play activities, we predict that the larger the group, the more amplified the contagion effect, and the higher the proportion of troop members exhibiting SH simultaneously; Prediction #2: Since the diffusion of SH depends on age structure, we predict that a group with abnormal age structure (i.e., missing age classes) will show a lower proportion of stone handlers and a lower frequency of SH than normal groups with all age classes present.

Second, based on the surplus energy hypothesis (Barber, 1991), the premise that SH is a form of object play (Huffman, 1984), and due to the evidence from previous studies of an effect of age on SH (Huffman, 1996; Huffman and Hirata, 2003; Nahallage and Huffman, 2007), we hypothesized intra-group variation in SH reflected more age- than sex-related differences. Accordingly, we will test the six following predictions: Prediction #3: SH occurrence will be higher in young than in older troop members, whereas no significant sex differences in SH occurrence is expected; Prediction #4: SH frequency will be higher in young than in older troop members, whereas no significant sex differences in SH frequency is expected; Regarding SH form, SH episodes will be shorter (Prediction #5) and more vigorous (Prediction #6) in young than in older troop members; SH patterns will be less diverse (Prediction #7) but more complex (Prediction #8) in mature than in immature individuals.

To address these questions, we conducted a systematic comparative investigation of the occurrence, frequency, duration, and form of SH among ten troops of Japanese macaques characterized by high variability in size and age structure. We will discuss the implications of our findings for the possible role of SH in neuro-motor and cognitive processes across age classes (after Nahallage and Huffman, 2007). We will draw conclusions that can be generalized to the performance and diffusion of SH at the species level, and provide insights into the origin of object play and stone-tool use in hominids.

Materials and methods

General study conditions

The species under study was the Japanese macaque (*Macaca fuscata*). The first two authors, occasionally assisted by M.A.H. and C.A.D. Nahallage, observed a total of ten troops at six geographically isolated sites in Japan from August 2003 to February 2005. Four troops lived in large outdoor enclosures in Inuyama, Aichi Prefecture (PRI Arashiyama = Ara.A, Wakasa = Wak.A, Takahama = Takh., and Japan Monkey Centre Yakushima macaques = JMC), and six troops were free-ranging (Koshima, Miyazaki Prefecture = Kosh., Arashiyama, Kyoto Prefecture = Ara.E, Shodoshima, Kagawa Prefecture = Sho.A and Sho.B, Takasakiyama, Oita Prefecture = Tak.B and Tak.C).

Captive troops were mainly 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 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. Regarding the ethical treatment of the study subjects, we complied with the policies, regulations, and guidelines implemented under protocols developed by the Kyoto University Primate Research Institute.

We used two types of age classifications to divide age groups for observation, analysis, and description (Table 1). Six age classes were used for observations (yearling, juvenile, subadult, young adult, middle-aged adult, and old adult: after Fedigan et al., 1983), and three broader age group categories (young, growing, and grown-up) for the purpose of some analyses, according to the size of the data set. For each troop, demographic variables including troop size and the distribution of troop members according to age and sex classes are shown in Table 2. The ten studied troops varied both in size and composition: two small-sized captive troops (Ara.A and Wak.A), two medium-sized captive troops (Takh. and JMC), two medium-sized free-ranging troops (Kosh. and Ara.E), and four large-sized free-ranging troops (Sho.A, Sho.B, Tak.B, and Tak.C). The proportion of individuals belonging to each of the different age and sex classes also varied. For only Ara.A, Wak.A, Takh., Kosh., and Ara.E were subjects individually identified. The exact age in years of each individual and their matrilineages were known. For JMC, Sho.A, Sho.B, Tak.B, and Tak.C, every sampled subject was categorized according to its sex and estimated age class. Observations were conducted between 7:00 and 18:00. Visibility was excellent. We sampled captive troop members from observation platforms overhanging the enclosures. Free-ranging troop members could be approached and sampled within 3–5 m.

Data collection

We used the same observation procedure for all troops, except Tak.B and Tak.C (see below for details). The two main observational methods used were continuous focal-animal sampling and instantaneous group scan sampling (Altmann, 1974). Behavioral data collection was supplemented with *ad libitum* sampling when necessary (Altmann, 1974).

Focal sampling

We video-recorded every focal session using Sony digital video cameras (DCR-TRV22 and DCR-TRV33). Whenever possible, the focal individual was filmed from the front, within a one-meter square area. We focused on all the behaviors and interactions of the focal individual. Since the field observation conditions did not allow us to use a totally random focal sampling method, we selected the focal individual using a semi-random procedure. The daily observation period was divided into one-hour blocks. To select the focal individual independently of its activity, the subject (or member of each age and sex class, when focal subjects were not individually identified) with least cumulative data was given priority.

We recorded the starting time of each focal session. Following protocol used in previous surveys carried out at Takasakiyama and Arashiyama (see Huffman, 1996), the typical duration of a focal session was 15 minutes. If the focal individual performed SH activity during the last 2 minutes of this period of time, the observation was extended for 5 minutes and continued until the SH bout ended.

Scan and ad libitum *samplings*

Before and after each focal session, the troop was scanned for evidence of any SH activity. For each scan-sampled stone handler, we recorded individual identity or age and sex class, and whenever possible, the SH patterns observed (Table 3). The observer recorded scans on data sheets, visually scanning across the enclosure for captive troops, or by walking from one side of the free-ranging troop to the other, in a set direction, so that each individual was sampled only once in a given scan session.

To supplement each troop's SH data set, observers devoted an average of 38.8 ± 31.8% of total observation time to the collection of *ad libitum* data on individuals performing SH. Whenever possible, *ad libitum* sessions were video-recorded, or otherwise collected on a notepad. For Tak.B and Tak.C,

Table 1
Two types of age classifications used in the observations, analyses, and descriptions

Age in years	1 year	2–3 years	4–6 years	7–10 years	11–15 years	16–years
Classification 1	Young		Growing		Grown-up	
Classification 2	Yearling	Juvenile	Subadult	Young adult	Middle-aged adult	Old adult

Table 2
Distribution of individuals according to age and sex classes in each studied troop. F: Female; M: Male; Asterisk: In large-sized troops, figures were approximately assessed during yearly surveys (Sho.A and Sho.B: after Watanabe, pers. comm.; Tak.B and Tak.C: after Kurita, pers. comm.)

	Age and sex classes												
	Yearling		Juvenile		Subadult		Young adult		Middle-aged adult		Old adult		Total number of individuals
Troop	Female	M	Female	M	Female	M	Female	M	Female	M	Female	M	
Ara.A	1	2	1	2	0	0	0	0	4	0	5	3	18
Wak.A	0	1	2	2	4	3	3	0	2	0	2	0	19
Takh.	3	6	4	2	1	4	7	2	4	0	10	3	46
JMC	3	1	9	12	8	14	15	5	11	9	11	4	102
Kosh.	2	3	11	10	7	8	7	12	4	7	8	9	88
Ara.E	7	5	10	5	15	4	20	5	30	2	31	7	141
Sho.A*	20	20	80	80	60	50	30	10	40	10	40	10	450
Sho.B*	10	10	60	60	50	40	30	20	30	10	20	10	350
Tak.B*	30	35	60	60	50	20	37	10	60	16	50	10	438
Tak.C*	68	69	96	95	80	20	70	10	86	20	50	12	676
Total	144	152	333	328	275	163	219	74	271	74	227	68	2328

Table 3
Thirty-six SH patterns performed by Japanese macaques and categorized according to general activity patterns (after Nahallage and Huffman, 2007)

Category	Name	Definition
Investigative activities	Bite	Bite a stone
	Hold	Pick up a stone in one's hand and hold on to it, away from the body
	Lick	Lick a stone
	Put in mouth	Put a stone in one's mouth and keep it for some time
	Move inside mouth	Make a stone move inside one's mouth with tongue or hands
	Sniff	Sniff a stone
Locomotion activities	Carry	Carry a stone grasped in hand from one place to another
	Carry in mouth	Carry a stone in mouth while locomoting
	Grasp walk	Walk with one or more stones in the palm of one or both hands
	Move and push/pull	Push/pull a stone with one or both hands while walking forward/backward
	Toss walk	Toss a stone ahead (repeatedly) and pick it up while walking
Collection (gathering) activities	Cuddle	Take hold of, grab, or cradle a stone against the chest
	Gather	Gather stones into a pile in front of oneself
	Grasp with hands	Clutch a stone or a pile of stones gathered and placed in front of oneself
	Pick up	Pick up a stone and place it into one's hand
	Pick and drop	Pick up a stone and drop it repeatedly
	Pick up small stones	Pick up small stones and hold them between fingertips (like the picking up of wheat grains)
Complex manipulative activities[*]	Clack	Clack stones together (both hands moving in a clapping gesture)
	Combine with object	Coordinated use of a stone with an object different from a stone (food, piece of wood, leaf, metal, etc.)
	Flint	Strike a stone against another held stationary
	Flint/rub/in mouth	Strike or rub a stone against another held in mouth
	Flip	Turn a stone over with both hands
	Pound on surface	Pound a stone on a substrate
	Roll in hands	Roll a stone in one's hands
	Rub/roll on surface	Rub or roll a stone on a substrate
	Rub stones together	Rub stones together
	Rub with hands	Hold a stone in one hand and rub it with the other (like potato-washing)
	Rub with mouth	Rub a surface with a stone held in mouth
	Scatter	Scatter stones about, on a substrate, in front of oneself
	Shake in hands	Take stone(s) in one's open palm hand and shake the stone(s) with the hand moving back and forth
	Slap	Slap, tap, or pound a stone with one's fingertips or palm of hand
	Spin	Spin a stone around on the ground using two fingers of one hand or both hands (one moving forward and the other backward)
	Stone groom	Self or allo-groom with a stone (put/rub a stone on fur)
	Swipe	Swipe stones together (both hands moving in a sweeping gesture)
	Throw	Throw a stone
	Wash	Put a stone in water or pick up a stone from water and rub it with hands

[*] Combine a stone with other stones, other objects, or substrate and/or perform behavioral patterns involving percussive actions or a series of at least three different actions, repeated or not.

we did not collect focal sessions, but only video-recorded *ad libitum* sessions during the periods after feeding, when SH is most likely to occur (Huffman, 1996). In some cases, we were able to record complete *ad libitum* sessions. The sampled individual was filmed through the entire sequence of SH, from start (a few minutes after provisioning time, immediately after the macaque left the feeding site and picked up or touched stones) to finish (five minutes after the last stone was discarded).

Data analysis

Based on video-records, J.-B.L. transcribed each focal session onto a data sheet and measured the duration of all activities to the second (feeding, foraging, locomoting, resting, socializing, SH, non-stone object exploring, and other). Each SH pattern was also recorded. Data were then entered into a computer for processing and statistical analysis.

We distinguished two types of SH records: SH bouts collected from focal sessions or complete *ad libitum* video-recorded sessions, and SH notes collected from scan sessions or incomplete *ad libitum* sessions. A *SH bout* (Huffman, 1996) is defined as the display of SH activity with possible pauses of no longer than 120 seconds. If the individual resumed SH within 120 seconds after pausing, then the two SH episodes were considered as a single SH bout. If SH was resumed more than 120 seconds after pausing, this would mark the start of a new SH bout. A SH bout could consist of several SH phases interspersed with pauses of no longer than 120 seconds. We defined a *SH phase* as the uninterrupted display of SH activity within a SH bout.

We defined the total troop observation time as the total time spent observing each troop, including focal time, scan time, and time spent collecting *ad libitum* data (Table 4). When multiple observers were present (i.e., during focal and *ad libitum* sessions), two types of observation time were distinguished. First, observation time during focal sessions was animal-based, and calculated by adding up the focal hours the animals were observed. Second, observation time during *ad libitum* sessions was observer-based, and calculated by adding up the times each observer viewed the animals. The occurrence of SH behavior and the presence of specific SH patterns were determined by taking into account focal time, scan time, and *ad libitum* time. The frequencies of SH patterns, as well as the duration and general form of SH bouts, were estimated from focal sessions and complete *ad libitum* sessions. The frequencies of SH bouts were calculated from focal time only.

To qualify as unequivocally present in a particular troop, SH behavior must have been observed at a rate of at least one record (SH bout or SH note) over 20 hours of total observation time (after Whiten et al., 1999, 2001). We defined *SH frequency* as the number of SH bouts per focal hour. We referred to *SH prevalence* as the mean percentage of stone handlers among individuals sampled in scan sessions collected during the most frequent SH activity period. For troops in which provisioning had no significant effect on SH frequency (Ara.A, Wak.A, JMC, and Kosh.; cf. Leca et al., 2006), all scan sessions were taken into account. Since provisioning had a significant effect on SH frequency and/or SH prevalence in other troops (cf. Leca et al., 2006), only scan sessions collected within 30 minutes after provisioning were taken into account for Ara.E, Sho.A, Sho.B, Tak.B, and Tak.C, and only scan sessions collected during non-provisioning periods were considered for Takh.

To assess *SH occurrence* at the individual level, we ascribed each troop member to one of the three following SH categories: verified stone handler, verified non-stone handler, or non-verified individual. In troops with individually identified members (Ara.A, Wak.A, Takh., Kosh., and Ara.E), an individual was labeled a verified stone handler if it had been observed to SH at least once during the troop's total observation time. In a middle-sized troop with unidentified members (JMC), J.-B.L. determined the number, age, and sex of verified stone handlers based on a comparison of physical features, age, and sex class of video-recorded stone handlers (67 different individuals identified out of 131 SH bouts and 91 SH notes). In the large-sized troops with unidentified members (Sho.A, Sho.B, Tak.B, and Tak.C), we determined the number, age, and sex of verified stone handlers based on the maximum number of stone handlers sampled during scan sessions. We labeled an individual as a *verified non-stone handler* if it had been sufficiently sampled (at least 2 hours of focal session and 50 scan sessions) but was never observed SH. When an individual was not observed SH but was insufficiently sampled, it was labeled as *non-verified*.

We used several variables to assess the form of SH. We evaluated *SH persistence* by calculating the mean duration of SH bouts, and duration and number of SH phases per bout. To evaluate *SH vigorousness*: 1) we measured the simultaneous performance of two SH patterns by the same individual, defined as double SH patterns, 2) we calculated the number of changes in the sequence of SH patterns performed per SH bout, defined as SH pattern turnover, and 3) we calculated the number of different SH patterns performed per SH bout defined as SH pattern variety per bout. For example, in the following sequence of SH patterns: clack, bite, clack, and bite, the SH pattern turnover is three, and the SH pattern variety per bout is two. To assess *SH pattern diversity*, we calculated the total number of different SH patterns observed in each age class, and derived from all available SH bouts and notes, defined as age-specific inclusive diversity of SH patterns. To evaluate *SH pattern complexity*, we measured the frequency of SH patterns grouped into three levels based on the four categories of general activity patterns (Table 3): simple SH patterns (belonging to the investigative and locomotion activities, such as lick, sniff, or carry a stone), intermediate SH patterns (collection/gathering activity patterns, such as cuddle or gather stones), and complex SH patterns (complex manipulative activities, such as combine with object, wash, clack, or rub stones together).

In Table 4, we present the total data sets per age class and per troop. For analyses regarding SH frequency, we drew on all focal sessions. The Sho.B, Tak.B, and Tak.C troops were

Table 4
Data sets collected according to age classes in each studied troop. Total: All age classes pooled; T.O.T.: total observation time; FT: Focal time (total duration in hours of focal sessions); SH Bt (F, CAL): Number of SH bouts collected during focal sessions (n.a.: not available), and during complete *ad libitum* sessions; SH Nt (IAL): Number of SH notes collected during incomplete *ad libitum* sessions

	Age class							
Troop	Yearling	Juvenile	Subadult	Young adult	Middle-aged adult	Old Adult	Total	T.O.T.
Ara.A								179.9
FT	23.3	23.3	n.a.	n.a.	31.5	62.0	140.1	
SH Bt (F, CAL)	12, 0	1, 0	n.a.	n.a.	0, 1	1, 0	14, 1	
SH Nt (IAL)	10	15	n.a.	n.a.	2	1	28	
Wak.A								224.6
FT	10.0	39.3	59.8	27.8	19.8	18.0	174.7	
SH Bt (F, CAL)	2, 4	16, 14	35, 36	0, 4	4, 1	2, 3	59, 62	
SH Nt (IAL)	18	45	140	3	5	13	224	
Takh.								449.2
FT	70.2	42.7	39.9	73.1	31.1	96.6	353.6	
SH Bt (F, CAL)	108, 6	68, 5	38, 4	56, 6	17, 3	22, 4	309, 28	
SH Nt (IAL)	267	254	206	190	72	210	1199	
JMC								99.1
FT	4.3	7.5	12.3	10.5	13.8	6.3	54.7	
SH Bt (F, CAL)	2, 6	6, 38	10, 27	1, 24	3, 4	0, 0	22, 99	
SH Nt (IAL)	4	33	24	27	3	0	91	
Kosh.								339.7
FT	13.3	38.0	30.3	42.5	38.0	53.3	215.4	
SH Bt (F, CAL)	5, 8	4, 6	0, 0	0, 0	0, 0	0, 0	9, 14	
SH Nt (IAL)	2	5	0	0	0	0	7	
Ara.E								431.3
FT	14.2	14.9	19.6	21.1	38.4	52.4	160.6	
SH Bt (F, CAL)	39, 8	57, 8	39, 3	56, 7	50, 2	76, 7	317, 35	
SH Nt (IAL)	57	97	75	106	106	138	579	
Sho.A								77.6
FT	5.0	3.9	3.8	0.5	3.1	0.5	16.8	
SH Bt (F, CAL)	13, 4	8, 3	6, 3	0, 0	3, 0	0, 0	30, 10	
SH Nt (IAL)	3	4	8	4	4	4	27	
Sho.B								51.5
FT	0.0	0.5	0.5	0.0	0.3	0.0	1.3	
SH Bt (F, CAL)	0, 1	3, 10	1, 8	0, 4	0, 2	0, 1	4, 26	
SH Nt (IAL)	10	32	16	4	4	1	67	
Tak.B								22.8
FT	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	
SH Bt (F, CAL)	0, 9	0, 11	0, 17	0, 9	0, 11	0, 2	0, 59	
SH Nt (IAL)	17	14	14	15	13	2	75	
Tak.C								73.8
FT	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.	
SH Bt (F, CAL)	0, 14	0, 67	0, 44	0, 32	0, 18	0, 7	0, 182	
SH Nt (IAL)	64	163	70	51	41	2	391	

excluded from these analyses because focal data were insufficient or not available. Among the other troops, focal sessions lasting less than 15 minutes (i.e., when the focal subject was lost) were excluded from these analyses. We drew on all SH bouts available for analyses on SH persistence and vigorousness. We drew on all SH bouts and SH notes available for analyses about SH pattern diversity per age class (defined as the number of different SH patterns observed in all individuals belonging to the same age class). For captive troops, we only used scans sessions in which at least 80% of troop members were sampled. For free-ranging troops, we only considered scans sessions taking into account at least 60% of troop members. Individuals aged less than one year old were not taken into account in the analyses.

We verified inter-observer reliability between the two main observers, J.-B.L. and N.G. using the kappa coefficient (Martin and Bateson, 1993). Based on individual identities, activities, and interactions, we found k = 0.88, 0.92, and 0.96, respectively. To measure the extent to which a single observer obtains consistent results when transcribing the same video-recorded behaviors on different occasions, J.-B.L. transcribed two times the same samples of SH video-records, involving a total of 630 sample points. A good intra-coder reliability kappa coefficient was also obtained: k = 0.84 (cf. Martin and Bateson, 1993). In most analyses, we reported mean values ± the standard deviation (SD). When the assumptions of normality, independence, and homogeneity of variances were verified, we used one-way ANOVAs to test the effect of age on the frequency and form of SH. When these assumptions were not verified, we used non-parametric tests (Mann-Whitney tests if two age classes were tested, and Kruskal-Wallis tests if more than two age classes were tested). We used Spearman rank-order correlation tests to evaluate the relationships between troop size and SH prevalence or SH frequency. To test the sex differences in SH occurrence among age classes, we used a chi-square test of independence from a contingency table (cf. Siegel and Castellan, 1988). Statistical analyses were performed using the SPSS 12.0 analytical program. Tests were two-tailed and significance levels were set at $\alpha = 0.05$.

Results

Effect of troop size and composition on SH prevalence and occurrence

We found a statistically significant positive correlation between troop size and SH prevalence (Spearman rank-order correlation test, N = 10, $r_s = 0.842$, $p = 0.002$). The correlation was still significant after excluding the outlier dot Sho.A that was outside the range of ± 2 SD around the regression line (N = 9, $r_s = 0.800$, $p = 0.010$). We verified Prediction #1 stating that the larger the group, the higher the proportion of troop members exhibiting SH simultaneously (Fig. 1a). By contrast, troop size was not significantly correlated with SH frequency (N = 7, $r_s = 0.679$, $p = 0.094$; Fig. 1b), SH persistence, defined as the mean duration of SH bouts (N = 10, $r_s = 0.588$, $p = 0.074$), or inclusive diversity of SH patterns at the group level (N = 10, $r_s = -0.061$, $p = 0.867$).

In Fig. 2a–j, we present an inter-troop comparison of the distribution of stone handlers and non-stone handlers according to age and sex class. We verified Prediction #2 that a group with abnormal age structure will show a lower proportion of stone handlers and a lower frequency of SH than groups with all age classes present. Ara.A was the only troop with an age gap in the distribution of group members: The growing age class (subadult and young adult) was missing. Interestingly, among the troops in which SH was present in all age classes (i.e., all the studied troops except Kosh.), Ara.A showed the highest proportion of verified non-stone handlers and the lowest SH frequency in the grown-up class (Fig. 2 and Table 5).

Although SH was found to be present in all troops studied, we found marked differences in the presence of SH according to age classes. For troops in which the focal data set was sufficient (at least 50 focal hours), except for Kosh. (i.e., Ara.A, Wak.A, Takh., JMC, and Ara.E), most verified non-stone handlers were aged 11 or more (i.e., middle-aged or old adults; eight individuals out of eight verified non-stone handlers in Ara.A, one out of two in Wak.A, three out of three in Takh., eight out of nine in JMC, and nine out of nine in Ara.E). Conversely, among immature individuals (yearlings, juveniles, and subadults), 100% of verified individuals in these troops were stone handlers. In troops with few non-verified individuals, (i.e., to the exclusion of Sho.A, Sho.B, Tak.B, and Tak.C), we found no significant sex difference among age classes in the proportion of verified stone handlers (Ara.A: $\chi^2_2 = 5.8$,

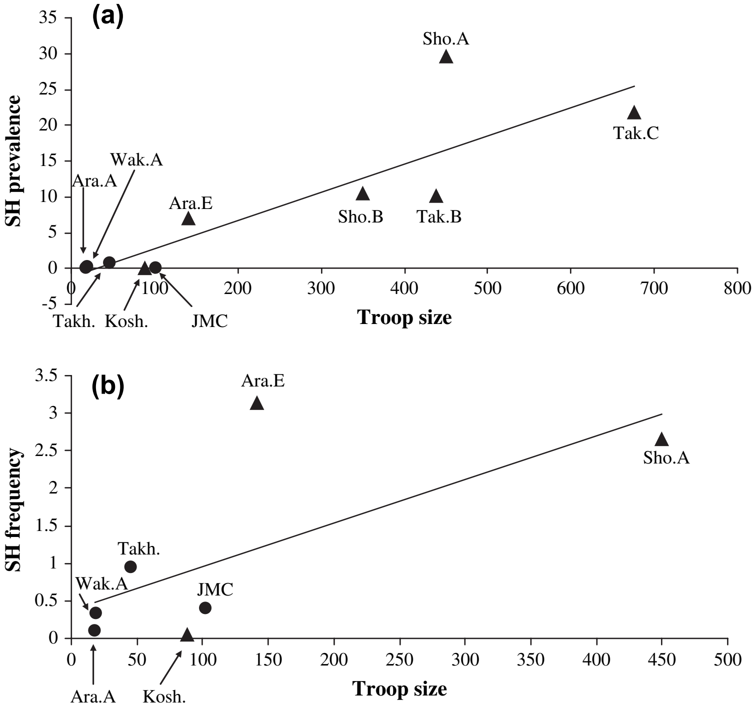
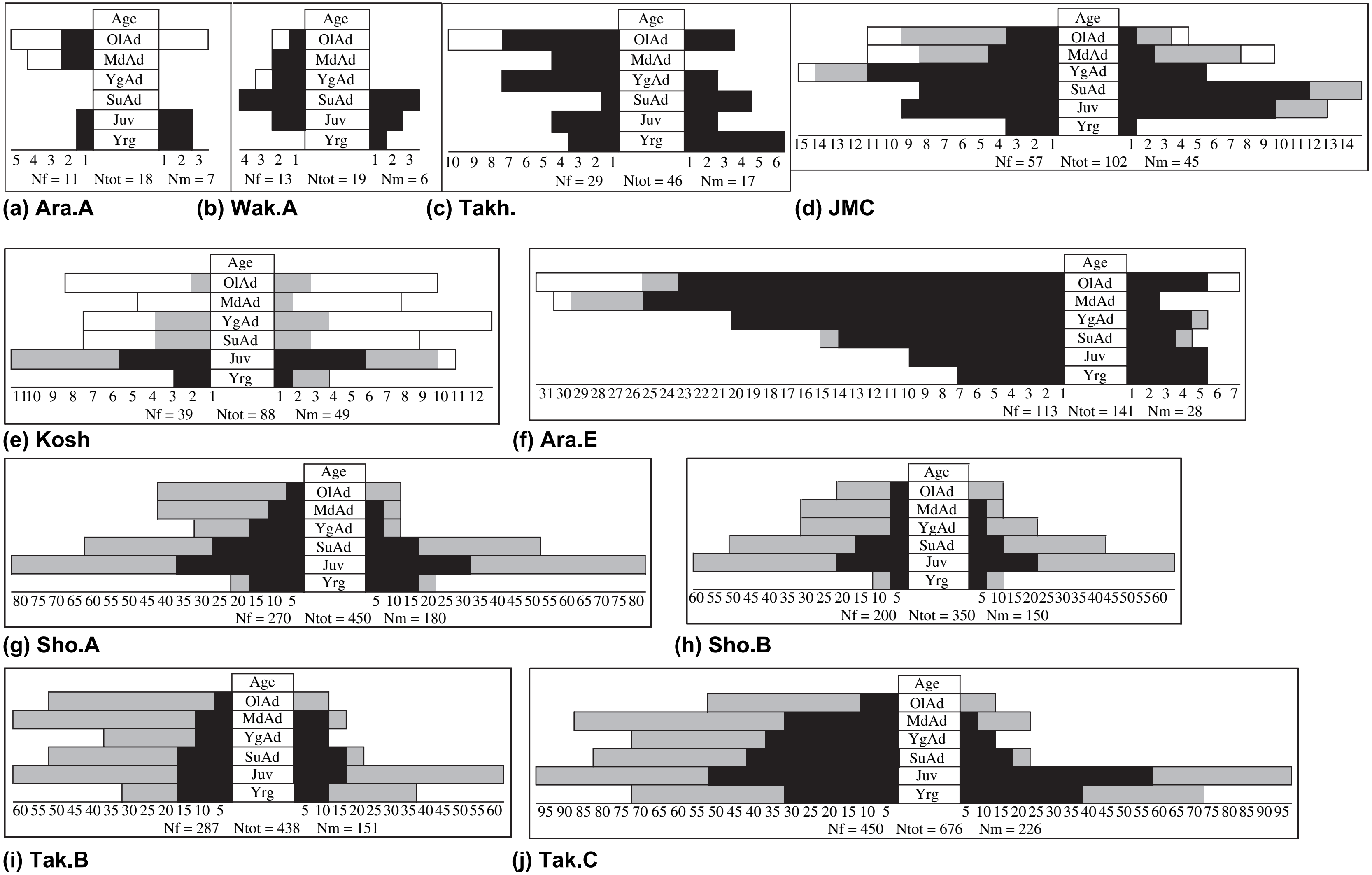


Fig. 1. SH prevalence (a), defined as the mean percentage of stone handlers among individuals sampled in scan sessions collected during the most frequent SH activity period, and SH frequency (b), defined as the number of SH bouts per focal hour, according to troop size; Slopes for line of best fit = 0.039 and 0.006, respectively; Round shapes represent captive troops and triangular shapes represent free-ranging troops.



(a) Ara.A (b) Wak.A (c) Takh. (d) JMC

(e) Kosh (f) Ara.E

(g) Sho.A (h) Sho.B

(i) Tak.B (j) Tak.C

Fig. 2. Inter-troop comparison of the distribution of stone handlers and non-stone handlers according to age and sex classes. Yearling, Juv: Juvenile, SuAd: Subadult, YgAd: Young adult, MdAd: Middle-aged adult, OlAd: Old adult; Left part of the distributions represents the number of females (Nf), right part represents the number of males (Nm); Ntot: Total number of individuals; Black areas indicate verified stone handlers, white areas indicate verified non-stone handlers, grey areas indicate non-verified individuals.

Table 5

SH frequency (mean ± SD), defined as the number of SH bouts per focal hour, according to the two degrees of age classes (see Methods for detail). n/a: Age class not present; Yng: Young, Grg: Growing, Gup: Grown-up, Yrg: Yearling, Juv: Juvenile, SuAd: Subadult, YgAd: Young Adult, MdAd: Middle-aged Adult, OlAd: Old Adult; Three types of tests were used (see Data analysis for detail): Mann-Whitney tests (MW, z value), Kruskal-Wallis tests (KW, chi-square value), and one-way ANOVAs (F values); Figures in brackets: Number of focally-sampled individuals

Troop							
	Ara.A	Wak.A	Takh.	JMC	Kosh.	Ara.E	Sho.A
Age classes # 1							
Young	0.28 ± 0.28 [6]	0.36 ± 0.34 [5]	1.67 ± 0.56 [15]	0.68 ± 1.73 [20]	0.18 ± 0.24 [13]	4.19 ± 2.03 [24]	3.36 ± 2.96 [22]
Growing	n/a	0.38 ± 0.48 [10]	0.80 ± 0.73 [14]	0.44 ± 1.40 [32]	0.00 ± 0.00 [25]	3.28 ± 2.46 [36]	2.35 ± 2.77 [10]
Grown-up	0.01 ± 0.04 [12]	0.15 ± 0.19 [4]	0.32 ± 0.40 [17]	0.15 ± 0.76 [22]	0.00 ± 0.00 [25]	2.13 ± 1.89 [67]	1.23 ± 1.87 [9]
Test	MW = −2.669	KW = 0.808, df = 2	$F_{2,45} = 24.301$	KW = 6.235, df = 2	H = 25.020, df = 2	$F_{2,126} = 9.070$	KW = 5.985, df = 2
p	0.032	0.668	<0.001	0.034	<0.001	<0.001	0.040
Sig. diff.	Yng > Gup*		Yng > Grg* Yng > Gup* Grg > Gup*	Yng > Gup** Yng > Grg*	Yng > Grg* Yng > Gup*	Yng > Gup* Grg > Gup*	Yng > Gup**
Age classes # 2							
Yearling	0.52 ± 0.13 [3]	0.20 ± 0.00 [1]	1.67 ± 0.64 [9]	0.71 ± 1.57 [4]	0.40 ± 0.35 [3]	4.00 ± 1.57 [12]	3.17 ± 3.34 [14]
Juvenile	0.04 ± 0.07 [3]	0.40 ± 0.38 [4]	1.69 ± 0.47 [6]	0.67 ± 1.84 [16]	0.12 ± 0.17 [10]	4.40 ± 2.45 [12]	3.69 ± 2.31 [8]
Subadult	n/a	0.54 ± 0.49 [7]	0.93 ± 0.40 [5]	0.67 ± 1.72 [17]	0.00 ± 0.00 [10]	3.37 ± 3.14 [15]	2.61 ± 2.80 [9]
Young Adult	n/a	0.00 ± 0.00 [3]	0.73 ± 0.88 [9]	0.19 ± 0.86 [15]	0.00 ± 0.00 [15]	3.21 ± 1.92 [21]	0.00 ± 0.00 [1]
Middle-aged Adult	0.00 ± 0.00 [4]	0.20 ± 0.28 [2]	0.63 ± 0.57 [4]	0.22 ± 0.92 [13]	0.00 ± 0.00 [11]	2.02 ± 1.64 [30]	1.59 ± 2.00 [7]
Old Adult	0.02 ± 0.05 [8]	0.10 ± 0.14 [2]	0.23 ± 0.30 [13]	0.00 ± 0.00 [9]	0.00 ± 0.00 [14]	2.22 ± 2.08 [37]	0.00 ± 0.00 [2]
Test	KW = 12.006, df = 3	KW = 7.153, df = 5	$F_{5,45} = 9.853$	KW = 13.734, df = 5	H = 27.739, df = 5	$F_{5,126} = 3.633$	KW = 9.041, df = 5
p	0.007	0.210	<0.001	0.012	<0.001	0.004	0.039
Sig. diff.	Yrg > MdAd* Yrg > OlAd*		Yrg > SuAd* Yrg > YgAd* Yrg > MdAd* Yrg > OlAd* Juv > SuAd* Juv > YgAd* Juv > MdAd* Juv > OlAd* SuAd > OlAd*	Yrg > OlAd* Juv > OlAd* SuAd > OlAd** SuAd > YgAd* MdAd > OlAd*	Yrg > SuAd* Yrg > YgAd* Yrg > MdAd* Yrg > OlAd*	Yrg > MdAd* Yrg > OlAd* Juv > MdAd* Juv > OlAd* SuAd > MdAd*	Yrg > MdAd* Yrg > OlAd* Juv > MdAd* Juv > OlAd* Juv > OlAd* SuAd > OlAd*

*$p < 0.05$
**$p < 0.025$

$p = 0.055$; Wak.A: $\chi^2_1 = 0.0$, $p = 1.000$; Takh.: $\chi^2_4 = 4.4$, $p = 0.358$; JMC: $\chi^2_5 = 1.6$, $p = 0.899$; Kosh.: $\chi^2_1 = 0.8$, $p = 0.363$; Ara.E: $\chi^2_5 = 0.5$, $p = 0.992$). Therefore, we found that SH occurrence was higher in young than in older troop members but did not significantly differ in males and females (Prediction #3).

Effect of age and sex on SH frequency

In Table 5, we present SH frequency according to the two age class classifications used, from the broader to the more detailed age group differences. Overall, younger individuals showed higher SH frequencies than older individuals. In Ara.A, Takh., JMC, Kosh., Ara.E, and Sho.A, SH frequency was significantly higher in young than in grown-up individuals, and in Takh., JMC, and Kosh., SH frequency was significantly higher in young than in growing individuals. In Takh. and Ara.E, growing individuals showed significantly higher SH frequencies than grown-up individuals.

More detailed analyses showed that in all troops, except Wak.A, SH was significantly more frequent in yearlings than in old adults. In some troops, SH frequency was significantly higher in yearlings than in middle-aged adults (Ara.A, Takh., Kosh., and Ara.E), young adults (Takh. and Kosh.), and subadults (Takh. and Kosh.). In some troops, SH frequency was significantly higher in juveniles than in old adults (Takh., JMC, Ara.E, and Sho.A), middle-aged adults (Takh., Ara.E, and Sho.A), young adults (Takh.), and subadults (Takh.). In Takh., JMC, and Ara.E, SH was significantly more frequent in subadults than in old or middle-aged adults.

In Table 6, we present SH frequency according to sex classes and within each of the following age classes: young, growing, and grown-up. Among all of the sex differences tested, only one was statistically significant: In growing Takh. troop members, SH was more frequent in males than in females. We found no statistically significant sex difference in other troop age classes. In sum, we found that SH frequency was higher in young than in older troop members but did not significantly differ between males and females (Prediction #4).

Effect of age on SH form

SH persistence and vigorousness. In Table 7, we present an inter-troop comparison of the general form of SH according to the following age classes: young, growing, and grown-up. In each troop (except Kosh., because the data set was insufficient), we tested the effect of age on several variables related to SH persistence and the vigorousness of SH performance. In Ara.E, Sho.A, Tak.B, and Tak.C, grown-up individuals displayed significantly longer SH bouts or total SH phases than growing individuals. In Takh., JMC, Tak.B, and Tak.C, growing or grown-up individuals performed significantly longer SH bouts and total SH phases, and/or more numerous SH phases than young individuals (Table 7). Overall, we verified Prediction #5 stating that SH episodes will be shorter in young than in older troop members.

Table 6
SH frequency (mean ± SD), defined as the number of SH bouts per focal hour, according to sex classes and within each age class. MW: Mann-Whitney test z value; Figures in parentheses: Number of focal sessions

Troop							
Age/Sex classes	Ara.A	Wak.A	Takh.	JMC	Kosh.	Ara.E	Sho.A
Young Female	0.19 ± 0.87 (62)	0.70 ± 1.89 (80)	1.59 ± 2.68 (186)	0.74 ± 1.93 (27)	0.17 ± 0.79 (118)	4.73 ± 2.40 (36)	2.80 ± 2.70 (10)
Young Male	0.32 ± 1.08 (124)	0.14 ± 0.73 (117)	1.67 ± 2.50 (224)	0.60 ± 0.1.47 (20)	0.18 ± 0.84 (87)	3.80 ± 2.95 (20)	3.83 ± 3.19 (12)
MW	−0.705	−1.732	−0.231	−0.035	−0.311	−0.671	−0.690
p (two-tailed)	0.481	0.200	0.867	0.972	0.836	0.491	0.539
Growing Female	n/a	0.35 ± 1.27 (257)	0.45 ± 1.52 (225)	0.71 ± 1.83 (34)	0.00 ± 0.00 (93)	3.41 ± 3.32 (81)	1.60 ± 2.19 (5)
Growing Male	n/a	0.52 ± 1.59 (92)	1.21 ± 2.35 (166)	0.29 ± 1.04 (56)	0.00 ± 0.00 (198)	2.17 ± 2.06 (9)	3.11 ± 3.32 (5)
MW	–	−0.590	−2.075	−1.184	0.000	−0.632	−0.565
p (two-tailed)	–	0.667	0.043	0.236	1.000	0.543	0.690
Grown-up Female	0.01 ± 0.24 (281)	0.16 ± 0.78 (151)	0.36 ± 1.36 (364)	0.08 ± 0.57 (50)	0.00 ± 0.00 (146)	2.24 ± 2.44 (167)	2.78 ± 1.89 (4)
Grown-up Male	0.00 ± 0.00 (93)	n/a	0.15 ± 0.76 (81)	0.27 ± 1.01 (30)	0.00 ± 0.00 (219)	1.49 ± 1.96 (24)	0.00 ± 0.00 (5)
MW	−0.577	–	−.0902	−1.057	0.000	−0.401	−2.183
p (two-tailed)	0.564	–	0.432	0.291	1.000	0.688	0.063

Table 7
Inter-troop comparison of SH persistence and SH vigorousness according to age classes. Yng: Young, Grg: Growing, Gup: Grown-up; Three types of tests were used (see Data analysis for detail): Mann-Whitney tests (MW, z value), Kruskal-Wallis tests (KW, chi-square value), and one-way ANOVAs (F values); N: Number of SH bouts; DurBt: Duration of SH bouts (sec), DurPh: Duration of all SH phases pooled per SH bout (sec); NbPh: Number of SH phases per SH bout; PatTnr: SH pattern turnover; PatVar: SH pattern variety per bout; DurDbPat: Duration of double SH patterns per SH bout (sec); Figures represent mean ± SD; Asterisks and sharps indicate significant post-hoc paired comparisons

Troop	Age	N	Duration SH bouts	Duration SH phases	Number SH phases	SH pattern turnover	SH pattern variety	Duration double SH patterns
Ara.A	Yng	13	14 ± 14	13 ± 12	1.2 ± 0.4	0.9 ± 1.9	1.8 ± 1.4	0 ± 1
	Grg	0	–	–	–	–	–	–
	Gup	2	101 ± 119	69 ± 73	1.5 ± 0.7	4.5 ± 4.9	2.0 ± 0.0	0 ± 0
	MW		−1.533	−1.701	−0.774	−1.769	−1.129	−0.392
	p		0.171	0.114	0.571	0.114	0.381	0.933
Wak.A	Yng	36	71 ± 102	49 ± 77	1.6 ± 1.1	4.9 ± 7.9	3.5 ± 2.6	6 ± 31
	Grg	75	70 ± 192	62 ± 186	1.3 ± 0.6	4.9 ± 9.5	3.6 ± 3.4	5 ± 12
	Gup	10	113 ± 128	102 ± 119	1.4 ± 0.7	9.7 ± 11.7	5.9 ± 3.3	22 ± 56
	KW/$F_{2,16}$		KW = 3.496	KW = 3.145	F = 0.223	F = 0.258	F = 0.290	KW = 3.023
	p		0.174	0.208	0.803	0.776	0.752	0.221
Takh.	Yng	187	73 ± 113*	49 ± 66*	1.8 ± 2.0*	5.7 ± 9.0	4.1 ± 3.4	2 ± 11
	Grg	104	210 ± 342*	161 ± 260*	2.6 ± 2.8*	5.0 ± 8.2	3.1 ± 2.8	6 ± 19
	Gup	46	132 ± 163	87 ± 96	2.1 ± 2.1	11.9 ± 16.2	5.4 ± 4.3	10 ± 31
	KW/$F_{2,34}$		KW = 17.364	KW = 19.025	KW = 6.269	KW = 2.944	F = 0.779	KW = 3.644
	p		< 0.001	< 0.001	0.044	0.229	0.467	0.162
JMC	Yng	52	47 ± 93*	41 ± 89*	1.3 ± 0.7	3.4 ± 7.2	2.6 ± 2.1	0 ± 1
	Grg	62	85 ± 115*	72 ± 100*	1.6 ± 1.1	3.2 ± 4.3	2.8 ± 2.0	0 ± 1
	Gup	7	67 ± 51	42 ± 32	1.9 ± 1.2	1.3 ± 1.7	1.9 ± 1.2	0 ± 1
	KW		10.830	11.757	2.639	1.441	1.724	0.140
	p		0.004	0.003	0.267	0.487	0.422	0.932
Kosh.	Yng	23	37 ± 45	33 ± 41	1.2 ± 0.7	4.0 ± 7.4	3.0 ± 2.2	0 ± 0
	Grg	0	–	–	–	–	–	–
	Gup	0	–	–	–	–	–	–
	KW		–	–	–	–	–	–
	p		–	–	–	–	–	–
Ara.E	Yng	112	227 ± 249	163 ± 213	4.3 ± 4.4	27.4 ± 34.0	6.4 ± 4.0$^{\#}$	12 ± 26$^{\#}$
	Grg	105	187 ± 257*	115 ± 163*	4.8 ± 6.4	15.8 ± 22.4*	3.9 ± 2.7*$^{\#}$	4 ± 13*$^{\#}$
	Gup	135	275 ± 301*	195 ± 231*	4.4 ± 4.1	25.1 ± 38.3*	5.0 ± 2.7*	19 ± 44*
	KW/$F_{2,98}$		KW = 10.577	KW = 13.919	F = 0.049	KW = 6.797	KW = 18.543	KW = 23.125
	p		0.005	0.001	0.952	0.033	< 0.001	< 0.001
Sho.A	Yng	28	319 ± 343	269 ± 303	4.0 ± 4.0	30.3 ± 35.4	6.9 ± 3.3	11 ± 24
	Grg	9	132 ± 86	72 ± 68*	5.0 ± 3.5	15.2 ± 16.1	5.0 ± 2.9	4 ± 10
	Gup	3	592 ± 330	544 ± 367*	7.0 ± 4.2	49.0 ± 2.8	7.0 ± 0.0	1 ± 1
	KW		5.292	7.247	2.492	4.553	1.501	0.675
	p		0.071	0.027	0.288	0.103	0.472	0.713
Sho.B	Yng	14	44 ± 22	41 ± 20	1.5 ± 1.3	3.7 ± 3.2	3.0 ± 2.0	1 ± 2
	Grg	13	116 ± 148	86 ± 99	3.1 ± 4.4	8.3 ± 10.1	4.6 ± 2.9	18 ± 45
	Gup	3	26 ± 7	26 ± 7	1.0 ± 0.0	2.5 ± 0.7	3.0 ± 1.4	0 ± 0
	KW		1.597	1.611	1.875	1.634	1.762	0.841
	p		0.450	0.447	0.392	0.442	0.414	0.657
Tak.B	Yng	20	221 ± 150$^{\#}$	206 ± 156	2.5 ± 1.5$^{\#}$	30.5 ± 22.3	7.9 ± 2.1*	43 ± 71
	Grg	26	194 ± 146*	168 ± 127*	3.0 ± 2.2*	15.7 ± 13.9*	6.1 ± 2.4*	12 ± 24
	Gup	13	391 ± 275*$^{\#}$	343 ± 260*	5.7 ± 2.8*$^{\#}$	40.9 ± 38.8*	7.7 ± 3.2	63 ± 101
	KW/$F_{2,21}$		F = 3.974	F = 3.515	F = 4.868	KW = 7.706	F = 3.725	F = 0.612
	p		0.036	0.040	0.020	0.021	0.043	0.553
Tak.C	Yng	81	111 ± 77$^{\#}$	99 ± 68$^{\#}$	2.0 ± 1.4	18.8 ± 14.2	6.0 ± 2.3	9 ± 17
	Grg	76	109 ± 93*	98 ± 86*	2.2 ± 1.8	16.6 ± 14.5	5.9 ± 2.2	4 ± 9
	Gup	25	186 ± 178*$^{\#}$	172 ± 170*$^{\#}$	2.3 ± 2.0	28.4 ± 22.4	6.2 ± 2.1	6 ± 10
	KW/$F_{2,40}$		F = 7.592	F = 9.133	F = 0.715	KW = 5.448	F = 1.100	KW = 1.011
	p		0.002	0.001	0.496	0.066	0.343	0.603

However, Prediction #6 proposing that SH will be more vigorous in young than in older troop members was not verified. In the Ara.A, Wak.A, Takh., JMC, Sho.A, Sho.B, and Tak.C, we found no statistically significant difference in SH vigorousness according to age classes (Table 7). In Ara.E and Tak.B, we found no consistent effect of age on SH vigorousness. In Ara.E, SH pattern turnover, SH pattern variety per bout, and the duration of double SH patterns per bout were significantly higher in grown-up than in growing individuals, whereas SH pattern variety per bout and the duration of double SH patterns per bout were higher in young than in growing individuals. In Tak.B, SH pattern turnover was higher in grown-up than in growing individuals, whereas SH pattern variety per bout was higher in young than in growing individuals (Table 7).

Given the link between SH and feeding activities (see Huffman, 1984; Huffman and Quiatt, 1986; Huffman, 1996), the fact that SH persistence and vigorousness were considerably higher in most free-ranging troops (Ara.E, Sho.A, Sho.B, Tak.B, and Tak.C) than in captive troops may be due to the influence of repeated food provisioning with hard coated cereal grains (in these free-ranging troops) on the duration of SH activity (Leca et al., 2006).

SH pattern diversity and complexity. To further investigate the effect of age on the form of SH, we examined the total number of different SH patterns observed in each of the six age classes (yearling, juvenile, subadult, young adult, middle-aged adult, and old adult) of each troop (Fig. 3). In troops in which all six age classes were represented (i.e., all troops except Ara.A), we found that yearlings showed lower inclusive diversity of SH patterns than juveniles (except in Takh., where both age classes showed an equal number of SH patterns). In each troop, the age classes exhibiting the highest SH pattern diversity were the juvenile (Takh., JMC, Kosh., Ara.E, Sho.B, and Tak.C), subadult (Wak.A and Takh.), or young adult (Tak.B) classes. In all studied troops, old adults showed the lowest SH pattern diversity, except in Wak.A and Ara.E, in which the age classes showing the lowest SH pattern diversity were underrepresented in terms of SH records compared to other age classes (middle-aged adults: 10 out of a total of 345 SH bouts and notes; subadults: 117 out of a total of 931 SH bouts and notes, respectively; see Table 4). In Takh., JMC, Sho.B, Tak.B, and Tak.C, SH pattern diversity tended to decrease as a function of age (from young to old adults). Therefore, we verified Prediction #7 stating that SH patterns will be less diverse in mature than in immature individuals.

To examine potential age differences in the complexity of SH patterns performed, we compared the frequency of SH patterns in each of the four pattern categories and according to age classes. For each troop, we drew on all available SH bouts and calculated the sum of SH patterns performed in each category per SH bout. As presented in Table 8, we found a consistent tendency for grown-up individuals to perform complex SH patterns more frequently than younger individuals in most troops (Ara.A, Wak.A, Takh., Ara.E, Sho.A, Tak.B, and Tak.C). In Ara.A, grown-up individuals performed significantly more complex SH patterns than young individuals. In Wak.A, Takh., and Tak.C, complex SH patterns were significantly more frequent in grown-up than in growing and young troop members. In JMC, growing individuals performed complex SH patterns significantly more often than young individuals. In Ara.E, complex SH patterns were significantly more frequent in grown-up than in growing troop members. In sum, we verified Prediction #8 stating that SH patterns will be more complex in mature than in immature individuals.

By contrast, when considering simple SH patterns (belonging to the investigative and locomotion activities), we found no major age difference, except in Ara.E, where investigative and locomotion SH patterns were significantly more frequent in young than in growing and grown-up individuals. Regarding intermediate SH patterns (belonging to the collection activity), no clear, consistent difference appeared among the study troops. In Takh. and Sho.B, collection patterns were significantly more frequent in growing than in young individuals, whereas the converse was found in Tak.B. In Ara.E, grown-up individuals performed significantly more collection patterns than growing individuals.

Discussion

We provided new evidence on the effect of group size, composition in age classes, and age-related differences on SH in Japanese macaques. We verified the two predictions generated by the first hypothesis that patterns of inter-troop variation in SH reflect variability in group size and age structure. First, the larger the group, the higher the proportion of troop members exhibiting SH simultaneously (Prediction #1). The positive effect of troop size on the synchronized performance of SH suggests the contagious nature of play. Seeing group members playing is a reliable cue for more individuals that the current environmental conditions are safe enough to engage in play

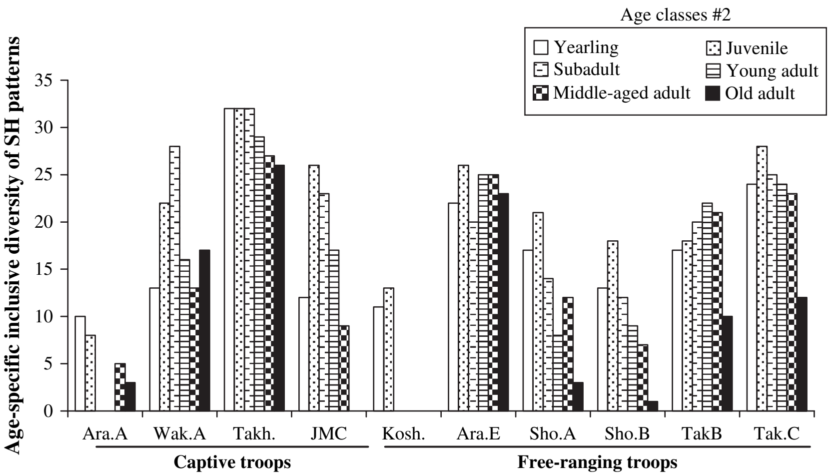


Fig. 3. Inter-troop comparison of age-specific inclusive diversity of SH patterns, defined as the total number of different SH patterns observed in each age class.

Table 8

Inter-troop comparison of the frequency of the four SH pattern categories according to age classes. Yng: Young, Grg: Growing, Gup: Grown-up; Three types of tests were used (see Data analysis for detail): Mann-Whitney tests (MW, z value), Kruskal-Wallis tests (KW, chi-square value), and one-way ANOVAs (F values); N: Number of SH bouts; Figures represent the number of SH patterns per bout (mean ± SD); Asterisks and sharps indicate significant post-hoc paired comparisons

Troop	Age	N	Investigative activities	Locomotion activities	Collection activities	Complex manipulative activities
Ara.A	Yng	13	0.5 ± 0.8	0.1 ± 0.3	1.5 ± 1.8	0.0 ± 0.0
	Grg	0	–	–	–	–
	Gup	2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	5.5 ± 4.9
	MW		−0.874	−0.392	−2.050	−3.732
	p		0.571	0.933	0.076	0.019
Wak.A	Yng	36	1.6 ± 2.8	0.4 ± 0.9	1.3 ± 1.7	2.8 ± 4.3*
	Grg	75	1.9 ± 3.6	0.3 ± 1.3	1.0 ± 1.7	3.2 ± 5.3$^{\#}$
	Gup	10	2.5 ± 4.2	0.7 ± 1.6	1.6 ± 2.7	8.2 ± 10.1*$^{\#}$
	$F_{2,16}$		0.286	0.640	0.662	3.953
	p		0.664	0.529	0.518	0.022
Takh.	Yng	187	1.7 ± 3.4	1.0 ± 1.8	1.2 ± 1.9*	3.4 ± 5.5*
	Grg	104	1.9 ± 3.9	0.6 ± 1.3	2.2 ± 3.4*	3.2 ± 5.8$^{\#}$
	Gup	46	8.8 ± 39.8	2.2 ± 6.4	5.3 ± 18.2	8.3 ± 25.4*$^{\#}$
	KW/$F_{2,34}$		KW = 5.019	KW = 4.587	KW = 8.199	F = 4.388
	p		0.081	0.101	0.017	0.013
JMC	Yng	52	0.6 ± 1.1	1.0 ± 2.2	1.0 ± 1.6	1.8 ± 3.6*
	Grg	62	0.4 ± 0.8	0.4 ± 0.9	0.9 ± 1.3	2.7 ± 2.6*
	Gup	7	0.1 ± 0.4	0.0 ± 0.0	0.7 ± 1.1	1.4 ± 0.5
	KW		2.502	4.929	0.933	10.629
	p		0.286	0.085	0.627	0.005
Kosh.	Yng	23	0.1 ± 2.5	0.5 ± 0.8	2.3 ± 2.9	1.1 ± 2.1
	Grg	0	–	–	–	–
	Gup	0	–	–	–	–
	KW		–	–	–	–
	p		–	–	–	–
Ara.E	Yng	112	1.3 ± 2.3*$^{\#}$	3.1 ± 4.9*$^{\#}$	10.4 ± 15.8	7.5 ± 16.6
	Grg	105	0.4 ± 1.1*	1.0 ± 2.2*	9.2 ± 14.1*	4.7 ± 8.6*
	Gup	135	0.5 ± 1.3$^{\#}$	1.0 ± 2.1$^{\#}$	14.0 ± 17.2*	11.0 ± 24.0*
	$F_{2,98}$		9.216	16.515	2.966	3.656
	p		<0.001	<0.001	0.043	0.027
Sho.A	Yng	28	3.5 ± 5.9	3.3 ± 3.5	9.5 ± 21.2	8.6 ± 13.9
	Grg	9	0.3 ± 0.5	0.9 ± 1.5	6.7 ± 12.6	2.9 ± 3.1
	Gup	3	2.7 ± 4.6	4.7 ± 4.2	14.3 ± 12.4	12.3 ± 10.7
	KW		5.099	5.180	0.748	2.881
	p		0.078	0.075	0.688	0.237
Sho.B	Yng	14	0.3 ± 0.7	0.6 ± 0.9	1.3 ± 2.1*	1.1 ± 1.3
	Grg	13	0.2 ± 0.4	0.3 ± 0.9	3.6 ± 5.7*	2.5 ± 3.6
	Gup	3	0.0 ± 0.0	0.3 ± 0.6	1.3 ± 1.2	1.0 ± 1.0
	KW		0.498	2.070	6.019	1.004
	p		0.780	0.355	0.049	0.605
Tak.B	Yng	20	1.2 ± 1.5	2.2 ± 2.6	15.0 ± 13.4*	10.6 ± 11.3
	Grg	26	1.1 ± 2.0	1.7 ± 1.7	5.8 ± 5.6*	6.9 ± 8.0
	Gup	13	4.2 ± 8.4	2.5 ± 2.4	11.4 ± 15.5	18.9 ± 17.4
	KW/$F_{2,21}$		KW = 0.472	F = 0.559	F = 3.874	KW = 5.901
	p		0.790	0.575	0.027	0.052
Tak.C	Yng	81	1.1 ± 2.0	1.3 ± 1.7	6.6 ± 6.7	8.9 ± 8.7*
	Grg	76	0.7 ± 1.6	1.2 ± 1.7	5.7 ± 5.2	8.7 ± 11.1$^{\#}$
	Gup	25	0.4 ± 0.9	1.8 ± 3.0	9.6 ± 9.6	16.1 ± 15.0*$^{\#}$
	KW/$F_{2,40}$		F = 1.984	F = 1.208	KW = 2.161	KW = 7.093
	p		0.140	0.301	0.339	0.029

(Spinka et al., 2001). Although SH is primarily a solitary activity, the sight of nearby stone handlers and even the loud noise generated by percussive patterns (Leca, pers. observ.) may increase an individual's probability to start handling stones. This stimulation effect may be amplified by an increasing number of troop members and eventually result in a form of ''hysterical contagion'' (Kerckhoff, 2002). This may help to explain the increase in number of SH individuals (synchronized occurrence) around feeding time in free-ranging provisioned troops, as this is the only time when most troop members are all together in the same location.

Regarding the effect of troop size on the synchronized performance of SH, we should bear in mind the more limited percentages of troop members sampled during scans collected in free-ranging troops compared with scans collected in captive troops. Due to lower visibility in free-ranging than in captive conditions, the consideration threshold for the percentage of scan-sampled troop members was lower in the former than in the latter (see Methods for details). Although this may affect, to some extent, the value of SH prevalence in free-ranging troops, we do not consider it a serious confounder of our results for two reasons: 1) as previously mentioned, scans sessions in free-ranging troops were conducted within 30 minutes after food provisioning, when almost all troop members are gathered around the feeding site; this is why yearly censuses of most free-ranging populations are conducted during provisioning time (Shodoshima: Watanabe, pers. comm.; Takasakiyama: Kurita, pers. comm.); 2) most free-ranging troops are considerably larger than most captive troops, and even 60% sampled troop members in the former represent 1.5 to 30 times more individuals than 80% sampled troop members in the latter.

Second, we verified that a group with abnormal age structure showed lower proportion of stone handlers and lower frequency of SH than normal groups (Prediction #2). The very low occurrence and frequency of SH in Ara.A, a troop with no subadults and young adults, strongly support the view that a group's age structure may affect the diffusion and maintenance of SH behavior. When a behavioral practice is restricted to a particular class of group members, it is supposed to spread very slowly and its maintenance may be jeopardized (Huffman and Hirata, 2003; Leca et al., 2007b). Huffman (1984, 1996) noted that the acquisition of SH and its further diffusion to the whole group require several years of practice by different age classes. To become established in a troop, SH needs to be passed from mother to infant ("tradition phase"). As long as young and middle-aged mothers continue to practice SH, this behavior will persist in young individuals (Huffman and Hirata, 2003). Moreover, as no individuals over five years old were seen to acquire SH behavior, there would be a critical period after which SH cannot be acquired (Huffman, 1984). We suggest that the age gap in the Ara.A troop might have constrained the diffusion of SH from the young to the grown-up age class. The restricted practice of SH by young individuals and only very occasional practice by older troop members may not be sufficient to maintain the behavior in this troop in the long-term.

Likewise, our data show that SH occurs in the Kosh. troop, but is only observed very occasionally in young individuals, compared to our other study troops. The question arises as to whether this behavior has only recently appeared in this troop, or if these findings also reflect an effect of the age of stone handlers on the diffusion of the behavior. We suggest that SH might have appeared at some time, but somehow has never become well-established and widespread within the Kosh. troop. One reason may be the poor nutritional conditions experienced by the monkeys on Koshima Island (Mori et al., 1997), which may lead adults to primarily focus on survival activities such as foraging instead of devoting time to such leisure activities as SH. If adults do not adopt this non-directly adaptive behavior because of local ecological pressures, SH may eventually disappear from the Kosh. troop, and possibly reappear under more favorable environmental conditions. In the Ara.A and Kosh. troops, the very low frequency of interaction with stones and the simple patterns exhibited are more likely to reflect a baseline level of interest in stones by macaques (Leca et al., 2007a) than ecological constraints such as shortage of stones (Leca, unpublished data). These are also relatively small troops, with lower chance of contagion than larger-sized troops such as Ara.E or Tak.C, where SH has persisted for the last 30 years. In white-faced capuchins, the durability of traditional behaviors was found to be readily disrupted by socio-demographic changes (Perry et al., 2003).

We verified five of the six predictions generated by the second hypothesis that intra-group variation in SH reflects more age- than sex-related differences. We found that SH occurrence and frequency were higher in young than in older individuals, regardless of sex (Predictions #3 and 4). In all troops, almost all individuals under the age of seven years were observed handling stones at least once, whereas most verified non-stone handlers were aged 11 or more. As individuals grow in age, they tend to handle stones less often than younger monkeys. This is in agreement with earlier findings from the Arashiyama and Takasakiyama troops (Huffman, 1996). Our results were consistent with the surplus energy hypothesis (Barber, 1991), and extensive reports that young animals typically play more than older ones (Fagen, 1981). We found limited evidence for an effect of sex on the occurrence and frequency of SH. Other studies have failed to find sex differences in socially learned behaviors (e.g., Pedersen et al., 1990; Bugnyar and Huber, 1997).

Although we failed to verify Prediction #6 (age did not seem to affect SH vigorousness), the other predictions about the effect of age on SH form were verified. We found that young individuals engaged in shorter SH episodes than older troop members (Prediction #5). The diversity of the comprehensive SH patterns displayed tended to increase between one, two, or three years of age and then gradually decline as adults age (Prediction #7). We also showed that complex SH patterns were more frequently performed by old rather than younger individuals (Prediction #8). Overall, our results are consistent with previous findings about the effect of age on SH frequency and form in captive and free-ranging troops of Japanese macaques (Huffman, 1984; Huffman and Quiatt, 1986; Huffman, 1996; Nahallage and Huffman, 2007), and further emphasize the view of SH as object play. SH is mainly practiced by young individuals but is also continued into adulthood. In macaques, SH is probably the only example of routine object play among adults.

However, much care is required when discussing our results in subadults and young adults. We acknowledge that our second age classification may be regarded as problematic since it fails to consider one of the most significant factors of life history and demography in the Japanese macaque (as well as other macaques and most Cercopithecines), namely sexual bimaturism. Although it may be quite reasonable to ascribe a four- to ten-year-old male to the subadult or young adult age class, a five- or six-year-old female is already fully mature and almost certainly not nulliparous. They are neither socially nor physiologically equivalent to a five- or six-year-old male. We are aware that this age classification possibly affects our results in an unknown direction (e.g., the patterns may be more pronounced, less pronounced, or even qualitatively different).

Developmental research conducted on other animal species consistently show that play is most common in immatures (Fagen, 1981), but animals can continue to play well into adulthood (Pellis and Pellis, 1991; Pellis and Iwaniuk, 2000). When considering the ecological constraints imposed on young and older animals, the energy-regulation approach generates predictions about the adaptive consequences of play in terms of an anti-predator strategy, and resistance to pathogens or to cold exposure (Barber, 1991). New mechanistic hypotheses suggest that animals would actively seek and create unexpected situations in play through self-handicapping (e.g., deliberately relaxing control over their movements) which would enable them to develop flexible kinematic and emotional responses to stressful events (Spinka et al., 2001). As in many types of play, our comparative results provide an additional line of evidence that there are age-related differences in the underlying motivational processes, and potential physiological and behavioral consequences of the practice of SH. We suggest that all monkeys, regardless of age, may simply enjoy manipulating stones, and pleasurable feedback potentially gained from the activity may be an immediate reinforcement.

However, our comparative results from multiple troops also provide wider support for the findings from the long-term studied Takh troop. As Nahallage and Huffman (2007) pointed out, there may be an age-related difference in the complex emotional state that is referred to as ‘‘having fun’’ in human folk psychology (see also Spinka et al., 2001): namely *excitement* in young individuals and *feeling relaxed* in older individuals. As a form of object play, SH may promote the development of motor skills in young monkeys and contribute to slow down the impairment of cognitive functions in older individuals (Nahallage and Huffman, 2007). Both of these possible proximate causes and ultimate functions may account for the age-related differences found. First, more frequent and shorter SH episodes, with more diverse patterns observed in juveniles, may promote the development of motor skills through physical excitement. Second, longer SH episodes including more complex patterns may enable older monkeys to maintain cognitive functions through a relaxation activity (Nahallage and Huffman, 2007).

The relative lack of diversity in the patterns of SH observed in yearlings and oldest individuals may simply reflect physical limitations (such as lack of strength or manual coordination): body size, developmental constraints, and experience in the former, whereas it may relate to a form of behavioral conservatism in the latter (Huffman and Quiatt, 1986; Nahallage and Huffman, 2007). However, the overall differences in the inclusive-pattern diversity across the studied troops (Fig. 3) are not really surprising. Contrary to most other socially-transmitted stone-tool using behaviors in primates, such as nut-cracking techniques observed in wild capuchins (Fragaszy et al., 2004) and chimpanzees (e.g., Boesch and Boesch, 1984), or the use of intentionally modified stones as tools by early hominids (Panger et al., 2002), there is no optimal SH pattern. Provided some form of social learning, the non-adaptive nature of SH may allow particular SH pattern preferences to emerge at the group level (Leca et al., 2007a).

These findings can be considered in the light of previous research in Japanese macaques on SH behavior and other forms of play. The consistent effect of age on the occurrence and frequency of SH is in agreement with surveys conducted several years ago and at different points in time in two of the free-ranging studied troops (Ara.E: Huffman, 1984; Huffman and Quiatt, 1986; Huffman, 1996; Tak.C: Huffman, 1996), and a more recent long-term study on one of the captive studied troops (Tak.h.: Nahallage and Huffman, 2007). Based on cross-sectional and longitudinal analyses on a several-year time scale, these studies also showed that most non-stone handlers were advanced age individuals, and young monkeys handled stones more often than older ones. When considering the patterns of diffusion of SH among long-term observed identified troop members, it appeared that this behavior first spread laterally among young individuals, probably peer playmates. Second, as young individuals become older, it could be acquired vertically from mother to offspring through observational learning (Huffman, 1984, 1996). Therefore, SH can be regarded as one of the seldom studied, culturally-mediated object play behaviors in non-human primates. A few other instances have been recently reported, such as the ‘‘toy game’’ in white-faced capuchins (Perry et al., 2003) and ‘‘leaf-pile pulling’’ in chimpanzees (Nishida and Wallauer, 2003). Like SH, these traditional play behaviors mainly occur in young individuals, among which they initially spread, but are also present in adults. However, contrary to SH, which is a solitary form of object play, the toy game and leaf-pile pulling can be labeled as social object play since they consist of using non-edible natural objects (such as sticks, pieces of bark, or dead leaves) in social playful interactions (Nishida and Wallauer, 2003; Perry et al., 2003).

Although age-related effects are expected over a wide range of behavioral domains, some behaviors, such as play and tool-use, should be more strongly influenced by age than others. The significance of our results can be interpreted from the perspective of demographic constraints on culturally-transmitted object play and stone-tool using behaviors in non-human primates and hominids. Age and sex affect material culture in many primate species, including humans (Choleris and Kavaliers, 1999; Reader and Laland, 2001; Walker et al., 2002). Cross-generational studies of traditional practices in monkeys (SH: Leca et al., 2007a; fish-eating: Leca et al., 2007b) and apes (handclasp grooming: Bonnie and de Waal, 2006) could enable evaluation of whether non-human primates show the cumulative cultural evolution found in humans, and also called the ‘‘ratchet effect’’ (Boesch and Tomasello, 1998).

Our findings urge the use of an inter-populational comparative approach based on multivariate analyses when addressing the question of the evolution of behavioral traditions in primate and human populations. In addition to demographic constraints (Lefebvre, 1995; this study), ecological factors (Boesch et al., 1994; McGrew et al., 1997) and social influences (van Schaik, 2003; Leca et al., 2007a) should be jointly considered to identify the sources of behavioral diversity in general, and variation in object play and stone-tool use in particular. Like all stone-related behaviors in non-human primates, further investigation of the various factors constraining the occurrence of SH may provide new insights into the emergence of hominid material culture through stone-tool technology (cf. Foley and Lahr, 2003).

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RESEARCH ARTICLE

Age-Specific Functions of Stone Handling, a Solitary-Object Play Behavior, in Japanese Macaques (*Macaca fuscata*)

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Stone handling (SH) in Japanese macaques, a form of solitary-object play, is newly acquired only by young individuals, and is the first example of a directly nonadaptive behavior that is maintained as a behavioral tradition within free-ranging provisioned social troops. We report here the first systematic investigation of this behavior in a stable captive social troop, the Takahama troop, which is housed in an outdoor enclosure of the Primate Research Institute (PRI), Kyoto University, Japan. This study was conducted to evaluate relevant competing hypotheses regarding the function of object play (e.g., misdirected foraging behavior and motor training) to explain the proximal causes and ultimate function(s) of SH. The ''misdirected foraging behavior'' hypothesis can be ruled out because of the lack of a clear temporal relationship between feeding and the occurrence of SH in any age class. Age-related differences in SH performance and behavioral patterns were observed, suggesting possible differences in the immediate cause and ultimate function between young and adults. Young individuals engaged in frequent bouts of short duration, involving locomotion and vigorous body actions throughout the day, which is typical for play by young in general. This pattern of behavior is consistent with the motor training hypothesis, which states that play occurs during the development of motor and perceptual skills and is thus potentially critical for neural and cognitive development. This practice is continued by those who acquire it at an early age, with adults engaging in significantly fewer but longer bouts that involve more stationary, complex manipulative patterns, almost exclusively in the late afternoon. We propose that for adults, at the proximate level SH is psychologically relaxing, but ultimately functions to maintain and regenerate neural pathways, and potentially helps to slow down the deterioration of cognitive function associated with advanced age in long-

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INTRODUCTION

Stone handling (SH) by provisioned Japanese macaques at Takagoyama was first briefly reported in 1975 [Hiraiwa, 1975]. More intensive investigations began independently at Arashiyama and Takasakiyama in 1979 after it was first recognized to occur there [Huffman, 1984, 1996; Huffman & Quiatt, 1986]. Currently, SH behavior can be seen in four captive troops and 11 provisioned free-ranging troops in Japan (Fig. 1). This activity has yet to be observed in nonprovisioned troops, and despite long-term research there are also provisioned troops in which SH has not been recorded (e.g., at Yakushima, Katsuyama, and Minoo). At Arashiyama, the behavior was documented to initially arise as the

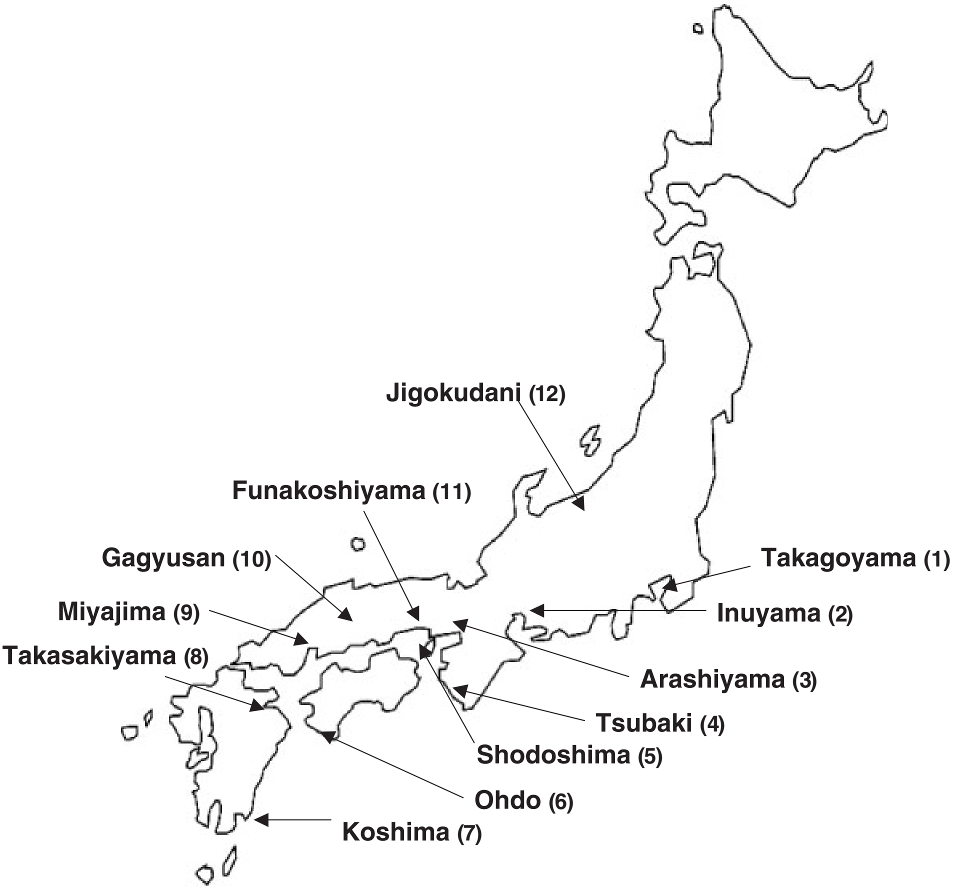

Fig. 1. SH site map of Japan. (Sources: Huffman and Hirata [2003] (sites 1, 3, 8, 10, 11, and 12); K. Watanabe, personal communication (sites 4, 5, 6, and 9); and C.A.D. Nahallage, personal observation (sites 2, 5, and 7).

innovation of a juvenile female that then spread to older immature kin relatives and peer playmates. As these individuals aged, the behavior was then transmitted to younger sibs or their own infants as a behavioral tradition [Huffman, 1984; Huffman & Quiatt, 1986]. At both Arashiyama and Takasakiyama, SH most frequently occurs after daily scheduled provisioning times, while individuals still have grain remaining in their cheek pouches [Huffman, 1984]. SH is defined as the repetitive manipulation of stones (e.g., gathering, picking up, and scattering them) and is considered as object play in Candland et al.'s [1978] terminology. According to Fagen [1981], object play is a ''divertive interaction with an inanimate object … including exploratory manipulation'' [cited in Hall, 1998, 45p].

While not every socially learned behavior has to be adaptive, the propensity to learn and adopt new behaviors certainly is. In the immediate sense, SH appears to be rewarding in itself, rather than the means to an end [Huffman, 1996]. Why the behavior persists in troops over many generations, despite the lack of any obvious function or direct adaptive value to those who practice it, has long been an elusive question. Two hypotheses regarding the occurrence of other types of object play in animals are the ''misdirected foraging behavior'' hypothesis and the ''motor training'' hypothesis. According to the misdirected foraging hypothesis, play in captive or domesticated animals is motivationally directed to objects as if they were food [e.g., Hall, 1998; Pellis, 1991; Pellis et al., 1988]. In the case of captive otters, they become increasingly excited by the approaching feeding time and devote less time to social play and more time to playing with objects as ''pseudo-feeding behavior'' [Pellis, 1991]. Object play by adult animals was described by Hall [1998] in a study of domestic cats as misdirected predatory behavior. A variety of objects were given to the cats, and those that most closely resembled mice were played with more than others.

The motor training hypothesis proposes a biological function for play, and states that object play modifies the developing neuromuscular system [Bekoff & Byers, 1981; Byers & Walker, 1995; Fairbanks, 2000]. In vervets and rhesus macaques, object play peaks at 3–6 months of age, coinciding with the time of motor neuron differentiation, rapid synaptogenesis, and peak cerebral activity [Jacobs et al., 1995; Rakic et al., 1986; Zecevic et al., 1989]. According to Fairbanks [2000], it is during this period of fine-motor development that the experience of object manipulation may play a role in shaping the neural connections that control precise hand movements. Moreover, object play continues at high rates during the second and third years of juvenile life. Another biological factor that determines the time course of object play is said to be the reduction of unmyelinated pathways in the central nervous system [Gibson, 1991]. Unmyelinated neural regions have a high potential for change, and a decline in the rate of object play was found to correlate with the age period (2–3 years) during which the number of unmyelinated pathways also begin to decline. Fairbanks [2000] was the first to clearly propose the neural selection model in these terms. The juvenile period is a time when heightened motivation to explore objects and their surroundings enhances input to the developing nervous system when the brain is still relatively plastic and is developing neural structures that can be modified by experience.

However, when SH was observed and reported for the Takagoyama and Arashiyama troops, it was exhibited only by infants and juveniles [Hiraiwa, 1975; Huffman, 1984]. At Arashiyama, despite over 29 years of continuous research prior to those observations, SH did not occur–at least not to the notice of many watchful observers [Huffman, 1991]. Furthermore, in the more than 25 years since its assumed innovation at Arashiyama in 1979, SH behavior has never been newly acquired by individuals over the age of 5 years, but the behavior continues to be practiced by individuals who acquired it when they were young into adulthood and old age [Huffman & Quiatt, 1986; Huffman & Hirata, 2003].

These long-term trends highlight the need for a closer systematic examination of SH behavior and beg for an explanation of the possible age-related differences in the function of this behavior. Here we analyze data from the first systematic study of SH behavior in a captive troop of Japanese macaques known to exhibit the behavior. First, a general behavioral description of SH and the prevalence of occurrence in the Takahama troop is presented. Next, the relationship between the occurrence of SH and feeding, and age-related differences in performance (i.e., duration, frequency, and number of patterns displayed) are analyzed and compared with those of the Arashiyama and Takasakiyama troops whenever possible. Based on these results, we reexamine the causes and possible functions of this behavior in young with regard to relevant existing hypotheses. Finally, we propose a new function for SH in adults, and assess the role of tradition in maintaining an innovated behavior of potential biological and psychological importance to those individuals that practice it.

MATERIALS AND METHODS

The Takahama troop of monkeys was introduced into the Primate Research Institute (PRI), Inuyama, from Takahama, Fukui Prefecture, in 1970. At the beginning of the present study there were 55 monkeys, but seven (two adult males, three adult females, one juvenile female, and one infant male) were removed at different times due to injury or death. Unless otherwise stated, only the 48 monkeys (18 males and 30 females) that remained to the end were used in the analyses presented here (Fig. 2). They are broken down into the following age-sex class distribution: infants (up to 12 months), yearlings (1 year), juveniles (2–4 years), young adults (5–15 years), and older adults (15–30 years). For analyses of broader age group differences, individuals are grouped as young (0–4 years) or adult (5 years and older) [Huffman, 1996].

Presently the troop is kept in a 960 m^2 outdoor enclosure with various metal climbing structures and shelter boxes for enrichment and protection from the weather.

Data collection began in June 2003 and continued up to November 2004, and all members of the troop were equally observed in all seasons of the year. The daily observation time was dependent on daylight length, which varied according to season. The observation time was divided into 1-hr time blocks, and individuals were sampled randomly in each time block. Equal numbers of focal samples were collected for each individual, in all time periods of the day in every month, to avoid sampling bias of certain age-sex classes and possible seasonal differences. Each individual was sampled 43 times, and a total of 878 focal observation hours were obtained. From this 434 SH sessions (focal sessions in which SH occurred) and 578 bouts of SH were recorded. A bout of SH is defined as the continuation of this behavior with pauses of no longer than 120 sec. If SH resumed after a more than 120-sec pause, it was counted as another bout.

Two sampling methods were used in the data collection: continuous focal animal sampling with video, and instantaneous scan sampling [Altamann, 1974; Martin & Bateson, 1993]. Each focal animal was video recorded for 15 min with a

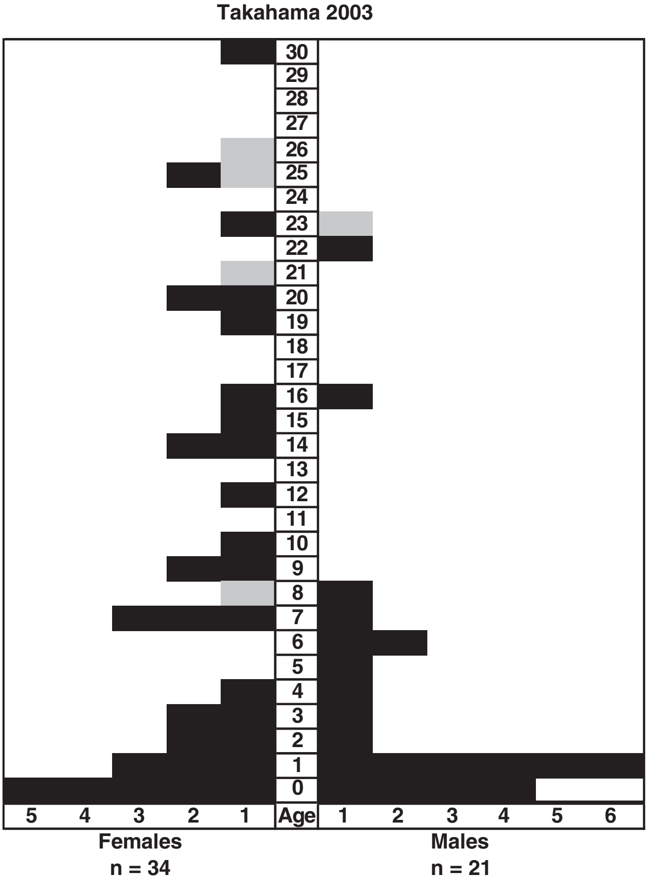

Fig. 2. Age-sex distribution of Takahama individuals. Black areas represent verified SH individuals. Gray areas represent non-SH individuals.

digital video camera (Sony Digital Handycam). The focal session was extended if SH was still in progress or started toward the end of the session. The session was extended for 5 min, but was terminated thereafter if there was no further contact with stones [Huffman, 1996]. In addition, before and after each focal session, 5-min scan samples were made to record the behavioral states of the troop as a control for average activity patterns of that time of the day for the troop. The scans were recorded on data sheets, and the observers moved from one side of the enclosure to the other so as not to sample each individual more than once. The recorded behaviors included resting, feeding, foraging, walking, grooming, playing, object handling, SH, aggression, and ‘‘other.’’ To determine the location of an SH session within the enclosure, the area was divided into 32 equal blocks labeled as a letter-number matrix. Each block was named accordingly (A1, A2, A3, A4, …, H4).

The videotapes were analyzed on a TV monitor and the duration of each focal sample, activity patterns exhibited, duration of SH bouts of each focal subject, and their location within the enclosure were recorded on the data sheets and then entered into a Microsoft Excel spread sheet for statistical analysis.

RESULTS

Prevalence of Stone Handlers and Behavioral Description

Of the 55 individuals present in the Takahama troop at the beginning of this study, 90% were verified to stone-handle at some point during the study (Fig. 2). All individuals 7 years or younger were observed to stone-handle. The oldest stone handlers present in the troop throughout the entire study were five females aged 20, 20, 23, 25, and 30 years. The five individuals that were never observed to stone-handle were all adults (four females aged 8, 21, 25, and 26 years, and one male aged 23). Only two of these individuals (the 23-year-old male and 26-year-old female) were removed before SH could be confirmed. However, we are confident that they were not stone handlers during the study because they had been observed for 4 and 6 months, respectively, prior to their removal.

In the Takahama troop, 45 SH patterns were recognized (see Table I for definitions of each behavior). This number far exceeds that reported by Huffman [1996] for Arashiyama (17 patterns) and Takasakiyama (16 patterns), even though similar methods of data collection and analysis were used. Of these behaviors, Pi, H, B, ROS, RIH, and SC were the most common, and these have also been reported as common object manipulation patterns for primates in general and macaque species in particular [Huffman, 1996; Torigoe, 1985]. Many individuals displayed all of the above-mentioned behavioral patterns when they manipulated food pellets, pieces of metal, and other novel objects they came across in the enclosure. On average, an individual was observed to perform 13.9 different behavioral patterns (SD = 5.2, n = 45) over the course of the study. Males performed an average of 15.2 patterns (SD = 4.3, n = 18), and females performed an average of 13.0 (SD = 5.6, n = 27); thus there was no statistically significant difference.

These 45 behaviors were classified into five categories according to their basic motor patterns (Table I). Of all of these behaviors, 17.7% were investigative activities. Locomotive and collecting/gathering activities accounted for 11.1%. The greatest number of behaviors were sound-producing activities, accounting for 33.3%. The majority of patterns exhibited produce sound, which can be interpreted as a possible immediate stimulus for their practice. The second-largest representative group of behaviors (26.7%) involved the manipulation of stones together with other objects.

No single individual in the troop displayed all 45 behavioral patterns given in Table I, and some were specific only to young individuals (e.g., MP, TH, PIW, WIL, RIM, RWH, ROF, and SGR) or adults (e.g., GH, SW, FLM, TR, SP, and TS). Infants at first exhibited only very basic behavioral patterns (CD, B, and H), but their number and complexity increased with time (ROS, RIH, CA, and MP). Juveniles engaged in behavioral patterns that involved more vigorous body movements (CA, TW, MP, and CL), while adults engaged in more complex manipulative behavioral patterns (e.g., PUS, F, FL, GA, and SC), as has also been observed at Arashiyama and Takasakiyama [Huffman & Quiatt, 1986].

Diurnal Variation of SH in Relation to Feeding Activity

The Takahama troop was provisioned with monkey chow only once a day in the late morning (1000–1100 hr). Only 5.6% (n = 24/434) of all SH sessions occurred between 1000–1100 hr. While SH was observed throughout the day, it occurred significantly more often in the afternoon between 1300 and 1900 hr than in the morning between 0700 and 1200 hr (Wilcoxon signed-rank test, Z = –5.36, n = 48, P = 0.001). Regardless of the provisioning time, the monkeys

TABLE I. Stone Handling Behaviors Classified by Activity Patterns

Investigative activities
Pi (Pick): Pick
H (Hold): Pick up a stone and hold it away from the body
B (Bite): Bite a stone
L (lick): Lick a stone
SN (Sniff): Sniff a stone
CD (Cuddle): Take hold of, grab or cradle a stone for a few seconds[a,b]
PIM (Put In Mouth): Put a stone in one's mouth and keep it sometime
MIM (Move inside Mouth): Make a stone move inside one's mouth with tongue or hand
Locomotion activities
MP (Move and Push): Push/pull a stone with one or both hands while working forward/backward[a,b]
GW (Grasp Walk): Walk with one stone or more in the palm of one or both hands[a,b]
CA (Carry): Carry a stone cuddled in one's hand from one place to another[a,b]
CIM (Carry in Mouth): Carry a stone in one's mouth while locomoting
TW (Toss Walk): Toss a stone ahead (repeatedly) and pick it up while walking[a,b]
Collecting/gathering activities
GA (Gathering): Gather stones into a pile in front of oneself[a,b]
PU (Pick Up): Pick up a stone and placed it into one's hand[a,b]
PUS (Pick Up a Small stone): Pick up a small stone and hold it between finger tips (like wheat grains)[a,b]
PUD (Pick Up and Drop): Pick up a stone and drop it repeatedly[a,b]
GH (Grasp with Hands): Clutch a pile of stone gathered and placed in front of one self[a,b]
Sound producing activities
ROS (Rub on Surface): Rub or roll a stone on a surface[a,b]
RIH (Roll in Hands): Roll a stone in one's hand[a,b]
RT (Rub Together): Rub stones together[a,b]
SC (Scatter): Scatter stones about, on a substrate, in front of oneself[a,b]
CL (Clacking): Clack stones together (Both hands moving in a clapping gesture)[a,b]
RWH (Rub with Hands): Hold a stone in one hand and rub it with the other[a,b]
POS (Pound on a surface): Pound a stone on a substrate
SL (Slapping): Slap or pound a stone with ones fingertips or palm of ones hand
RWM (Rub With Mouth): Rub a surface with a stone held in mouth
RIM (Rub in Mouth): Rub a stone against another held in mouth
TIM (Tap in Mouth): Put a stone in ones mouth and tap it slightly with one's finger tip or palm
FL (Flinting): Strike a stone against another held stationary[a,b]
FP (Flip): Flip a stone
SW (Swiping): Swipe stones together in a sweeping gesture
FLM (Flint in Mouth): Strike a stone against another held in mouth
Combination of stone and other object activities
PIW (Put in Water): Put a stone in water
WIL (Wrap in Leaves): Wrap stones in leaves
ROF (Rub on Fur): Rub or put a stone on one's fur
COO (Combine stones with other objects): Combine a stone with other objects that can be found in the enclosure e.g., pellets, pieces of strings, metals etc.
TH (Throw): Throw without jumping and running
SGR (Stone groom): Groom somebody with a stone
SIH (Shake in Hand): Take small stones into ones hand and shake it
W (Wash): Wash a stone in water
SP (Spin): Spin a stone with one hand or both hands
THS (Throw and Sway): Throw a stone and sway from front to back
JT (Jump and Throw): Jump and throw a stone forward or backward
TR (Run and throw): Run and throw a stone or vise versa

[a] Observed in Arashiyama.
[b] Observed in Takasakiyama.

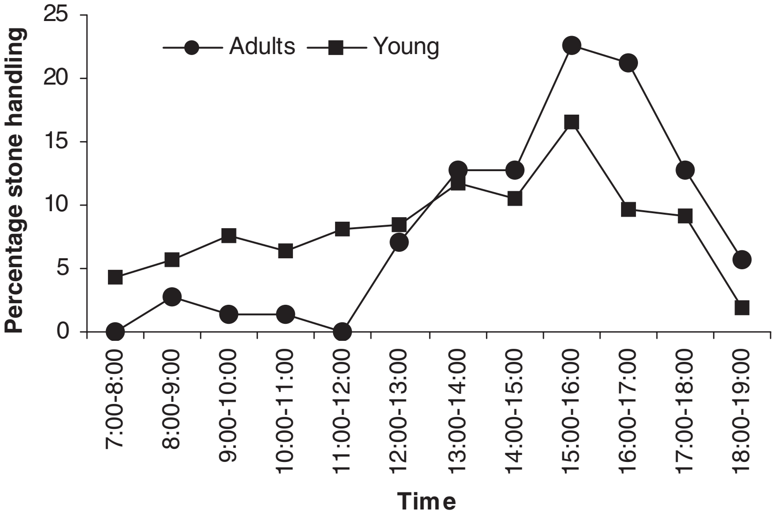

Fig. 3. Effect of age on the diurnal variation of SH.

TABLE II. Summary of Stone Handling Behavior in Different Age and Sex Categories

	Average bouts/ individual (SD)	Average time/ bout (sec)	Average frequency/ hour (SD)	Average number of patterns/ individual (SD)	n
Young	15.92 (7.76)	82.29	1.48 (0.72)	16 (4.74)	24
Adult (5–15 years)	8.81 (6.5)	136.16	0.81 (0.60)	12 (4.6)	14
Old adult (16–30 years)	9.57 (10.43)	273.68	0.89 (0.97)	10 (5.36)	7
Adult females	6.87 (7.79)	188.02	0.64 (0.72)	10 (4.36)	15
Young females	18.25 (8.03)	73	1.69 (0.75)	17 (4.94)	12
Adult males	14.33 (4.88)	180	1.33 (0.45)	15 (4.26)	6
Young males	13.58 (7.02)	94.19	1.26 (0.65)	15 (4.65)	12

were observed to have food in their mouths in only 24.0% of all recorded SH sessions. The peak time for SH was between 1500 and 1600 hr. Young individuals tended to stone-handle throughout the day, but with increasing age, adults restricted their SH more to the latter part of the day (Fig. 3). In particular, 77.8% (28/36) of all SH sessions observed in old adults occurred after 1500 hr.

Effects of Age on the Occurrence of SH

Marked age and sex class differences in the frequency of SH, number of patterns, and bouts performed were recognized (Table II). Young monkeys (0–4 years old) stone-handled significantly more often (Mann-Whitney, U = 69.5, n1 = 24, n2 = 21, $P = 0.001$) and displayed a significantly greater number of behavioral patterns compared to adults (Mann-Whitney, 0–4 years, n1 = 24, adults n2 = 21, U = 126, $P = 0.004$). This is supported by a statistically significant negative correlation between age and the number of patterns displayed (Spearman rho = –0.376, $P = 0.011$, n = 45, Fig. 4a). Similar trends were recorded in both the Arashiyama and Takasakiyama troops [Huffman, 1996].

Young individuals displayed twice as many bouts compared to adults (young mean = 15.9, SD = 7.8, n = 24, adults mean = 9.0, SD = 7.8, n = 21). A statistically significant difference was also recognized in the number of bouts performed by young and adults (Mann-Whitney, 0–4 years n1 = 24, adults n2 = 21, U = 131, *P* = 0.006). This is supported by a significant negative correlation in the average number of bouts performed by age (Spearman rho = –0.320, *P* = 0.032, n = 45; Fig. 4b).

When compared by sex, juvenile females performed the highest number of bouts per individual, and there was little difference between adult males and juvenile males. However, adult females performed the lowest number of bouts as well as the fewest number of patterns of all individuals (Table II).

Young individuals tended to exhibit many bouts of short duration, while adults exhibited fewer bouts of longer duration (Fig. 5). There was a statistically positive correlation between age and average time spent per bout (Spearman rho = 0.538, *P* = 0.001, n = 45, Fig. 4c). The time spent in a bout increased with age (Mann-Whitney, 0–4 years n1 = 24, adults n2 = 21, U = 113, *P* = 0.002).

Old adults stone-handled the longest per bout. Individuals tended to have their own specified small number of behavioral patterns, which they habitually exhibited at the same location in the enclosure. There is a statistically significant negative correlation between age and number of different places used within the enclosure to stone-handle (Spearman rho = –0.484, n = 45, *P* = 0.001; Fig. 4d). Younger individuals tended to use more different places in the enclosure than adults (Mann-Whitney, 0–4 years n1 = 24, adults n2 = 21, U = 107, *P* = 0.001).

There were no statistically significant differences between males and females in the number of bouts displayed or the average time spent per bout (bouts displayed: Mann-Whitney, males n1 = 18, females n2 = 27, U = 198.5, *P* = 0.302; average time per bout: males n1 = 18, females n2 = 27, U = 189.5, *P* = 0.215).

DISCUSSION

The results presented in this study provide us with information necessary to evaluate the possible function(s) of SH in Japanese macaques from the perspective of hypotheses proposed for object play in other species, and to formulate a relevant new hypothesis that may explain age differences in the performance of this behavior. Though many theories have been proposed regarding the function of play behavior [Smith, 1978], no single one can be applied across the board to all play behaviors in all species. Indeed, there are differences in play activities exhibited by the same species living under different environmental conditions [e.g., Ramsey & McGrew, 2005]. SH is no exception, as evidenced by the contrasts and similarities of the behavior between free-ranging and captive provisioned troops, and age-class differences within the same troop reported here.

The underlying function of play is expected to vary according to the content of the behavior itself, potential motivational differences brought about by differences in social and natural environments, and species' level characteristics. For example, Hall [1998] described object play in predatory species as boisterousness and enjoyable. However, SH in Arashiyama Japanese macaques occurs under low-arousal conditions [Huffman, 1984, 1996]. This was confirmed for Takahama macaques also, in that the frequency of SH was significantly greater on clear days than on cloudy or rainy days, as well as during warmer seasons of the year, and the monkeys suppressed SH for days following periods of

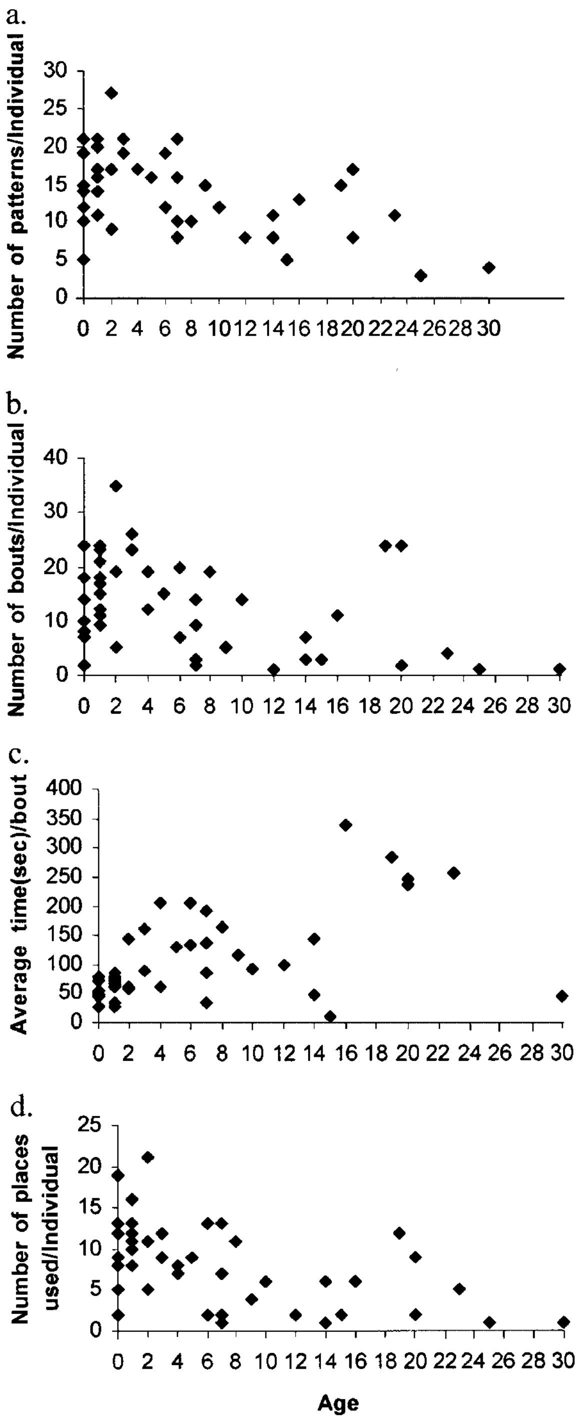

Fig. 4. Distribution of (**a**) number of patterns displayed, (**b**) number of bouts, (**c**) average time spent per bout, and (**d**) number of places used for SH by age of the stone handler.

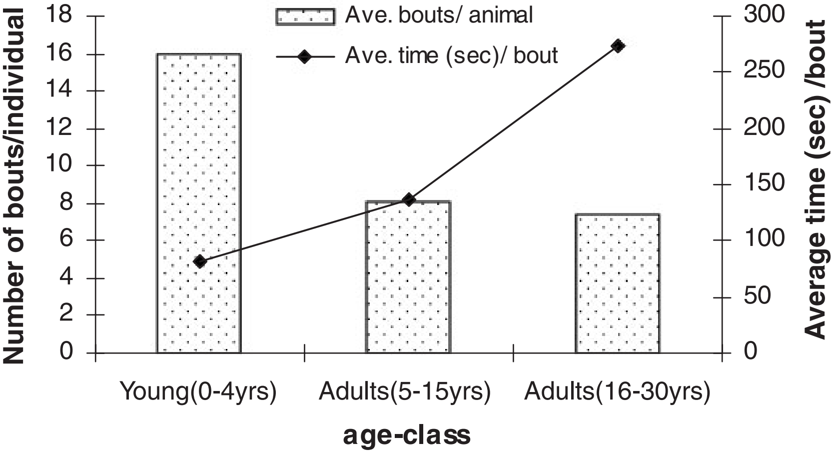

Fig. 5. Relationship between number of bouts displayed and average time spent per bout by age.

externally induced intense stress (e.g., capturing the entire troop for annual checkups, or moving a group temporarily into a new enclosure) [Nahallage, 2005] (Nahallage, personal observation).

SH, as described here, is not consistent with the misdirected foraging behavior hypothesis (pseudo-feeding behavior) proposed by Pellis [1991]. Even in provisioned free-ranging macaques (e.g., at Arashiyama and Takasakiyama [Huffman, 1984] and Shodoshima (Nahallage, unpublished data), SH occurs predominantly after feeding, not before. Therefore, we conclude that this behavior is not elicited by the anticipation of food, as has been described for captive otters and other zoo animals [Hediger, 1964; Pellis, 1991].

When we compare age-class differences in SH, the possible motivations for performing the behavior appear to differ between young and adults. This is of particular interest to us, given that the behavior is acquired only by young individuals. This leads us to speculate that unlike other play behaviors that disappear from the repertoire of most primates when they reach adulthood, presumably because they no longer serve a function, biological and cultural selective forces may be acting on individuals that have acquired the SH behavior to maintain the practice throughout life.

As regards SH in young macaques, it has been observed in many other examples of object play that young individuals are naturally curious and readily explore new objects and environments [Hall, 1998]. The immediate motivation for young to stone-handle, like any other form of object play, is most likely that it is intrinsically an enjoyable activity. Young individuals are naturally curious about what others are doing, and often desire to play with an object that has been made "popular" by others' use of it [Huffman, 1984]. At the functional level, playing with stones allows them to develop and practice the interactive use of motor and perceptual skills that support physical and neurophysiological development. In macaques, a surge of synaptogenesis occurs roughly 2 months before birth and continues up to 3 years of age [Bourgeois et al., 1994; Rakic et al., 1986]. The overall trend in the increasing complexity of SH behaviors (pattern and number of behaviors) over time from infancy into the juvenile period is consistent with this increase in neural-motor developmental activity. Young macaques displayed many behavioral patterns that required more vigorous body movements compared to adult behaviors, and performed many short bouts of SH throughout the day. These findings are consistent with Fairbanks' [2000] model describing the heightened frequency of object manipulation in correlation with synaptic development in juvenile vervets and rhesus macaques [e.g., Rakic et al., 1986]. We believe that this model is the best functional explanation for SH in young Japanese macaques.

The immediate motivation of adults to stone-handle appears to differ from that of young. With age, adults exhibit fewer bouts of longer duration, and these bouts involve relatively more complex behavioral patterns than those of the young. They concentrate on these more-demanding manipulative activities with seemingly intense concentration, often to the extent of ignoring or avoiding attempts of their offspring and other social partners to interact with them. They carry stones from various parts of the enclosure to their individually preferred locations to stone-handle in an unhurried, seemingly ''leisurely'' manner. Sometimes older individuals sit near their preferred location, waiting for others to leave, before going there to stone-handle. At Takahama SH is performed most often in the afternoon, and we suggest that adults may temporarily divert their attention away from the social interactive network of associations with others by concentrating on this solitary activity. In captive conditions, less time is required for feeding and locomotion. This leaves more time for social interactions, perhaps to the point that some animals experience a ''social overload'' by the end of the day, and adult monkeys may seek to engage in activities that divert their attention away from the routine of being in close proximity to one another.

Since adults have already acquired the necessary motor skills during early life, we propose that the ultimate function of SH differs between adults and young. However, an equally important neurophysiological benefit may be gained by adults from the practice of SH. As macaques grow older, a decline in memory and cognitive impairment, and associated pathology (e.g., senile plaque or synapse loss) of the prefrontal cortex occurs (see Hof and Duan [2001] for review). In humans, this process is similarly associated with cognitive decline, dementia, and Alzheimer's disease [Hof & Duan, 2001]. Recently a number of clinical studies have shown that elderly humans can significantly reduce the risk of acquiring such diseases by engaging in regular leisure activities involving concentrated mental activity (e.g., reading, and playing board games, cards, and musical instruments) [e.g., Verghese et al., 2003]. The neurological mechanism for this is not yet fully understood, but in simple terms, you either use it or you lose it. It has been suggested that the mental exercise of such leisure activities may stimulate new neural growth around damaged parts of the brain caused by aging [Coyle, 2003]. In fact, voluntary physical exercise has also been associated with increases in the production of brain-derived neurotrophic factor and other growth factors that stimulate neurogenesis and improved learning and mental performance in the elderly [Cotman & Berchtold, 2002; Laurin et al., 2001]. Given the close similarities in behavioral, physiological, and neurological aging processes between human and nonhuman primates [Hof & Duan, 2001], these processes of compensation for cognitive degeneration in older adult humans may be synonymous in macaques, making the potential benefits significant to all who stone-handle. A shift in the role of SH activity from neural-motor development in the young to basic maintenance in adults and regeneration of neurophysiological pathways in aging adults may be the prominent functions behind the sustained practice of this seemingly nonadaptive behavior in macaques.

SH may have significant positive implications for individuals that practice it from birth, and provide yet-unmeasured benefits if continued into old age. The benefits outlined here by the newly proposed ''neural maintenance and regeneration'' hypothesis could perhaps be partially tested by behavioral, demographic, and postmortem neuroanatomical investigations of individuals in provisioned SH and control study troops to look for possible differences in behavioral developmental rate, cognitive performance, population-level differences in longevity, and anatomical/pathological differences in the brain. This remains to be done in future studies.

For both young and adults, SH is considered the consequence of provisioning and a reflection of the spare time that is freed up from maintenance and survival activities [Huffman, 1984]. This is supported by the fact that it occurs only in captive and provisioned free-ranging troops, and not in wild troops. Differences in the relative amount of free time among captive and free-ranging troops of stone handlers are reflected by the data in various ways. In the captive Takahama troop, time spent per SH bout was significantly longer in older individuals. The opposite trend was observed in the free-ranging Arashiyama troop, where time spent per bout decreased with age and an increase in age/rank-related social activities. At Arashiyama, monkeys come to the feeding area mainly at provisioning time (four times a day), and it is after feeding that SH is most reliably seen. This is their window of free time, during which they socialize and rest before moving back into the forest [Huffman, 1984; Huffman & Quiatt, 1986]. Increased infant care within the first 6 months and the maintenance of social bonds in both males and females were two major reasons given for a decrease in SH time for adults at Arashiyama [Huffman, 1996]. However, Takahama monkeys are confined to a much smaller space without natural vegetation and are fed only once a day. This frees up significantly more time for socializing, resting, and infant care. In this light, the two different functions hypothesized here to explain why young and adults perform SH are interpreted to be due to a change in the combination of social and biological conditions associated with developmental and aging processes. To the best of our knowledge, while tool use provides important immediate gains in nutrition to those who practice it, only a few other behaviors of such potentially significant biologically adaptive value (e.g., animal self-medication [Huffman, 2001]) have been reported to be maintained within a primate group as a behavioral tradition.

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Acquisition and development of stone handling behavior in infant Japanese macaques

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Summary

In this study we systematically investigate the mode of acquisition and the developmental process of stone handling, a form of solitary object play, in a captive troop of Japanese macaques (*Macaca fuscata*) housed in an outdoor enclosure at the Kyoto University Primate Research Institute, Japan. This study was conducted to evaluate two alternative hypotheses regarding the mode of acquisition of stone handling in infants: (1) environmental stimuli (availability of and exposure to stones) and (2) social stimuli (exposure to stone handling individuals). Early exposure to stones in the environment had no significant effect on when infants acquired the behavior. No significant correlations were recognized between the age of stone handling acquisition and number of stones encountered per hour from birth to acquisition, or the time spent in a specific area of the enclosure as a function of the number of available stones therein. However, being exposed to a stone handling model(s) was a social stimulus that had an effect on the age of acquisition, with a significant negative correlation between a mother's stone handling frequency and the age of acquisition by her infant. Infants of non-stone handling mothers acquired the behavior much later than others. Infant peers who acquired stone handling earlier played no significant role as stone handling models. Of the factors tested here, the timing of acquisition depended mainly on the level of proximity to a demonstrator and the frequency at which those available demonstrators performed the behavior.

Keywords: solitary object play, proximity, behavioral model, stimulus enhancement, transmission.

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Introduction

In group-living animals, one way of acquiring a new behavior by a naïve individual is to watch an experienced individual perform it. How quickly a naïve individual can acquire the behavior depends on how frequently it can observe the experienced individual (model) perform that behavior. Therefore, for the acquisition process, proximity (tolerance of the model), frequency of the behavior performed, and the attention paid to the behavior are very important factors which increase the possibility for socially biased learning (Coussi-Korbel & Fragazy, 1995; Whiten, 2000; van Schaik, 2003; van Schaik et al., 2003; Perry & Manson, 2003; Londsdorf, 2006; Moscovice & Snowdon, 2006; Range & Huber, in press). For most behaviors, social affiliation plays an important role in the acquisition and pathway of transmission (Old World Monkeys: Kawai, 1965; Huffman & Hirata, 2003; New World Monkeys: Perry et al., 2003a,b; Chimpanzees: de Waal, 2001; Matsuzawa et al., 2001; Biro et al., 2003; Bonnie & de Waal, 2006; Dolphins: Mann & Sargeant, 2003). Affiliation can be measured as the amount of time two individuals spend in proximity to one another or engage in positive interactions (Mason, 1966; Bonnie & de Waal, 2006). Thus, individuals who have strong affiliative ties, and spend more time in proximity, are more likely to show similar behaviors.

If socially biased learning is to be evoked as the primary mode of acquisition for a given behavior, acquisition of that behavior by naïve individuals should be faster in those individuals with greater opportunity to observe and learn from experienced models (van Schaik et al., 2003; Perry & Manson, 2003). However confounding this are environmental, social, and developmental constraints that can affect the efficiency and speed by which a particular behavior is individually acquired and diffused through the group (Huffman & Hirata, 2003). When considering the acquisition of new behaviors by infants, it is assumed that the mother is the key source of information in the first few months of life due to a total dependence on her for all basic survival needs, and many of these behaviors are food related, e.g., food preferences or feeding techniques for food items difficult to eat (Hall, 1963; Itani & Nishimura, 1973; Watts, 1985; Goodall, 1986; Whitehead, 1986; Aisner & Terkel, 1992; Fragaszy & Visalberghi, 1996; Laland et al., 1996; Schuchmann, 1999).

There are some behaviors displayed by primates that do not have any direct adaptive value for the performer but are still transmitted to successive generations (Goodall, 1986; de Waal & Seres, 1997; van Schaik et al., 2003; Matsusaka et al., 2006). One such behavior acquired by infant Japanese macaques is stone-handling, which is a form of solitary object play (see Huffman, 1984, 1996; Nahallage & Huffman, 2007). In the free-ranging Arashiyama troop outside of Kyoto Japan, stone-handling behavior was first documented in 1979 as an innovation of a juvenile female. The behavior subsequently spread horizontally to peer playmates and older immature kin relatives over several years in what was termed the 'transmission phase' (Huffman, 1984). As female stone handlers matured, their infants began to exhibit the behavior within the first six months of life. It was proposed that mothers were the primary route of transmission to young during the subsequent 'tradition phase' (Huffman, 1984, 1996; Huffman & Quiatt, 1986). This makes sense, as individuals highly tolerant of each other are most likely to observe the activity of each other in more detail, affording a greater potential for learning (e.g., Huffman & Quiatt, 1986; Aisner & Terkel, 1992; van Schaik, 2003; Huffman & Hirata, 2003). Social life in group-living animals is complex, and this makes it essential to view the dynamics of social learning from the perspective of the social group's interactive network. Thus, understanding the process of acquiring stone-handling behaviors is expected to increase our knowledge on the role that demonstrators play in the learning and transmission processes of social living animals (e.g., Lefebvre, 1995).

Details of the mode of acquisition and the developmental process of stone handling have not yet been systematically clarified. This is in large part due to the difficulty of conducting systematic longitudinal observations on individuals in free-ranging troops. In captivity, there are also logistical and ethical limitations to the study of social living primate groups such as invasive manipulations to mother-infant pairs at critical periods of infant development. Working within these limitations, this study is the first to systematically investigate the acquisition and development of a behavioral tradition in a social living troop of monkeys maintained under semi-natural conditions. We adopt the Coussi-Korbel & Fragazy (1995) framework of social learning in terms of behavioral coordination between individuals, and in terms of the kind of information that may be acquired by an observer from a demonstrator without considering the underlying psychological mechanism. A captive stone-handling troop was chosen to facilitate detailed observations and environmental quantification. We examine the relative influence of an infant's exposure to stones in the environment, and the exposure to active stone handling models or demonstrators, on the acquisition and development of stone-handling behavior. We test two alternative hypotheses for the acquisition of stone handling behavior: (1) environmental stimuli hypothesis predicts that the total time spent in areas with high stone availability and, therefore, being exposed to more stones, increases the likelihood that an infant acquires stone-handling behavior and (2) social stimuli hypothesis predicts that the age at which infants acquire stone-handling behavior is influenced by the frequency the behavior is exhibited by their mothers.

Materials and methods

This study was conducted on the Takahama troop of Japanese macaques kept in a 960 m^2 outdoor enclosure at the Primate Research Institute, Kyoto University, Inuyama City, Japan. This is part of an on-going systematic study on the social, ecological and functional aspects of stone handling (Nahallage & Huffman, 2007). The data presented were collected over two study periods: June 2003 to November 2004 (18 months) and May 2005 to December 2005 (6 months). The age-sex class distribution of the troop during the study periods is given in Table 1.

All data were collected using the continuous focal animal sampling method (Altmann, 1974). Basic protocol for recording stone handling behavior in this study was adopted from Huffman (1996). In a previous study, 45 different stone handling behaviors were recorded and described (Nahallage & Huffman, 2007; see Table 2). Each focal session was recorded in its entirety by video (Sony Digital Handycam) for a minimum of fifteen minutes. The focal session was extended for 5 min if stone-handling was still in progress or began near the end of the session, and it was terminated if no further contact with stones was made. Stone-handling behavior was recorded as bouts, and a bout was defined as the continuation of the behavior with pauses of no longer than 120 s. If stone handling resumed after a 120-s pause, it was considered a separate bout (Huffman, 1996).

A total of 14 infants were born into the troop from 12 mothers during the study and observations for all were recorded. They accounted for eight mother-infant pairs in 2003 (172 h observation) and six mother-infant pairs in 2005 (72 h). With the exception of one particular mother, all mothers and

Table 1. Age/sex class distribution of individuals in Takahama troop.

Class category (Age)	Number of individuals in 2003 (No. sampled)	Number of individuals in 2005 (No. sampled)*
Adult males (over 10 years)	1 (1)	1
Adult females (over 7 years)	18 (18)	15 (6)
Adolescent males (5-9 years of age)	5 (5)	6
Adolescent females (5-6 years of age)	—	2
Juvenile males (1-4 years of age)	9 (9)	11
Juvenile females (1-4 years of age)	7 (7)	11
Infant males (0-1 years of age)	3 (3)	3 (3)
Infant females (0-1 years of age)	5 (5)	3 (3)
Total	48 (48)	52 (12)

* Only the new born infants and their mothers were sampled.

Table 2. Stone handling behavioral repertoire of the Takahama troop (modified from Nahallage, 2005; Nahallage & Huffman, 2007).

Bite: Bite a stone
Carry in Mouth: Carry a stone in one's mouth while locomoting
Carry: Carry a stone cuddled in one's hand from one place to another
Clacking: Clack stones together (Both hands moving in a clapping gesture)
Combine stones with other objects: Combine a stone with other objects that can be found in the enclosure eg. pellets, pieces of strings, metals etc.
Cuddle: Take hold of, grab or cradle a stone for a few seconds
Flint in Mouth: Strike a stone against another held in mouth
Flinting: Strike a stone against another held stationary
Flip: Flip a stone
Gathering: Gather stones into a pile in front of oneself
Grasp Walk: Walk with one stone or more in the palm of one or both hands
Grasp with Hands: Clutch a pile of stone gathered and placed in front of one self
Hold: Pick up a stone and hold it away from the body
Jump and Throw: Jump and throw a stone forward or backward
Lick: Lick a stone
Move and Push: Push/pull a stone with one or both hands while working forward/backward

Table 2. (Continued.)

Move inside Mouth: Make a stone move inside one's mouth with tongue or hand
Pick Up a Small stone: Pick up a small stone and hold it between finger tips (like wheat grains)
Pick Up and Drop: Pick up a stone and drop it repeatedly
Pick Up: Pick up a stone and placed it into one's hand
Pick: Pick
Pound on a surface: Pound a stone on a substrate
Put in Mouth: Put a stone in one's mouth and keep it sometime
Put in Water: Put a stone in water
Roll in Hands: Roll a stone in one's hand
Rub in Mouth: Rub a stone against another held in mouth
Rub on Fur: Rub or put a stone on one's fur
Rub on Surface: Rub or roll a stone on a surface
Rub Together: Rub stones together
Rub with Hands: Hold a stone in one hand and rub it with the other
Rub With Mouth: Rub a surface with a stone held in mouth
Run and throw: Run and throw a stone or vise versa
Scatter: Scatter stones about, on a substrate, in front of oneself
Shake in Hand: Take small stones into ones hand and shake it
Slapping: Slap or pound a stone with ones fingertips or palm of ones hand
Sniff: Sniff a stone
Spin: Spin a stone with one hand or both hands
Stone groom: Groom somebody with a stone
Swiping: Swipe stones together in a sweeping gesture
Tap in Mouth: Put a stone in ones mouth and tap it slightly with one's finger tip or palm
Throw and Sway: Throw a stone and sway from front to back
Throw: Throw without jumping and running
Toss Walk: Toss a stone ahead (repeatedly) and pick it up while walking
Wash: Wash a stone in water
Wrap in Leaves: Wrap stones in leaves

infants were observed to handle stones in both years. In 2005, observations were conducted in the peak period of stone handling activity for the whole troop, i.e., between 15:00 and 17:00 h (Nahallage & Huffman, 2007). In both 2003 and 2005 infants stayed very close to their mothers during their first three months of life and were, therefore, recorded together in full monitor view at all times. Mother and infant behaviors collected from the same video record were later transcribed into two separate data sheets, and considered independent of each other since different data were transcribed and analyzed for mother and infant. Infants began to move further away from their mothers after 3 months and, therefore, separate focal sessions were recorded for each at these times. Mother stone-handling frequency per hour was calculated from the transcribed focal records. An infant's proximity to other individuals, stone-handling behaviors displayed and time spent in each location of the enclosure were transcribed. Proximity was defined as being within one meter to another individual, and the identity of that individual was recorded.

For the analysis of the development of stone handling behavior in infants and a comparison with other age groups, only data from the first study period were used, and included all members of the troop. A total of 516 h of focal observations (43 focal observation sessions per individual) distributed equally across time of day (7:00 to 19:00) and season were used in the analysis.

The entire monkey enclosure floor area was divided into 32 blocks that ranged in size of 18.9 m^2 and 24 m^2, depending on the enclosure's boundaries, to determine the location of infant stone-handling bouts within the enclosure, and the relative effect of the number of stones on the first observed stone-handling behavior by individual infants. Each plot was assigned a letter and number code, e.g., A1, A2, A3, A4, etc. The enclosure had three terrace or flat areas at different elevations that were separated by two cement slopes, but stones could only be found on the flat areas. Stones were not distributed equally across all plots in the enclosure because individuals have preferred stone handling sites that they repeatedly return to (Nahallage and Huffman, 2007). In addition, inter-plot differences exist because gravitational force may contribute to the clustering of stones in certain areas. The average number of stones per plot was 604 ± 784 (range 0 to 3228). We estimated the distribution of stones in the enclosure by counting the number of stones in each block at the end of each study period, and only stones within the size range observed during stone handling, i.e., $8 \times 10 \times 7$ mm and $92 \times 62 \times 41$ mm, were counted. For data analysis we used the mean number of stones per each respective plot over the two years since there was no statistically significant difference between years in the distribution and number of stones in each block (Wilcoxon signed-ranks test: $T = 1.07$, $N = 32$, $p = 0.284$).

Non-parametric two-tailed tests were used and significance was at $p < 0.05$. SPSS (version 10) was used for analyses.

Results

Infant's proximity to the mother and other individuals

The mother was the primary determinant of an infant's early exposure to the physical and social environment. For the first three months, the average percent of time the infant spent in proximity to its mother (75 ± 12.72%, $N = 14$ infants) was greater than that spent with any other troop member (Figure 1, Table 3). Mothers kept their young infants from wandering off alone by picking them up or by holding onto a leg or arm. Thus, infants had very little contact with older juveniles or with other adults in the group during early life.

After 3 months, the average percent of time an infant spent within 1 m proximity to its mother decreased (58 ± 15.50%, $N = 14$) while proximity to peers increased (22 ± 13.23%, $N = 14$). Around this time, infants also started to interact with other members (older juveniles and adults) of the group (5 ± 3.76%). A low level of contact between infants and their siblings (2 ± 3.87%) across the first six months occurred because 6 out of 14 infants had no siblings. Siblings were between two to three years old and spent more time with their peers than with their mothers and newborn infants.

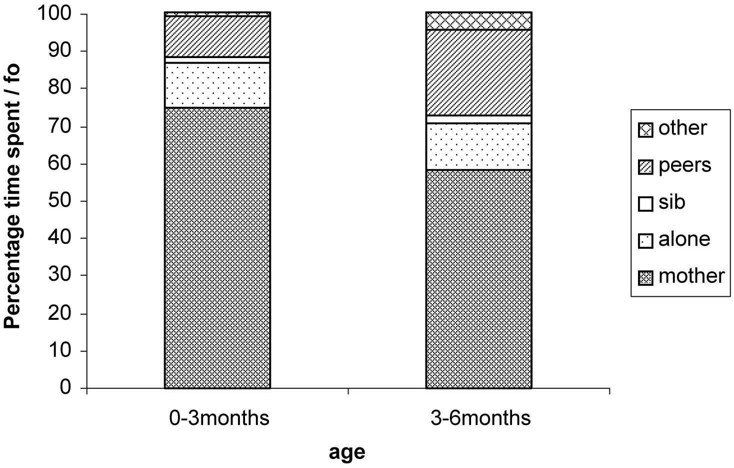

Figure 1. Infant's average time spent in proximity (1 m) to others in the first 6 months of life.

Table 3. Percentage of time spent by infants with mother, peers and others between 0-3 months and 4-6 months of life by a mother's frequency of stone handling (SH).

Age	*N*	Mother's frequency of SH	Time spent with mother	Time spent with peers	Time spent with others
0-3 months	2	High (4)	0.74	0.18	0
	10	Moderate-Low (0.05-1.09)	0.73	0.10	0.01
	2	Non-SH (0)	0.86	0.02	0
4-6 months	2	High (4)	0.78	0.13	0.05
	10	Moderate-Low (0.05-1.09)	0.54	0.25	0.10
	2	Non-SH (0)	0.59	0.20	0.01

Environmental effects on infant's acquisition of stone handling

We analyzed environmental factors that might contribute to the acquisition of stone handling. Exposure to stones in the environment did not have a significant effect on stone handling behavior (Figure 2). There was no significant correlation between the amount of time spent in plots and the approximate number of stones in plots (Spearman rank correlation: $r_S = 0.016$, $p = 0.741$, $N = 445$, Figure 2a), or the approximate number of stones encountered per hour from the time the first stone handling observation bout by an infant was recorded and the age (weeks) at which an infant was first observed stone handling (Spearman rank correlation: $r_S = 1.137$, $p = 0.641$, $N = 14$, Figure 2b). These data suggest that spending time in places with many, or few stones does not influence the timing of an infant's acquisition of stone-handling behavior.

Effect of mother's stone handling frequency on infant's age at first stone handling

All but one of the 14 infants started stone handling within the first 6 months after birth. Their age at first stone handling ranged from as early as 6 weeks to as late as 31 weeks (15.78 ± 7.0, $N = 14$). We calculated the percentile of stone handling frequencies by mothers, and individuals falling above 75 were classified as frequent stone handlers (2 mothers), while females falling below this level were classified as less-frequent stone handlers (10 mothers). One female did not stone handle and was classified as non-handler. Infants of

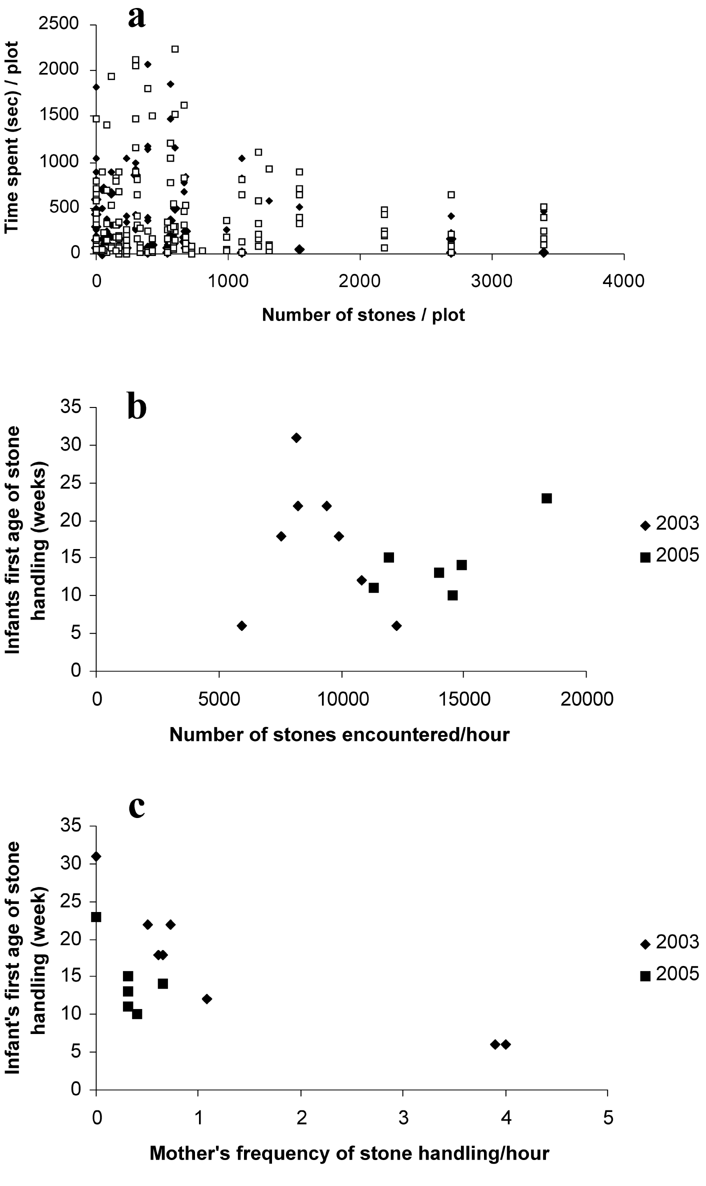

Figure 2. Relative influence of encountering stones versus exposure to active stone handling model on the acquisition of stone handling; (a) mother's frequency of stone handling bouts/h (Spearman rank correlation: $r_S = -0.630$, $N = 14$, $p = 0.016$); (b) number of stones encountered/h (pearman rank correlation: $r_S = 1.137$, $N = 14$, $p = 0.641$); (c) time spent per plot, before stone handling for the first time (Spearman rank correlation: $r_S = 0.016$, $N = 445$, $p = 0.741$).

frequent stone handling mothers generally exhibit the behavior earlier than infants of less-frequent stone handling mothers. There was a statistically significant negative correlation between the mothers' frequency of stone handling bouts per hour and the age at which infants first started stone handling (Spearman rank correlation: $r_S = 0.630$, $N = 14$, $p = 0.016$, Figure 2c). Furthermore, the average stone handling time per bout for frequent stone handling mothers was 133 ± 57.25 s (range 42-267 s, $N = 7$ bouts), and for less-frequent stone handling mothers it was 73 ± 72.95 s (range 5-194 s, $N = 16$ bouts). Also, the infants of frequent stone handling mothers were watching their mothers' stone handling in 83% (931 s) of the mother's total time handling stones, and in 75% of these stone-handling bouts they tried to take the stones away. Infants of less frequent stone handling mothers watched their mother stone handle in only 42% (1183 s) of their time handling stones, and tried to take stones away in 33% of these bouts. One effect of the difference in a mothers' stone handling frequency is that some infants have longer exposure to stone-handling, more opportunities handling stones, and more practice stone-handling than other infants.

Only three adult females out of the total 48 individuals in Takahama troop did not stone handle. Two of these three adult females were 25 and 21 years old, and gave birth for the last time in 1999 and 2002, respectively. The third, an 8 year old female is the only reproductively active non-stone handling female in the troop, and she gave birth for the first time in 2003 and then again in 2005.

The two infants of the only non-stone handling mother were the last to acquire the behavior among their peers. In the first study period, this non-stone handling mother was highly protective of her infant, which spent 88% and 70% of its time within 1 m of her in the first 0-3 month and 3-6 month periods, respectively. Consequently, the infant spent relatively little time with peers. It first displayed stone handling 31 weeks after birth, and after it had begun to spend more time with peers (13%). When this female gave birth again in the second study period, she appeared less protective and the infant spent less time in proximity after the first 3 months (3-6 months: 47%), and more than twice as much time in proximity with peers (28%) than its older sibling. This infant first displayed stone handling 23 weeks after birth, which is 8 weeks earlier than its older sibling. This finding highlights the fact that in this semi-natural troop, mothers were the primary stone-handling models for infants, and suggests that peers play a secondary role as models in the acquisition of stone handling behavior when a mother does not display the behavior. This is consistent with the hypothesized effect of early proximity to a stone-handling model on the acquisition of this behavior. Acquisition of stone handling was substantially delayed if the mother was a non-stone handler.

The infants that acquired stone handling behavior between 10 and 22 weeks spent 73% of their time in proximity with their mothers during the first 3 months, but later gradually spent more time with peers and others. Two possible sources for the acquisition of stone handling exist for these individuals: (1) the mother is the primary influence but with a lower frequency of stone handling displayed per hour; since her impact is less than high frequency stone handling mothers, it may take more time for infants to reach a critical level of exposure before acquisition, or (2) increased time spent in proximity with peers already stone handling may increase the acquisition of the behavior. However, proximity with older juveniles or other stone-handling adults was extremely low and they were not considered likely to have had any significant role in the transmission of stone handling to infants in this early period of their lives.

To evaluate the potential influence that infants which have already acquired stone-handling may have on acquisition of infants that have not yet done so, we assessed the average frequency of stone handling per hour of stone handling infants while in proximity to the non-stone handling infants. There was no significant correlation between the average frequency of stone handling infant peers per hour and the age at which the non-stone handling infant peers in proximity acquired the behavior (Spearman rank correlation: $r_S = 0.362$, $N = 10$, $p = 0.304$, Figure 3a). The average frequency of stone handling per hour and the amount of time spent in proximity to stone handling infant peers was also not correlated (Spearman rank correlation: $r_S = 0.512$, $N = 10$, $p = 0.130$, Figure 3b). These data suggest that exposure to stone handling peers had little effect on the timing of these infants' first acquisition of stone handling behavior, and that delay in acquisition was a consequence of their mother's low stone handling frequency.

The two infants of the non-stone handling mother spent more time with her than other individuals, and only displayed the behavior after 21 and 31 weeks of age, respectively, when they began to spend more time with peers. For them the primary models are definitely troop members other than their mother. In these cases, it was shown that the individuals found to be in closest proximity to the infants were their peers (Table 3).

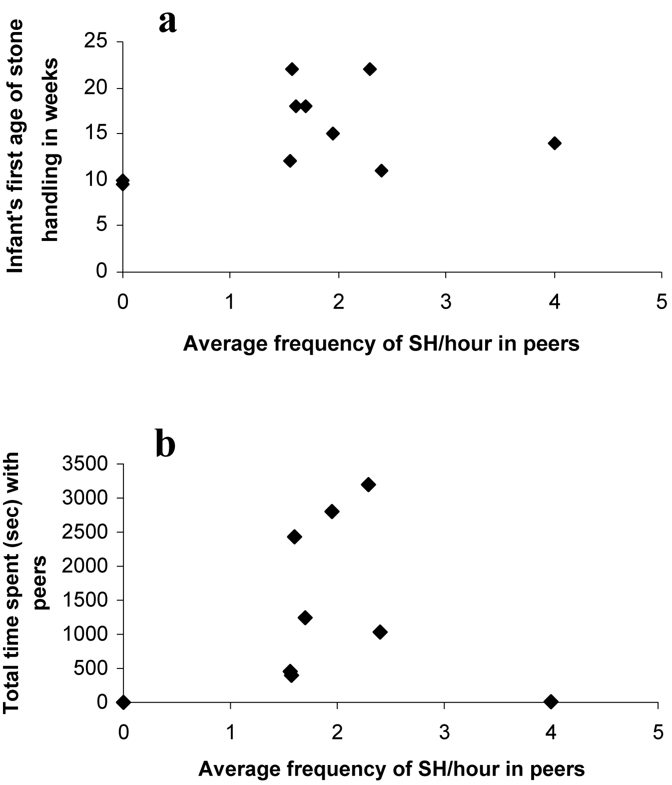

Figure 3. Influence of stone handling infant peers for the acquisition of SH by late stone handling infants; (a) peers average frequency of stone handling and infant's first age of stone handling (Spearman rank correlation: $r_S = 0.362$, $N = 10$, $p = 0.304$); (b) total time spent with SH peers (Spearman rank correlation: $r_S = 0.512$, $N = 10$, $p = 0.130$).

Development of stone handling behavior

We found a gradual increase in the number and complexity of stone handling patterns displayed by infants, which reveals a developmental phase of this behavior. During the first six months of life the average number of patterns displayed by individuals was 3.75 ± 1.90, and these simple patterns involving minimal manipulation included Pickup, Cuddling, Biting and Holding (Table 4).

After six months, individuals started to engage in more manipulative actions with stones, and the average number of patterns displayed by an individual between ages seven and twelve months increased to 8.85 ± 2.26. Patterns included combining more than one stone in the same action such as

Table 4. Development of those stone handling patterns displayed in infants over the first 18 months of life compared with juveniles.

Patterns displayed	Up to 6 months	7-12 months	13-18 months	24-48 months
Pick	x	x	x	x
Cuddle	x	x	x	x
Hold	x	x	x	x
Bite	x	x	x	x
Lick	x	x	x	x
Carry	x	x	x	x
Rub on Surface	x	x	x	x
Wrap in Leaves	x	x	x	x
Scatter	x	x	x	x
Rub in Hand	—	x	x	x
Put in Mouth	—	x	x	x
Carry in Mouth	—	x	x	x
Sniff	—	x	x	x
Rub Together	—	x	x	x
Move and Push	—	x	x	x
Grasp Walk	—	x	x	x
Clack	—	x	x	x
Rub on Fur	—	x	x	x
Combine with Object	—	—	x	x
Rub with Hand	—	—	x	x
Slap	—	—	x	x
Toss Walk	—	—	x	x
Flint	—	—	x	x
Gather	—	—	x	–
Tap in Mouth	—	—	x	x
Wash	—	—	x	x
Shake in Hand	—	—	x	x
Pick up and Drop	—	—	—	–
Pick up Small Stones	—	—	—	x
Throw stones	—	—	—	x
Flip	—	—	—	x
Pound	—	—	—	x
Move in Mouth	—	—	—	x
Rub in Mouth	—	—	—	x
Rub with Mouth	—	—	—	x
Jump and Throw	—	—	—	x
Stone Groom	—	—	—	x
Total	9	18	27	35

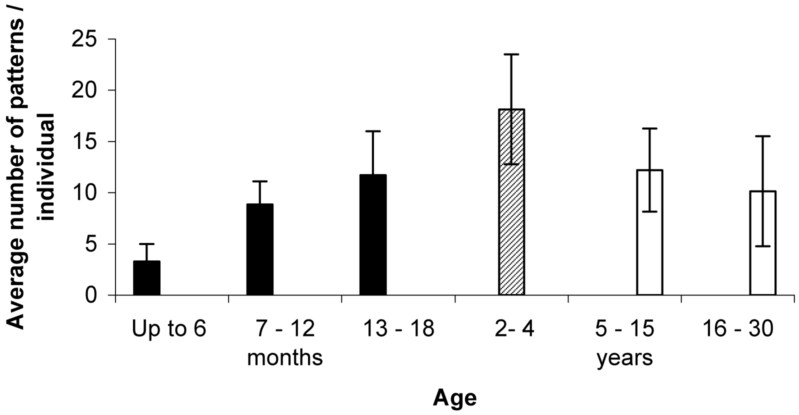

Figure 4. Comparison of average number of stone handling patterns performed by individuals during their early period of development with other age classes.

clacking or rubbing stones together, or rubbing stones on other substrates. Also, individuals started to carry stones with their hands and/or feet, and pushed them with both hands while walking (Table 4).

The average number of patterns displayed by an individual over 12 months was 11.71 ± 4.30, and the most common pattern was to combine stones with other objects. At this age individuals were more familiar with their environment and attempted to combine stones with other objects. For example, they tried wrapping leaves around stones or other metallic and plastic objects found within the enclosure. In addition, patterns such as flinting of stones together, shaking stones in the palm of the hand like dice, or washing stones in water were recorded (Table 4).

The number of behavioral patterns displayed by individuals gradually increased up to four years of age. Older juveniles displayed the highest number of patterns among all age classes, but the number of patterns displayed decreased into adulthood (Figure 4).

Discussion

Our study found no support for the effect of environmental stimuli, i.e., exposure to stones in the environment, for the acquisition of the behavior in infants. Instead, our data strongly supported the social stimuli hypothesis that predicts infants acquire stone handling behavior by means of exposure to stone handling models, i.e., the behavior is transmitted socially.

Transmission of information about a behavior from one individual to another can be addressed in two ways. One way is to identify the underlying learning mechanism involved in the information transfer such as imitation, emulation, stimulus and/or local enhancement (Whiten, 2000). Although this method is widely applied it requires controlled experimental settings, which are difficult to achieve in field studies (Perry & Manson, 2003) or in situations where separation of individuals from others in their social group is not preferred. The second complementary and equally important approach is to explore not how, but from whom a behavior is learned, and traditionally this has been addressed with observational methods (Kawai, 1965; Huffman, 1984; Hirata et al., 2001; Perry et al., 2003a,b; Lonsdorf et al., 2004).

There are no records of when stone handling started in the Takahama troop studied, but at the time the research presented here was being conducted the oldest stone handling individual was 30 years old. Long-term observations at Arashiyama suggest that individuals do not acquire the behavior after the age of 5 (Huffman, 1996), and if conditions were similar in our Takahama troop, it is likely that stone handling started nearly 25-30 years ago. Presently, and similar to the Arashiyama population, all the newborn infants and individuals in Takahama below the age of 7 stone-handle, and the behavior is passed down from older to younger individuals in each successive generation. Thus, our data suggest that stone handling has reached the 'tradition phase' in the Takahama group (see Huffman, 1984, 1996).

The proximity to an available model and the frequency of the behavior displayed by that model plays an important role in the process of acquiring stone handling behavior by infants. Infants are capable of 'copying' the behaviors of close associates even though they do not obtain any reward for performing them (Biro et al., 2003). The model for infants is frequently the mother since it is constantly exposed to the behaviors that she displays during the critical period of its early development. This motivation for wanting to act like the mother is explained as "education by master-apprenticeship". For example, chimpanzee infants are driven to copy not by motivation for food but simply to copy their mother's actions due to the strong affectionate bond of young with their mother and because of the mother's consistent tolerance toward her infant (Matsuzawa et al., 2001). This phenomenon is also described as Bonding and Identification-based Observational Learning (BIOL), where an infant's learning is "born out to be like others" (de Waal, 2001, p. 231). When the mother displays the behavior frequently and for a longer time the infant has more opportunity to observe her than an infant whose mother does not display the behavior as often and for a shorter time, or not at all. This is in agreement with van Schaik et al. (2003) in saying that the speed of acquisition of a behavior depends on the rate it was performed. The infant's desire to take part in the mother's action, by trying to take the stones from her, may result in stimulus enhancement learning. As a result, those infants were observed to stone handle considerably earlier. Stimulus enhancement (Spence, 1937; Thorpe, 1956) occurs when a naive animal is attracted to the object, or type of object that a conspecific has been manipulating. When the mother infant bond is strong and proximity is high, it leads to the infants' repeated observation and sometimes taking part in its mother's activity (Hirata & Celli, 2003). This gives the opportunity for stimulus enhancement and social facilitation. Similarly, Coussi-Korbel & Fragazsy (1995) stated that one of the first requirements for the occurrence of social learning is a stimulus that draws the naïve individual's attention and provide it with the information. This information could be provided from one animal to another through three forms of stimulation namely affective, physical and active stimuli. In the case of stone handling, though all three forms likely contribute, the most obvious form of stimulation may be affective stimuli produced by the percussive sounds of stone handling that draws an infant's attention to the mother's action. Coussi-Korbel & Fragazsy (1995) go on to say that if individuals can spend a long time in proximity they are more likely to acquire specific behavioral patterns from each other. That is the more frequent a certain behavior is displayed the more chance the naïve individual has to acquire it (van Schaik et al., 2003). Hence from our study we can say that it is not only proximity to a model but also the frequency that stone-handling behavior is displayed by the model that is important for acquisition. In the case of our study, mothers were the primary source of an infant's early information about stone handling. This form of information transmission is known as vertical/traditional transmission, in which information is transmitted from parent to offspring (Cavalli-Sforza & Feldman, 1981). Coussi-Korbel & Fragazsy (1995) named this type of learning as 'directed social learning' (i.e., "social learning that occurs differentially as a function of the identity of the active individual", p. 1444). According to them, the moderately hierarchical social system and strong matrilineal relationships prevailing in Japanese macaque society could assist directed social learning among group members.

In natural conditions an infant generally first acquires information about a behavior from its mother, but in situations where the mother does not display the behavior, an infant must acquire the information from another individual with whom it spends adequate time in proximity. In our study the other individual(s) were mainly peers. For example, the two infants born to the mother that did not display stone handling were the last among their peers to acquire the behavior, and did so only after they started interacting with other individuals that did stone handle. The difference in timing of acquisition of these two siblings, born in consecutive years, was also dependent on the relative amount of time each spent with stone handling peers versus their mother. The second infant spent more time with peers than the first infant and, as predicted, acquired the behavior considerably earlier. Similarly, at Arashiyama, the behavior first diffused among the young troop members, i.e., from a juvenile female to her peers and kin of relatively the same age (Huffman, 1984). In this case, because none of the mothers exhibited the behavior, it could only spread horizontally from the innovator to other young playmates.

The social learning process of stone handling in infants cannot be explained in terms of true imitation (reproducing the exact behavior of the model) since when stone-handling was first acquired infants did not display the same behavioral patterns as their mothers, and developmental constrains are considered to prohibit this possibility. Our data show that there is a gradual increase in the number and complexity of patterns displayed, and this varies according to age (Table 4). In general, immature primates need relatively long maturation periods to master tasks that require complex sensory-motor actions (Boinsky & Fragaszy, 1989; Visalbergi & Fragaszy, 1990; Drapier & Thiery, 2003). Among primates, the index of dexterity and the use of relatively independent finger movement (RIFM) is thought to reflect the degree to which motoneurons innervating the muscles acting on hand and fingers receive direct, monosynaptic projections from the cerebral cortex (Phillips, 1971; Kuypers, 1981; Bortoff & Strick, 1993). It is known that the earliest sign of RIFM occurred at 2-3 months, with mature patterns at 7-8 months (Lawrence & Hopkins, 1976; Olivier et al., 1997). Galea & Darian-Smith (1995) recently reported that performance on a reach and grasp test by a group of young macaques approach adult levels by 6 months. These results agree with our observations of the development of stone handling behavioral patterns. Although the infants in our study acquired the basic stone handling behaviors at around 2-3 months, they only started to display more demanding manipulative patterns from around 6 months. Even though the cortico-motoneuronal projections, responsible for RIFM, develop rapidly in the first neonatal months, they do not mature fully until the second year of life (Armand et al., 1996). This explains the observed increase in the number of stone handling patterns up to 3-4 years of age. The increase in the number of behaviors displayed with increasing age and the level of dexterity required to perform them are evidence in support of a gradual refinement of neuromotor skills over the first 18 months of an infant's life. Juveniles displayed the greatest number of behavioral patterns. By this age they are highly active and explorative by nature as well as physiologically capable of generating many different stone handling behavioral patterns. Combined, these factors could contribute to this increase in behavioral patterns displayed. Fragaszy & Adams-Curtis (1991), discuss this in terms of generativity aspects of object manipulation in tufted capuchin monkeys.

In general, as stone handling is not a means to an immediate functional end, there are no specific affordences guiding which behavioral patterns should be displayed over others. However, the fact that there is significant inter-site variation in the stone handling behavioral patterns displayed by Japanese macaques (Leca et al., 2007) suggests that innovation of new stone handling behavior patterns can occur. Given motoneuronal developmental constraints in the young and a trend toward increasing behavioral conservatism in adults, we predict that in the case of stone handling, the route of transmission (vertical or horizontal) of such new behavioral patterns is likely to be determined by the level of behavioral dexterity required to display the behavior and the social interactive network of the innovator. Investigation into the propagation of such new behaviors is needed to test this prediction in more detail.

Active teaching of stone handling to infants was not observed, unlike nut cracking in Tai chimpanzees (Boesch, 1991) or prey-handling skills in wild meerkats (Thornton & McAuliffe, 2006). However on rare occasions at both Takahama and Arashiyama when an infant approaches its mother while she is stone handling, she throws a stone towards it or allows the infant to take stones from her. The infants pick up these stones and start to stone handle. While anecdotal, such generalized actions of the mother are expected to increase an infant's opportunity and motivation to interact more with stones.

In conclusion, we can state that for stone handling, social learning in the form of stimulus enhancement plays a role in the acquisition of the behavior by infants. At this stage however, we do not rule out the possibility of true imitation of new behaviors or individual learning for the acquisition of behavioral variants between individuals of sufficient motorneuronal development to perform them. More detailed observations and analysis of this aspect is now underway. The timing of acquisition depends mainly on two factors, proximity to a demonstrator and the frequency at which the primary demonstrator performs the behavior. Mothers were found to be the primary models for infants, with the exception of those infants whose mother did not display stone handling behavior. Another factor that may contribute to acquisition is the degree of a mother's willingness to let the infant interact with others. Individual differences in the exposure to stones and their distribution in the environment did not influence the acquisition of stone handling.

Generalizing from our study, we conclude that acquisition of many socially learned behaviors can occur along multiple pathways from a variety of potential demonstrators. This may vary according to the phase of transmission of the behavior within the population, i.e., transmission, tradition, transformation (Huffman & Quiatt, 1986), the nature of the behavior, the individual's stage of social and physical development and, availability of appropriate and reliable models. The fabric of social life in-group living animals is indeed complex. The rules of social learning too are complex, making it essential to view the dynamics of social learning from the perspective of the social group's interactive network.

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Cultured Monkeys

Social Learning Cast in Stones

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ABSTRACT—*Sixty years ago, the notion that animals could have culture was unthinkable to most behavioral scientists. Today, evidence for innovation, transmission, acquisition, long-term maintenance, and intergroup variation of behavior exists throughout the animal kingdom. What can the longitudinal and comparative study of monkeys handling stones tell us about how culture evolved in humans? Now in its 30th year, the systematic study of stone-handling behavior in multiple troops of Japanese macaques has shown that socially mediated learning is essential to explain the spread, persistence, and transformation of individual behavioral innovations among group members. The integrative research paradigm presented here can be applied to the study of various candidate behavioral traditions in other species.*

KEYWORDS—*solitary object play; socially biased learning; development; behavioral tradition; cultural zones*

The concept of culture (also referred to as behavioral tradition) in animals was first proposed in 1952 by the founder of primatology in Japan, Kinji Imanishi, who predicted that culture should be present in all socially living animals. The first evidence for culture in primates came shortly thereafter from field research on Japanese macaques. The innovation by the juvenile female "Imo," for washing sandy sweet potatoes in seawater, and the behavior's subsequent transmission widely within the group (Kawai, 1965), is now a frequently cited example for social learning and culture in animals.

Evidence now exists for socially mediated learning and culture in many species including the great apes, New World monkeys, rats, cetaceans, birds, and fish (see Fragaszy & Perry, 2003). All of these studies have looked at determinants of cultural behavior, including innovation, transmission, acquisition, developmental constraints thereof, long-term maintenance, and intergroup variation. However, none have considered the role of all of these factors within an integrated framework of social learning.

There are two basic approaches to the study of social learning. The first focuses on underlying mechanisms—that is, *how* the information is transferred between two individuals. In a controlled experimental setting, a naive subject, faced with a problem-solving task, is given the opportunity to observe an experienced subject and learn from its behavioral strategies (Custance, Whiten, & Fredman, 1999). The second approach focuses on the pathway of behavioral diffusion under natural conditions in a stable social group—that is, *from whom* the information is transferred (Biro, Inoue-Nakamura, Yamakoshi, Sousa, & Matsuzawa, 2003). Interindividual tolerance allowing spatial proximity, frequency of the behavior performed, and the attention paid to the behavior are essential factors to predict the speed of diffusion of a novel behavior and pathway of transmission (Coussi-Korbel & Fragaszy, 1995; Huffman & Hirata, 2003; van Schaik, Fox, & Fechtman, 2003). However, not only social, but also environmental, demographic, and developmental constraints can affect the efficiency and speed of acquisition and diffusion of a particular behavior (Huffman & Hirata, 2003). Only the study of stone handling (SH) in Japanese macaques has embraced all of these determinants into the understanding of a single cultural behavior. Our long-term study supports the idea of SH culture and provides insights into the nature of social learning, its role in the spread of behavioral innovations, and the importance of culture in the process of behavioral evolution.

SH is a seemingly nonadaptive, solitary object-play activity (Huffman, 1984, 1996; but see Nahallage & Huffman, 2007a). SH consists of manipulation of stones in various ways, including rubbing or clacking them together; pounding them onto other hard surfaces; picking up and rolling them together in the hands; and cuddling, carrying, pushing, or throwing them (Fig. 1; Box 1). Currently, 45 different behavioral patterns are documented in Japanese macaques (Leca, Gunst, & Huffman, 2007a).

SH occurs in four captive troops and six provisioned free-ranging troops across Japan. This behavior has been followed for 30 years across multiple generations in the Arashiyama troop, Kyoto, Japan, beginning from its innovation in 1979 by a juvenile female named "Glance 6476" (Huffman, 1984;

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Fig. 1. **Four stone-handling behaviors: (a) carry, (b) clacking, (c) rub on surface, and (d) rub together.**

Huffman, 1996). Unlike potato washing, SH was first transmitted horizontally among playmates. Transmission began to occur vertically from elder to younger individuals around 1984. Since then, SH has been acquired by every infant in the group, but it was never acquired by individuals over 5 years of age in the years right after the behavioral innovation.

BOX 1

Representative Stone-Handling Behaviors

MP (Move and Push): Push/pull a stone forward/backward with one or both hands while walking
GW (Grasp Walk): Walk with one stone or more in the palm of one or both hands
CA (Carry): Carry a stone cuddled in one's hand from one place to another
GA (Gathering): Gather stones into a pile in front of oneself
ROS (Rub on Surface): Rub or roll a stone on a surface
RT (Rub Together): Rub stones together
RWH (Rub With Hands): Hold a stone in one hand and rub it with the other
SC (Scatter): Scatter stones about, on a substrate, in front of oneself
CL (Clacking): Clack stones together (both hands moving in a clapping gesture)
FL (Flinting): Strike a stone against another held stationary
POS (Pound on a Surface): Pound a stone on a substrate

ACCESS TO DEMONSTRATORS BY NAIVE INDIVIDUALS AND THE ACQUISITION OF BEHAVIORS

This long-term study at Arashiyama allows us to understand the pathways of diffusion of SH. Mothers were presumed to be the primary source of an infant's early exposure to SH (Huffman, 1984, 1996). Through controlled captive conditions, we were able to systematically evaluate the effect of pivotal individuals as demonstrators on the initial acquisition and development of SH behavior by focusing on interindividual interactions, particularly mother–infant pairs. We (Nahallage & Huffman, 2007b) studied a group of 48 Japanese macaques at the Primate Research Institute, Kyoto University, for 24 months spanning two breeding seasons over a 3-year period, during which 14 infants were born. In these 14 mother–infant pairs, all but one infant started SH within the first 6 months after birth. There was great variability among them in the age SH was first displayed (6–31 weeks). During their first 3 months of life, infants spent 75% of the time within 1 meter of their mother, significantly more time than they spent with other individuals. This high level of proximity to the mother had a significant impact on the age at which SH was acquired. Infants of mothers with higher SH frequencies exhibited the behavior earlier than did infants of less frequent SH mothers. Two infants born in consecutive years to the same non-SH mother were the last to acquire the behavior. These results suggest that the acquisition of SH behavior in infants was strongly influenced by the amount of time spent in proximity to a stone handler and the frequency of the behavior displayed by that model. Infants of frequent SH mothers spent twice as much time (83%) watching their mothers when she engaged in that behavior than did infants whose mother showed low SH frequency (42%). The former tried to take stones away from their mothers in 75% of the SH bouts whereas the latter tried to do so in only 33% of these bouts, resulting in a difference in the amount of time an infant took part in its mother's activity. Differences in mothers' SH frequency could affect their infants' exposure to SH, opportunities of handling stones, and practice of SH.

FACTORS RESPONSIBLE FOR INTERGROUP VARIATION

To better understand how the SH culture in Japanese macaques may appear, spread, and be maintained within a group over generations, we (Leca, Gunst, & Huffman, 2007a) investigated the roles of social and demographic factors in explaining intergroup similarities and differences in SH. We conducted a systematic comparison of SH in 10 troops of Japanese macaques, including two troops studied over a long period of time at Arashiyama and Takasakiyama. The analysis of 1,950 hours of observation revealed substantial variability in the frequency and form of SH between the troops. Most of the 45 SH patterns we documented were customary in some troops and rare or even absent in others even though they were ecologically possible (Leca, Gunst, & Huffman, 2008).

When we only considered the 33 SH patterns that were not observed in all 10 troops studied, we found cultural similarity to be significantly related to geographic proximity. Neighboring troops living at the same site, with overlapping home ranges and coming into occasional contact around the provisioning site—where SH activity most often occurs—tended to share similar SH patterns. The numbers of patterns showing the same occurrence in the two troops at Shodoshima and in the two troops at Takasakiyama were 26 and 25, out of 33, respectively. We propose the phenomenon of cultural zones, based on intertroop observation and possibly males transferring SH patterns when migrating from one troop to another. When such intertroop social influences do not exist (e.g., troops separated by substantial geographic distance in natural situations or by artificial barriers like concrete walls in captive conditions), the troops showed more differences in their SH repertoires: Their mean number of behaviors showing the same frequency of occurrence was only 12.1 ± 7.3.

To test the hypothesis that SH will be more prevalent in more cohesive groups, we calculated, for the 10 study troops, a group-level index of social tolerance, defined as the mean percentage of group members within 1 meter of each other, and recorded every 15 minutes by the observer visually or physically moving from one side of the troop to the other, in a set direction. Group-level social tolerance was not significantly correlated with the frequency and rate of diffusion of SH (Leca, unpublished data). In other words, the troops showing higher levels of positive social interactions (e.g., grooming and playing) were not necessarily the troops with more frequent episodes of SH and higher percentages of stone handlers. Instead, group size and group spatial cohesion after food provisioning was positively correlated with the prevalence of SH. Larger troops characterized by closer physical proximity among individuals feeding on provisioned food also showed higher percentages of troop members exhibiting SH simultaneously, which may reveal the contagious nature of play (Leca, Gunst, & Huffman, 2007b).

Another demographic factor, age structure of the group, may also affect the diffusion and maintenance of SH. Troops with abnormal age structure (e.g., missing age classes) showed a lower proportion of stone handlers and a lower frequency of SH than did more normally age-structured groups (Leca, Gunst, & Huffman, 2007b). These findings are consistent with long-term observations at Arashiyama suggesting that (a) after initial innovation by youngsters, SH behavior first spreads among young individuals, probably peer playmates; (b) there is a critical period after which SH cannot be acquired by an individual (> 5 years); and (c) when a behavioral practice is restricted to a particular class of group members, its propagation should be slow and its maintenance may be jeopardized (Huffman, 1996).

At Arashiyama and Takasakiyama, the SH culture has at least a 30-year history. By using similar methods of data collection in these troops, 13 and 15 years apart, respectively, we found that the size of the SH repertoire almost doubled in both troops. The SH patterns not recorded before involved complex manipulative actions, such as combining stones with other objects and grooming with a stone (Leca, Gunst, & Huffman, 2007a). These longitudinal data suggest a "ratchet effect," defined as an increase in the diversity and complexity of SH patterns compared to earlier generations of stone handlers. As the duration of a group's experience with SH increases, so does the variety of patterns displayed, possibly as a product of an increase in the number of "individual contributions" to the group's behavioral repertoire, which gradually diffuse through the group (e.g., shake-in-hands and stone-throwing patterns in the Takahama group).

Our comparative approach revealed that intergroup variability in SH may be best explained by demographic factors, opportunities for observational learning, and behavioral coordination at the group level.

CONSTRAINTS OF NEUROMOTOR DEVELOPMENT ON THE EXPRESSION OF SH BEHAVIORS

Few longitudinal studies have been conducted on the ontogeny of specific cultural behaviors; most research has tended to deduce development from cross-sectional observations (Lonsdorf, 2005). Furthermore, neuromotor development has rarely been considered as a constraint in the expression of matched behavioral patterns between experienced and naïve individuals. Our study shows that, though mothers have a strong influence on infants' initial acquisition of SH behavior, infants do not perform the same behavioral patterns as adults, mainly because of developmental constraints in the kinds of behaviors they can perform (Nahallage & Huffman, 2007b). There is a gradual increase in the number and complexity of SH patterns displayed by infants, which reveals a neuromotor developmental phase of this behavior. The infants we studied acquired the basic SH behaviors at around 2 to 3 months. Common to other behavioral traits observed during the early stages of infant development in macaques, stone-manipulation patterns are simple actions—mainly, picking them up or cuddling, licking, or biting them. Such actions are typically short in duration. Infants do not perform any complex manipulative action with stones during this time. The average number of patterns performed by an individual up to 6 months of age was 3.75 ± 1.90. Around 6 months, individuals started to perform clacking or rubbing two stones together or on a substrate. On average, they displayed 8.85 ± 2.26 patterns from 6 to 12 months of age. The earliest sign of relative independent finger movement occurs at 2 to 3 months, with mature patterns occurring at 7 to 8 months (Bortoff & Strick, 1993). Galea and Darian-Smith (1995) reported that performance on a reach-and-grasp test by a group of young macaques approached adult levels by 6 months. This agrees with our study showing infants starting with only the very basic SH behaviors between 2 and 3 months and performing activities that requires firm grasp of the stones around 6 months. Though the motoneuronal projections responsible for finger movement develop rapidly in the first months after birth, they do not mature until the second year of life. This explains the increase in the number of SH patterns up to 3 to 4 years of age. Older juveniles displayed the highest number of patterns among all age classes (18.14 ± 5.38), whereas the number of patterns displayed decreased into adulthood, which may reveal the appearance of individual preferences or behavioral routines over the years (Nahallage & Huffman, 2007b).

We concluded that at the time of acquisition, infants acquire a rudimentary form of SH but are constrained from matching specific behaviors due to their level of neuromotor development. Our findings support juvenile-primate developmental theories (Pereira & Fairbanks, 1993). Later on, however, this kind of matching does appear to occur, and is noticeable particularly in rare behaviors displayed by the mother, which are now being seen to diffuse among offspring and others.

FUTURE DIRECTIONS

SH is one of the longest-studied cultural behaviors in animals to date. Research on this behavior in both captive and free-ranging groups of monkeys has opened up new ways of addressing the complexities of learning in socially living animals through a deeper understanding of the dynamics of behavioral transmission. In order to understand the mechanisms associated with socially biased learning, future studies need to integrate this methodology with controlled experimentation on captive groups. This will allow us to more clearly address behavioral innovation and the underlying mechanism of diffusion within social groups.

Object manipulation provides a pool of behavioral variants that, if fortuitously reinforced, can become tool-use patterns. Long-term observations and documentation of the transformation of behavioral patterns are important to fully appreciate the potential transformation of noninstrumental use of objects into their instrumental use as tools. Longitudinal studies of SH already suggest that this could happen. The recent emergence of a unique behavior, stone throwing, may serve to augment the effect of intimidation displays. Research on such transformations may shed light on the evolution of stone-tool use in early hominids.

Recommended Reading

Fragaszy, D.M., & Perry, S. (Eds.). (2003). (See References). A collection of papers reviewing the current state of knowledge on animal traditions.

Huffman, M.A. (1984). (See References). The first detailed published account of SH in Japanese macaques.

Moscovice, L.R., & Snowdon, C.T. (2006). The role of social context and individual experience in novel task acquisition in cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour*, *71*, 933–943. Recent research article detailing the role of social attention in the acquisition of behaviors, of interest to those contemplating social-learning studies.

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Of Stones and Monkeys: Testing Ecological Constraints on Stone Handling, a Behavioral Tradition in Japanese Macaques

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KEY WORDS stone availability; terrestriality; culture; *Macaca fuscata*

ABSTRACT Japanese macaques are known to manipulate stones by displaying various seemingly functionless behavioral patterns, including carrying a stone, rubbing two stones together, or gathering several stones into a pile. This form of solitary object play called stone handling (SH) is a behavioral tradition in Japanese macaques, showing striking intertroop differences in frequency and form. Here, we evaluated two ecologically based hypotheses invoked to account for these differences. We hypothesized that the occurrence and form of SH would be affected by stone availability and the degree of terrestriality. We used standardized sampling methods to assess differences in SH and terrestriality among four captive and six free-ranging troops of Japanese macaques, and determine site-specific stone availability. Although we demonstrated that SH is almost exclusively a terrestrial activity, our comparative analyses showed that the number of stones readily available and the relative amount of time spent on the ground by the macaques were not associated with the intertroop differences in the occurrence of SH. Failure to accept the terrestriality and stone availability hypotheses suggests that the performance of SH and the motivation to engage in this activity are both more diverse and more complex than the direct links to time spent on the ground or the number of stones locally available. Other environmental influences and sociodemographic factors should be jointly considered to identify the sources of variation in SH, as a beginning to better understand the constraints on the appearance and subsequent diffusion of stone-use traditions in nonhuman primates. Am J Phys Anthropol 135:233–244, 2008. ©2007 Wiley-Liss, Inc.

During the past decade, primatologists have found evidence of interpopulational behavioral differences in several nonhuman primate species (e.g., McGrew et al., 1997; Whiten et al., 2001; Panger et al., 2002; van Schaik et al., 2003; Leca et al., 2007a). When obvious genetic and ecological causations can be ruled out, such behavioral variation is largely considered cultural (often labeled "traditional" in ethology). In recent years, attempts have been made to study such variability in behavioral traditions between populations, using similar methodologies, and in conjunction with rigorous documentation of the ecological context of occurrence of the behavior in question (Perry, 2003). The comparative method mainly involves accumulating information about several groups and then correlating specific environmental conditions with the populations' attributes, to draw conclusions concerning the ecological factors responsible for promoting the evolution of the phenomenon under study (Fragaszy and Perry, 2003).

Early studies have documented some features of the physical environment that favor the evolution of tool use in primates (see Beck, 1980, for a review). The critical ecological conditions are "embedded food" and "environmental opportunity" (Beck, 1980, p. 190 and 193; see also Parker and Gibson, 1977; Hamilton et al., 1978). According to the former, a diet including foods protected by hard husks or encased inside woody substrates requires extractive foraging techniques, among which tool use may have been promoted as an adaptive behavioral innovation (Beck, 1980), According to the latter, for a tool-related behavior to evolve, the environment must make it not only advantageous, but also possible. If the animals have more time to manipulate objects readily available in their habitat, they have more opportunities to discover a novel tool pattern (Hamilton et al., 1978; Beck, 1980).

Recently, these plausible explanations of how ecological factors may constrain the emergence of stone-tool use traditions in nonhuman primates have been integrated into three major hypotheses. First, the "necessity hypothesis" (after Fox et al., 2004) proposes that primary resource scarcity may force group members to exploit novel food sources that require the invention of new food-processing techniques, including the use of stones as tools to extract food from a substrate. For example, seasonal variation in main food abundance may explain

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the appearance of nut-cracking for oil-palm kernels as backup embedded foods in Bossou chimpanzees (Yamakoshi, 1998).

Second, the "stone availability hypothesis" (derived from the "environmental opportunity conditions": Beck, 1980, and the "opportunity hypothesis": Fox et al., 2004) proposes that favorable local conditions, such as the abundance of loose stones suitable to manipulation, enhance chances for stone-tool invention via repeated exposure to stones, and acquired familiarity with stone-related behaviors through the integration of stones with various daily activities. For instance, the common occurrence of *Coula* nut-cracking in Taï chimpanzees may correspond to the concomitant presence of stones, transportable by hand, as appropriate natural hammers, surface roots as adequate anvils, and *Coula* nuts, a staple food resource at this site (Boesch and Boesch, 1984).

Third, the "terrestriality hypothesis" proposes that engaging in various activities on the ground, rather than in the trees, increases an individual's chance of coming across stones, also present on the ground. This may provide significant opportunities for stone-tool use, such as the seed-cracking behavior observed in the brown capuchins of the Caatinga dry forest (Visalberghi et al., 2005). However, Beck (1980) highlighted the difficulty of associating terrestriality and tool use in primates. In some cases, time spent on the group may not be sufficient to account for the emergence of stone-tool behavior (Lee and Moura, 2005).

In primates, most cases of material culture and the majority of reported behavioral innovations involving stones occur under the context of foraging, probably because information about food is critical to every individual (see Reader and Laland, 2001 for a review). Instead of being labeled "cultural," some group-specific foraging variants could be more parsimoniously explained on ecological grounds, because of subtle site-specific differences in food, object and substrate availability (Laland and Hoppitt, 2003; Galef, 2004; Laland and Janik, 2006). In contrast, behaviors unrelated to subsistence, such as communicative signals, are likely to be more flexible in form and less affected by ecological differences than food-related behavioral traditions, and in that sense, they would make better candidates for culture (Perry et al., 2003; Moura, 2007).

The best-documented case of a nonsubsistence traditional activity in monkeys is stone handling (SH hereafter) in Japanese macaques, a form of solitary object play consisting of the manipulation of stones by performing various behavioral patterns (Huffman, 1984, 1996; Huffman and Quiatt, 1986; Huffman and Hirata, 2003; Leca et al., 2006, 2007a; Nahallage and Huffman, 2007a). For example, individuals in different troops may be observed repeatedly pounding a stone on a substrate, clacking two stones together, or gathering several stones into a pile in front of them. SH mainly occurs and is more frequent in young than in older individuals. SH episodes are shorter, more vigorous, and SH patterns are more diverse and less complex in immature than in mature individuals (Nahallage and Huffman, 2007a; Leca et al., in press). These age-related differences in the performance of SH could be attributed to possible age-specific benefits of this activity. As a form of object play strenuously performed by young monkeys, SH may promote the development of motor skills in immature systems (Nahallage and Huffman, 2007a). As a psychologically relaxing activity in older monkeys, SH could contribute to slow the impairment of cognitive functions in aging individuals (Nahallage and Huffman, 2007a).

In free-ranging provisioned troops, most SH activity occurs immediately after provisioning time, while monkeys chew cereal grains stored inside their cheek pouches (Huffman, 1984; Huffman and Quiatt, 1986; Leca et al., submitted[1]). In contrast, SH in captive troops can be observed throughout the day, regardless of feeding activity (Nahallage and Huffman, 2007a; Leca et al., submitted). Previous findings from two troops of free ranging and one captive troop of Japanese macaques showed that SH is socially transmitted from generation to generation as a behavioral tradition (Huffman, 1984, 1996; Huffman and Quiatt, 1986; Huffman and Hirata, 2003; Nahallage and Huffman, 2007b). A recent interpopulational comparison of this behavior from a systematic investigation of four captive and six free-ranging troops of Japanese macaques reported major differences in the frequency of occurrence and the form of SH, and discussed the phenomenon of cultural zones (Leca et al., 2007a).

The ecological factors that contribute to these differences require investigation. While the "necessity hypothesis" is relevant to explain tool-use traditions, which are behavioral adaptations potentially critical to individual survival (e.g., Whiten et al., 2001; van Schaik et al., 2003), it can be a priori ruled out to explain variation in SH behavior, which is regarded as the noninstrumental manipulation of stones with no direct survival value (Huffman, 1984, 1996; Leca et al., 2007a). Although SH does not meet the descriptive criteria of Beck's (1980) definition of tool use, the daily practice of stone-related combinatorial patterns by most members of a group could be considered as a behavioral precursor to the possible use of stones as tools (Huffman and Quiatt, 1986; Huffman, 1996; Leca et al., 2007a). Because stone-tool behaviors in nonhuman primates may reflect on the origin and evolution of lithic technology in hominids (Foley and Lahr, 2003), it is critical to identify the environmental sources of SH variation in Japanese macaques. However, the most obvious ecological differences which could affect SH, such as site-specific availability in stone number and size, and the degree of terrestriality of individuals have not been studied.

The present study is the first to use an intertroop comparative approach to explore ecological constraints on SH activity in Japanese macaques. On the basis of extensive research showing that SH may be affected by nonecological factors such as troop size, age-related differences, and social proximity (Leca et al., 2007a, in press; Nahallage and Huffman, 2007b), it is reasonable to assert that SH is not purely a function of stone availability and access to stones. However, variability in these environmental conditions may contribute to account for the major intertroop differences in SH (cf. Leca et al., 2007a). The goal of this study is to evaluate the influence of stone-related ecological factors on the occurrence and form of SH.

On the basis of 1) the fact that SH involves particular objects present in the local environment (i.e., stones), 2) the assumption that SH is primarily a terrestrial activity, and 3) the finding that Japanese macaques (*Macaca fuscata*) are considered semiterrestrial, behaviorally in-

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[1] Leca J-B, Gunst N, Huffman MA. Influence of food provisioning on the transformation phase of the stone handling tradition in Japanese macaques. Submitted for publication.

termediate between arboreal long-tailed macaques (*M. fascicularis*) and terrestrial pig-tailed macaques (*M. nemestrina*) (Chatani, 2003), we tested the two following hypotheses: 1) the "stone availability hypothesis," stating that the number and size of stones readily available in the local environment provides various SH opportunities, affecting the occurrence and form of the SH behavior, and 2) the "terrestriality hypothesis," proposing that the degree of terrestriality of individuals contributes to explain differences in the occurrence and form of SH. The two hypotheses are not mutually exclusive, since they both relate to the relative opportunity to encounter stones. Failure to accept these hypotheses would imply that the performance of SH and the motivation to engage in this activity are better explained by sociodemographic factors and ecological factors that are not stone-related than the number of stones locally available and the time spent on the ground.

Our specific objective was to test a series of predictions derived from these hypotheses. On the basis of the "stone availability hypothesis," we tested the following predictions. First, the availability in stone number should be positively correlated with the occurrence of SH namely SH frequency, prevalence, and diffusion rate (Prediction #1a), the persistence and diversity of SH namely SH duration, number of phases, pattern turnover, and number of different patterns (Prediction #1b), the number of stones used during SH bouts (Prediction #1c), and the frequency of SH patterns typically involving a great number of stones, such as gathering or scattering (Prediction #1d). Second, the availability of stones belonging to different size categories should be associated with the frequency of use applied to the stones in each size category during SH bouts (Prediction #2). On the basis of the "terrestriality hypothesis," we tested the following predictions. First, among all major activities, SH should be most often performed on the ground (Prediction #3). Second, the occurrence, persistence, and diversity of SH should be positively correlated with the time spent on the ground at the group level (Prediction #4a) and at the individual level (Prediction #4b).

To address these questions, we compared 10 troops of Japanese macaques by using a standardized observation procedure to assess quantitative differences and similarities across troops in the frequency, prevalence, and diffusion rate of SH, as well as the duration, sequence, and diversity of SH patterns. We used ecological sampling methods to determine the site-specific availability in stone number and size, and the degree of terrestriality at the activity, group, and individual levels.

METHODS

General study conditions

The species under study was the Japanese macaque (*Macaca fuscata*). The first two authors, occasionally assisted by M.A.H. and C.A.D. Nahallage observed a total of 10 troops at six geographically isolated sites in Japan from August 2003 to February 2005 (Fig. 1). Four troops lived in large outdoor enclosures in Inuyama, Aichi Prefecture (Kyoto University Primate Research Institute: Arashiyama = Ara.A, Wakasa = Wak.A, Takahama = Takh., and Japan Monkey Centre Yakushima macaques = JMC), and six troops were free-ranging (Koshima, Miyazaki Prefecture = Kosh., Arashiyama, Kyoto Prefecture = Ara.E, Shodoshima, Kagawa Prefecture = Sho.A and Sho.B, Takasakiyama, Oita Prefecture = Tak.B and Tak.C). This research was conducted in accordance with PRI's Rules and Guidelines for Animal Health and Welfare.

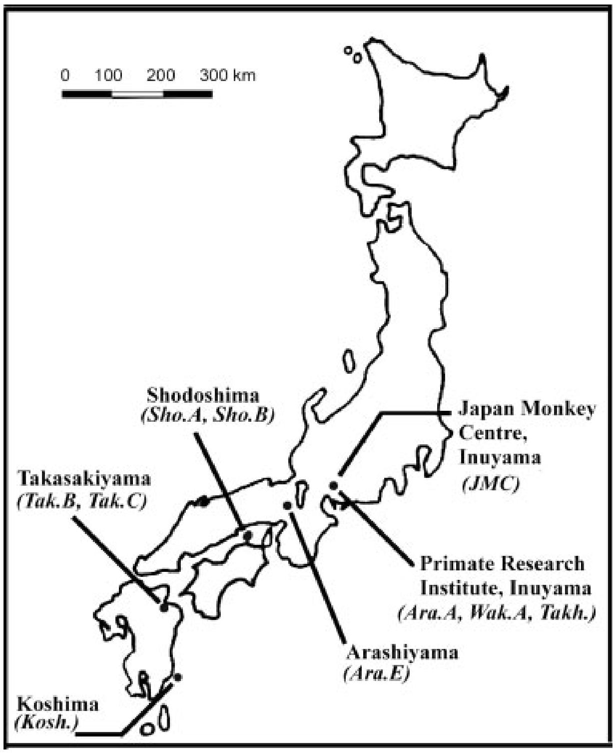

Fig. 1. Map of study sites in Japan, with abbreviations of studied troops mentioned in parentheses.

In Table 1, we present the general study conditions, including the troop ranging conditions, surfaces of enclosures or feeding sites, troop size, study periods, and number of observers. Captive animals were mainly supplied with commercial primate pellets, vegetables or fruits, scattered throughout large areas inside enclosures. Free-ranging troop members gathered regularly around feeding sites where they were artificially provisioned with cereal grains by technicians of the Koshima Field Station, Kyoto University or by the staff of monkey parks (Kosh., Ara.E, Sho.A, Sho.B, Tak.B, and Tak.C troops). Free-ranging animals were mainly supplied with cereal grains scattered throughout the feeding site.

Various stones occur at all study sites. A variety of vertical settings were present in the outdoor enclosures including climbing structures (e.g., metal or wooden rods, chains, ropes, spinning wheels, etc.), platforms, roofs, and elevated shelter boxes. Free-ranging troops could also use many vertical structures surrounding the feeding sites, either artificial structures such as roofs and wall ledges, or natural ones such as bushes and trees. There was no dramatic change in the environmental conditions of each troop over the past decade, including site-specific stone availability (e.g., stones artificially brought or removed by humans) and vertical settings.

The detailed distribution of all troop members according to age and sex classes is described elsewhere (Leca et al., 2007a, in press). Individual identifications were possible for only some of the study troops (Ara.A, Wak.A, Takh., Kosh., and Ara.E), and for them the exact age in years of each individual and their respective matrili-

TABLE 1. *Inter-troop comparison of study conditions and total data sets*

Troop name and ranging conditions	Surface of enclosure (CP) or feeding site (FR) in m^2	Study period	Observers	TS	TOT	FT	NS	SH Bt (F)	SH Bt (CAL)	SH Bt (IAL)
Arashiyama A (Ara.A), CP	850	Sep–Dec 2003	NG	18	179.9	140	644	14	1	28
Wakasa A (Wak.A), CP	500	Aug–Nov 2003	NG	19	224.6	174.5	809	59	62	224
Takahama (Takh.), CP	960	Sep–Dec 2003	JBL	46	449.2	353.6	1,593	309	28	1,252
Japan Monkey Centre (JMC), CP	4,000	Aug–Dec 2003, Mar–Apr 2004	JBL, NG	102	99.1	54.4	275	22	99	91
Koshima (Kosh.), FR	1,000	Jan–Feb 2004	JBL, NG	88	339.7	215.4	252	9	14	7
Arashiyama E (Ara.E), FR	400	May–Aug 2004	JBL, MAH,[a] CN[a]	141	431.3	160.6	1,010	317	35	579
Shodoshima A (Sho.A), FR	1,200	Feb 2005	JBL, NG, CN	450	77.6	16.8	66	30	10	27
Shodoshima B (Sho.B), FR	1,200	Feb 2005	JBL, NG, CN	350	51.5	1.3	42	4	26	67
Takasakiyama B (Tak.B), FR	1,000	Dec 2003 – Jan 2004	JBL, NG	438	22.8	0.0	58	n.a.	59	75
Takasakiyama C (Tak.C), FR	1,000	Dec 2003 – Jan 2004	JBL, NG	676	73.8	0.0	72	n.a.	182	391

In parentheses: abbreviation of troop name; CP: captive troop; FR: free-ranging troop; TS: troop size (number of troop members aged at least one year); TOT: total observation time in hours; FT: focal time (total duration in hours of focal sessions); NS: number of scan sessions; SH Bt (F): number of SH bouts collected during focal (F) sessions (n.a.: not available); SH Bt (CAL): number of SH bouts collected during complete *ad libitum* (CAL) sessions; SH Nt (IAL): number of SH notes collected during incomplete *ad libitum* (IAL) sessions.

[a] Occasionally assisted by M.A.H. and Mrs. Charmalie Nahallage. The first two authors were the main observers.

neages were known. For the other troops (JMC, Sho.A, Sho.B, Tak.B, and Tak.C), every sampled subject was labeled according to its age and sex class. Observations were conducted between 7:00 a.m. and 6:00 p.m. Visibility was excellent. We sampled captive troop members from observation platforms overhanging the enclosures. Free-ranging troop members could be approached and sampled within 3–5 m.

Data collection

We used the same observation procedure for all troops, except Tak.B and Tak.C (see below for details). The two main observational methods used were continuous focal-animal sampling and instantaneous group scan sampling (Altmann, 1974). Behavioral data collection was supplemented with *ad libitum* sampling when necessary (Altmann, 1974). We also collected data about a particular environmental feature which we proposed could have an influence on the occurrence and form of SH namely stone availability.

Focal sampling. We video-recorded every focal session with Sony digital video cameras (DCR-TRV22 and DCR-TRV33). Whenever possible, the focal individual was filmed head on and about one-meter square in-frame. We focused on all the behaviors and interactions of the focal individual. Since the field observation conditions did not allow us to use a totally random focal sampling method, we selected the focal individual using a semirandom procedure. The daily observation period was divided into 1-h blocks. We selected the focal individual, independently of its activity, in an ordered list of temporarily undersampled individuals or members of each age and sex class, when focal subjects were not individually identified.

We recorded the starting time of each focal session. Following protocol used in previous surveys carried out at Takasakiyama and Arashiyama (see Huffman, 1996), the typical duration of a focal session was 15 min. If the focal individual performed SH activity during the last 2 min of this period of time, the observation was extended for 5 min and ended thereafter unless SH was still in progress.

Scan and ad libitum samplings. Before and after each focal session, the troop was scanned to assess terrestriality at the group level and for evidence of any SH activity. All individuals located above 1-m height were labeled "off the ground," whereas others were labeled "on the ground." For each scan sampled stone handler, we recorded individual identity or age and sex classes, and whenever possible the SH patterns observed (see Leca et al., 2007a for a comprehensive list of SH patterns). The observer recorded scans on data sheets, visually scanning across the enclosure for captive troops, or by walking from one side of the free-ranging troop to the other, in a set direction, so that each individual was sampled only once in a given scan session.

To supplement each troop's data set, observers devoted an average of 38.8% ± 31.8% of total observation time to the collection of *ad libitum* data on individuals performing SH. Whenever possible, *ad libitum* sessions were video-recorded or otherwise, collected on notepad. For Tak.B and Tak.C troops, we did not collect focal sessions, but only video-recorded *ad libitum* sessions during the periods after feeding, when SH is most likely to occur (Huffman, 1996). In some cases, we were able to record complete *ad libitum* sessions. The sampled individual was filmed through the entire sequence of SH, from start (a few minutes after provisioning time, immediately after it left the feeding site and picked up or touched stones) to finish (5 min after the last stone was discarded). When a SH episode was recorded on notepad or when the sampled individual was not filmed through the entire sequence of SH, we referred to the *ad libitum* session as incomplete.

Site-specific availability in stone number and size. We assessed availability of stones (estimate abundance) at each site by using the quadrat method (Krebs, 1999). A total of ten 1-m^2 quadrats were alternately drawn on each side of a 10-m transect. In each quadrat, we counted the number of stones bigger than 2 mm × 2 mm × 2 mm. Likewise, we drew three 10-m transects at and around the feeding site of each study site. We estimated the site-specific availability in stone number by calculating the average number of stones per meter square, based on a total of thirty 1-m^2 quadrats surveyed. In these quadrats, we also randomly sampled the type of stones present (e.g., quartzite, granite, schist, sandstone, pumice, pebble and concrete block).

We estimated the site-specific availability in stone size from standardized video quadrats, defined as still images extracted from video-recorded focal sessions or, when not available, video records of SH bouts. In each video quadrat, the only filmed individual (always a juvenile) was located at the center of the image in a sitting posture, zoomed on about one-meter square in-frame, with no object or background blocking the view of the ground. We used particular parts of the sampled subject's hand (finger width, palm surface, and hand total length) as standards to estimate the size of stones present around it. We ascribed the stones to four size categories: S1 (2–10 mm), S2 (11–50 mm), S3 (50–100 mm), and S4 (more than 100 mm).

To test the reliability of the estimation of stone size from video records, we used a sample of stones collected in the field ($N = 86$, 19 S1 stones, 38 S2 stones, 24 S3 stones, and 5 S4 stones, respectively) and compared the estimated sizes with the actual sizes of the stones obtained by using a caliper. We found good correspondences between sizes estimated from video records and actual sizes: 100% for S1 and S4 stones, 95% for S2 stones, and 92% for S3 stones. In each video quadrat, we checked for the presence of at least one S2, S3, and S4 stones, and at least a dozen of S1 stones. We added up the frequency of presence of stones for each size category out of 100 randomly chosen video quadrats per study site (Qd_{S1}, Qd_{S2}, Qd_{S3}, and Qd_{S4}, respectively). We ascribed the same values of site-specific availability in stone number and size to the free-ranging troops living at the same site.

Data analysis

On the basis of video-records, J.-B.L. transcribed each focal session onto a data sheet and measured the duration to the second of all activities (feeding, foraging, locomoting, resting, socializing, SH, nonstone object exploring, and other), as well as each SH pattern, and the time spent on and off the ground. Data were then entered into a computer for processing.

We distinguished two types of SH records: SH bouts collected from focal sessions or complete *ad libitum* video-recorded sessions, and SH notes collected from scan sessions or incomplete *ad libitum* sessions. We defined a SH bout (Huffman, 1996) as the display of SH activity with possible pauses of no longer than 120 s. If the individual resumed SH within 120 s after pausing, then the two SH episodes were defined as two SH phases within a single SH bout. If SH was resumed more than 120 s after pausing, this would mark the start of a new SH bout. To assess the occurrence of SH at the group level, we used three variables namely SH frequency, prevalence, and diffusion rate. To describe the form of SH at the group level, we used six variables namely SH persistence, repetitivity, pattern turnover, pattern diversity per bout, pattern inclusive diversity, and pattern frequency (Table 2).

TABLE 2. Definition of different variables representing SH occurrence and form

Variable	Definition
SH occurrence	
Frequency[a]	Average number of SH bouts per focal hour
Prevalence	Mean percentage of stone handlers among individuals sampled in scan sessions
Diffusion rate	Total percentage of stone handlers per troop (either exactly calculated from SH bouts and notes in troops with individually identified members, or estimated by dividing the maximum number of stone handlers by the average number of unidentified troop members sampled during post-provisioning scans: cf., Huffman, 1996; Leca et al., in press)
SH form	
Persistence[b]	Mean duration of SH bouts in seconds
Repetitivity[b]	Average number of SH phases per SH bout
Pattern turnover[b]	Average number of changes in the sequence of SH patterns performed per SH bout
Pattern diversity per bout[b]	Average number of different SH patterns performed per SH bout
Pattern inclusive diversity[c]	Total number of different SH patterns observed in each troop or individual
Pattern frequency	For each SH pattern, average number of occurrence in 10 min of SH phases

[a] Were derived from all focal sessions and all troop members were considered.

[b] Were derived from all SH bouts available and only verified stone handlers were considered.

[c] Were derived from all SH bouts and SH notes available.

Number and size of stones handled. To test possible troop-specific preferences in the number of stones used during SH bouts, we calculated for each troop the frequency of SH bouts in which one or two stones were handled ($Nb_{1/2}$), from 3 to 5 ($Nb_{3/5}$), 6 to 10 ($Nb_{6/10}$), and more than 10 stones were handled (Nb_{+10}). These four categories are mutually exclusive. Regarding the size of stones, we also calculated the number of SH bouts during which one S1, S2, S3, or S4 stone was handled at least once ($Nb_{S1,}$ $Nb_{S2,}$ $Nb_{S3,}$ or $Nb_{S4,}$ respectively and not mutually exclusive).

Data sets and statistical analysis. In Table 1, we present the total data sets for each studied troop. We defined the total troop observation time as the total time spent observing each troop, including focal time, scan time, and time spent collecting *ad libitum* data. The cumulative time of multiple observers, when present, was calculated for total troop observation time. For the anal-

TABLE 3. Results of Spearman rank-order correlation tests (one-tailed) at the group level between site-specific availability in stone number (average number of stones/m^2) or troop-specific terrestriality (mean percentage of time spent on the ground drawn from focal sessions and mean percentage of troop members on the ground drawn from scan sessions) and different variables representing SH general occurrence and form in each corresponding troop

				Troop-specific terrestriality					
	Site-specific availability in stone number			Mean percentage of time on the ground			Mean percentage of troop members on the ground		
Variables	N	r_s	P	N	r_s	P	N	r_s	P
SH occurrence									
Frequency	7	0.429	0.169	7	0.321	0.241	7	0.321	0.241
Prevalence	10	0.421	0.113	7	0.285	0.213	10	0.285	0.213
Diffusion rate	10	0.000	0.500	7	−0.321	0.241	10	−0.297	0.202
SH form									
Persistence	10	0.396	0.128	7	0.429	0.169	10	0.358	0.155
Repetitivity	10	0.551	0.056	7	0.321	0.241	10	0.467	0.087
Pattern turnover	10	0.476	0.082	7	0.500	0.127	10	0.553	0.050
Pattern diversity per bout	10	0.506	0.068	7	0.500	0.127	10	0.532	0.064
Pattern inclusive diversity	10	0.291	0.207	7	−0.396	0.190	10	0.079	0.414

yses about the mean percentage of time spent on the ground at the group level, we drew on all focal sessions. To assess terrestriality at the individual level, only individuals with more than 120 min of focal data were considered. The Sho.B, Tak.B, and Tak.C troops were excluded from these analyses because focal data were insufficient or not available. Among the other troops, focal sessions lasting less than 15 min (i.e., when the focal subject was lost) were excluded from these analyses. We drew on all SH bouts available for analyses on the number and size of the stones handled. For analyses about the mean percentage of troop members on the ground, we drew on scan sessions. For captive troops, we only used scan sessions in which at least 80% of troop members were sampled. For free-ranging troops, we only considered scans sessions taking into account at least 60% of troop members. Individuals aged less than 1 year were not taken into account in the analyses.

We verified interobserver reliability using the kappa coefficient of Cohen (1960). On the basis of individual identities, activities, and interactions, we found $k = 0.92$ between the first two authors. We tested possible correlations between site-specific stone availability or terrestriality at the group and individual levels, and the different variables representing the occurrence and form of SH, by using a series of Spearman rank-order correlation tests (one-tailed, on the basis of directional hypotheses). To evaluate the relationship between site-specific availability in stone sizes and the corresponding troop preference in stone sizes, we used Kendall rank-order correlation tests (two-tailed). To assess troop preferences in the number of stones used during SH bouts, we used χ^2 goodness-of-fit tests. To test the association between troop-specific preference in the number of stones handled and site-specific stone availability, we used a χ^2 test of independence from a contingency table. For *post hoc* examination of χ^2 tests, we calculated the adjusted standardized residuals, and considered statistically significant those values of z-scores that were $\geq |1.96|$. Statistical analyses were performed using the SPSS 12.0 analytical program. Significance levels were set at $\alpha = 0.05$.

RESULTS

Stone availability hypothesis

Stones were available at all sites, but stone availability was highly variable according to the study site (average number of stones/m^2: Kosh. = 3; Takh. = 81; JMC = 92; Sho.A/Sho.B = 192; Ara.A = 236; Wak.A = 410; Tak.B/Tak.C = 620; and Ara.E = 855).

Prediction #1a: Number of stones and SH occurrence. We found no statistically significant correlation between site-specific stone availability and the different variables representing the occurrence of SH in each corresponding troop namely SH frequency, prevalence, diffusion rate (Table 3).

Prediction #1b: Number of stones and SH persistence and diversity. We found no statistically significant correlation between site-specific stone availability and the different variables representing the general form of SH in each corresponding troop namely SH persistence, repetitivity, pattern turnover, and pattern diversity per bout, and pattern inclusive diversity (Table 3). However, it should be noted that in a few instances, the P values were very close to 0.05 (e.g., repetitivity: $P = 0.056$ and pattern diversity per bout: $P = 0.068$).

Prediction #1c: Availability in stone number and number of stones handled. We found that each of the seven troops with sufficient data (more than 30 SH bouts) presented a strongly significant preference in the number of stones used during SH bouts (χ^2 goodness-of-fit tests, df = 3, Wak.A: $Nb_{1/2} = 89$, $Nb_{3/5} = 24$, $Nb_{6/10} = 5$, $Nb_{+10} = 3$, $\chi^2 = 161.02$, $P < 0.001$; Takh.: $Nb_{1/2} = 221$, $Nb_{3/5} = 58$, $Nb_{6/10} = 35$, $Nb_{+10} = 23$, $\chi^2 = 303.46$, $P < 0.001$; JMC: $Nb_{1/2} = 101$, $Nb_{3/5} = 11$, $Nb_{6/10} = 5$, $Nb_{+10} = 4$, $\chi^2 = 221.58$, $P < 0.001$; Ara.E: $Nb_{1/2} = 53$, $Nb_{3/5} = 32$, $Nb_{6/10} = 59$, $Nb_{+10} = 208$, $\chi^2 = 222.75$, $P < 0.001$; Sho.A: $Nb_{1/2} = 7$, $Nb_{3/5} = 5$, $Nb_{6/10} = 2$, $Nb_{+10} = 26$, $\chi^2 = 35.40$, $P < 0.001$; Tak.B: $Nb_{1/2} = 3$, $Nb_{3/5} = 1$, $Nb_{6/10} = 9$, $Nb_{+10} = 46$, $\chi^2 = 90.63$, $P < 0.001$, Tak.C: $Nb_{1/2} = 13$, $Nb_{3/5} = 13$, $Nb_{6/10} = 18$, $Nb_{+10} = 138$, $\chi^2 = 251.10$, $P < 0.001$). *Post hoc* examination of residuals showed that members of the captive troops (Wak.A, Takh., and JMC) were more likely to use fewer (one or two) stones over more than two stones, whereas members of the free-ranging troops (Ara.E, Sho.A, Tak.B, and Tak.C) were more likely to use a great number of stones (more than 10).

To test whether such troop preferences in the number of stones handled may also be related to stone availability, we conducted a χ^2 test of independence based on a contingency table representing the frequency of SH bouts involving different number of stones in two conditions of stone availability namely low (less than 250 stones/m^2, three captive and three free-ranging troops) and high (at least 250 stones/m^2, one captive and three free-ranging troops) (Table 4). We found a significant association between stone availability and the number of stones used during SH bouts (N = 1,280 SH bouts, Pearson χ^2 = 330.44, df = 3, P < 0.001). *Post hoc* examination of adjusted standardized residuals showed that when stone availability was low, significantly more SH bouts involved one or two stones and fewer involved more than 10 stones, whereas when stone availability was high, significantly more SH bouts involved more than 10 stones and fewer involved one or two stones. In total, these four cells accounted for 96.4% of the χ^2 value.

TABLE 4. Contingency table representing the frequency of SH bouts involving different number of stones (one or two, three to five, six to ten, and more than ten stones, respectively) in two conditions of availability in stone number, namely low (less than 250 stones/m^2) and high (at least 250 stones/m^2)

Availability in stone number	Number of SH bouts involving different number of stones			
	$Nb_{1/2}$	$Nb_{3/5}$	$Nb_{6/10}$	Nb_{+10}
Low (<250 stones/m^2)	370 (8.9)*	85 (1.9)	50 (−1.6)	61 (−9.9)*
High (>250 stones/m^2)	158 (−8.0)*	70 (−1.8)	91 (1.4)	395 (8.8)*

Adjusted standardized residuals are mentioned in parentheses and asterisks represent statistically significant values.

Prediction #1d: Number of stones and frequency of SH patterns involving numerous stones. This correlation between the number of stones readily available for the monkeys and the number of stones actually used by them during SH bouts led us to test a possible association between stone availability and the frequency of occurrence of particular SH patterns. Among the most representative SH patterns (recorded at least once in five of the 10 study troops), we tested the correlations between the pattern frequencies in each troop and the site-specific stone availability (Table 5). The SH patterns whose frequency presented a significant positive correlation with stone availability were patterns involving a great number of stones, either collected and manipulated simultaneously as a pile (GA, GH, PU, SC) or integrated one by one as part of a locomotion sequence (GW), or by sets of two stones successively handled then discarded (RT). All other SH patterns generally involved one or few stones and were not positively correlated with the site-specific stone availability.

TABLE 5. Relationships between pattern frequencies of the 25 most representative SH patterns[a] *and site-specific availability in stone number*[b]

Category name (code)	Definition	r_s	P
Investigative activities			
Bite (B)	Bite a stone	−0.677	0.016*
Hold (H)	Pick up a stone in one's hand and hold on to it, away from the body	0.085	0.407
Lick (L)	Lick a stone	−0.204	0.286
Move inside mouth (MIM)	Make a stone move inside one's mouth with tongue or hands	0.039	0.457
Pick (P)	Pick up a stone	0.069	0.425
Put in mouth (PIM)	Put a stone in one's mouth and keep it sometime	−0.125	0.365
Sniff (SN)	Sniff a stone	−0.232	0.260
Locomotion activities			
Carry (CA)	Carry a stone cuddled in hand from one place to another	−0.390	0.132
Carry in mouth (CIM)	Carry a stone in mouth while locomoting	−0.241	0.251
Grasp walk (GW)	Walk with one or more stones in the palm of one or both hands	0.628	0.026*
Move and push/pull (MP)	Push/pull a stone with one or both hands while walking forward/backward	−0.519	0.062
Toss walk (TW)	Toss a stone ahead (repeatedly) and pick it up while walking	0.099	0.393
Collection or gathering activities			
Cuddle (CD)	Take hold of, grab or cradle a stone against the chest	−0.189	0.300
Gather (GA)	Gather stones into a pile in front of oneself	0.585	0.038*
Grasp with hands (GH)	Clutch a stone or a pile of stones gathered and placed in front of oneself	0.665	0.018*
Pick up (PU)	Pick up a stone and place it into one's hand	0.707	0.011*
Percussive or rubbing sound producing activities			
Clack (CL)	Clack stones together (both hands moving in a clapping gesture)	−0.086	0.407
Combine with object (COO)	Combine (rub or strike) a stone with an object different from a stone (piece of wood, metal, etc.)	−0.052	0.443
Flint (FL)	Strike a stone against another held stationary	0.122	0.368
Pound on surface (POS)	Pound a stone on a substrate	0.044	0.452
Rub/roll on surface (ROS)	Rub or roll a stone on a substrate	−0.409	0.121
Rub stones together (RT)	Rub stones together	0.673	0.017*
Scatter (SC)	Scatter stones about, on a substrate, in front of oneself	0.616	0.029*
Other complex manipulative activities			
Roll in hands (RIH)	Roll a stone in one's hands	−0.043	0.453
Rub with hands (RWH)	Hold a stone in one hand and rub it with the other (like potato-washing)	−0.364	0.151

* P < 0.05.

[a] Defined and categorized according to general activity patterns: after Leca et al., 2007a; Nahallage and Huffman, 2007.

[b] Spearman rank-order correlation tests, one-tailed, N = 10.

TABLE 6. Quantification of the size of stones handled and available for each troop

	Stone size							
	S1		S2		S3		S4	
Troop	Nb	Qd	Nb	Qd	Nb	Qd	Nb	Qd
Ara.A	1	42	10	51	7	22	0	13
Wak.A	5	64	110	50	29	73	7	65
Takh.	67	67	218	44	114	30	15	11
JMC	8	71	71	57	47	36	20	22
Kosh.	0	21	11	15	9	5	4	4
Ara.E	83	73	341	42	112	22	7	14
Sho.A	25	67	34	58	6	40	2	15
Sho.B	5	67	27	58	17	40	0	15
Tak.B	31	79	45	59	24	34	9	12
Tak.C	79	79	152	59	73	34	16	12
Total	304	630	1019	493	438	336	80	183

Nb: number of SH bouts during which a stone of a particular size was handled at least once; Qd: percentage of quadrats containing at least a dozen of S1 stones, at least one S2, S3, and S4 stones (see Methods for details).

Prediction #2: Availability in stone size and size of stones handled. Table 6 shows that stones belonging to the four size categories were present at all sites and handled by most troops. Although these frequencies varied substantially across troops, we found no significant correlation between the site-specific availability in stone size and the corresponding troop preference in stone sizes, represented by the number of SH bouts during which S1, S2, S3, or S4 stones were handled at least once (Kendall rank-order correlation tests, $N = 4$, Ara.A: $T = 0.667$, $P = 0.174$; Wak.A: $T = 0.000$, $P = 1.000$; Takh.: $T = 0.333$, $P = 0.497$; JMC: $T = 0.000$, $P = 1.000$; Kosh.: $T = 0.000$, $P = 1.000$; Ara.E: $T = 0.333$, $P = 0.497$; Sho.A: $T = 0.667$, $P = 0.174$; Sho.B: $T = 0.333$, $P = 0.497$; Tak.B: $T = 0.667$, $P = 0.174$; Tak.C: $T = 0.667$, $P = 0.174$).

Several types of stones such as quartzite, granite, and schist rocks were sampled at the different natural sites (Arashiyama, Shodoshima, and Takasakiyama), with the exception of Koshima island where only sandstones and pumices were sampled. In addition to quartzite and schist rocks, a variety of pebbles and pieces of concrete blocks, artificially brought by humans, were sampled in the enclosures of the captive troops (PRI and JMC). Although the size and type of stones varied, we found that loose stones suitable for SH were available at all the study sites.

Terrestriality hypothesis

Prediction #3: SH as the activity most performed on the ground. On the basis of the focal sessions collected in seven troops, we calculated the percentage of time spent on and off the ground by the monkeys while involved in eight major types of activity (Fig. 2). Overall, we found that SH was the activity showing the greatest difference in terms of terrestriality, with 89.7% of the time devoted to SH being spent on the ground. This value came to 100.0% in four troops (Ara.A, JMC, Kosh., and Sho.A), 94.2% in Ara.E, and 83.6% in Takh. In the Wak.A troop, the relatively low terrestriality in SH (55.7%) could be attributed to the unique presence of a large central platform in a relatively small enclosure (see Table 1). Unlike narrow bars and branches or sloping roofs encountered at other sites, this flat surface may be regarded as a "ground above the ground," where the monkeys spent a comparatively great percentage of time resting and socializing (Fig. 2), and where they could readily find discarded stones to handle, even performing locomotion SH patterns typically observed on the ground, such as GW, MP, and TW (Gunst, personal observation).

The other activity close to SH in terms of terrestriality was object exploring, with an overall 88.2% of time spent on the ground. When considering the six other major activities together (feeding, foraging, locomoting, resting, socializing, and other), the overall percentage of time spent on the ground was 67.8%. The discrepancy between SH and most other activities found in the terrestriality profile led us to further explore a possible link between Japanese macaque terrestriality and SH activity.

Prediction #4a: SH and time spent on the ground at the group level. Terrestriality was highly variable according to the study troop, either defined as the mean percentage of time spent on the ground for all troop members sampled during focal sessions (Wak.A = 38.3%, Ara.A = 44.8%, Takh. = 72.7%, JMC = 73.3%, Ara.E = 76.7%, Kosh. = 77.9%, and Sho.A = 92.4%) or as the mean percentage of troop members on the ground during scan sessions (Wak.A = 35.0%, Ara.A = 43.2%, Sho.A = 69.5%, JMC = 69.9%, Sho.B = 70.9%, Takh. = 75.6%, Kosh. = 78.4%, Ara.E = 78.8%, Tak.C = 85.4%, and Tak.B = 88.0%). However, in both cases, we found no statistically significant correlation between troop-specific terrestriality and the different variables representing the occurrence and general form of SH in each corresponding troop (Table 3). It should be noted that in a few instances, the P values related to the mean percentage of troop members on the ground were equal or very close to 0.05 (e.g., pattern turnover: $P = 0.050$ and pattern diversity per bout: $P = 0.064$). The general tendency for captive troops to spend less time on the ground than free-ranging troops may be due to the abundance of climbing structures in the enclosures, such as bars, platforms, and shelter boxes.

Prediction #4b: SH and time spent on the ground at the individual level. In Wak.A, Takh., and Ara.E (where troop members were individually identified and SH relatively frequent), we found no significant positive correlation between the mean percentage of time spent on the ground by the different troop members and their SH frequency (Spearman rank-order correlation tests, Wak.A: $N = 19$, $r_s = 0.401$, $P = 0.050$; Takh.: $N = 45$, $r_s = -0.308$, $P = 0.020$; Ara.E: $N = 17$, $r_s = 0.064$, $P = 0.404$; all three troops: $N = 81$, $r_s = 0.182$, $P = 0.051$), pattern diversity per bout (Wak.A: $N = 17$, $r_s = -0.542$, $P = 0.013$; Takh.: $N = 39$, $r_s = -0.047$, $P = 0.389$; Ara.E: $N = 17$, $r_s = 0.182$, $P = 0.243$; all three troops: $N = 73$, $r_s = 0.057$, $P = 0.316$), and pattern inclusive diversity (Wak.A: $N = 17$, $r_s = -0.332$, $P = 0.097$; Takh.: $N = 39$, $r_s = -0.237$, $P = 0.073$; Ara.E: $N = 17$, $r_s = 0.187$, $P = 0.237$; all three troops: $N = 73$, $r_s = -0.100$, $P = 0.199$). Interestingly, significant negative correlations were found with SH frequency in Takh. and SH pattern diversity per bout in Wak.A.

DISCUSSION

In this study, we used an intertroop comparative approach to explore ecological constraints on SH activity in Japanese macaques, and tested a series of predictions generated from two hypotheses related to stone avail-

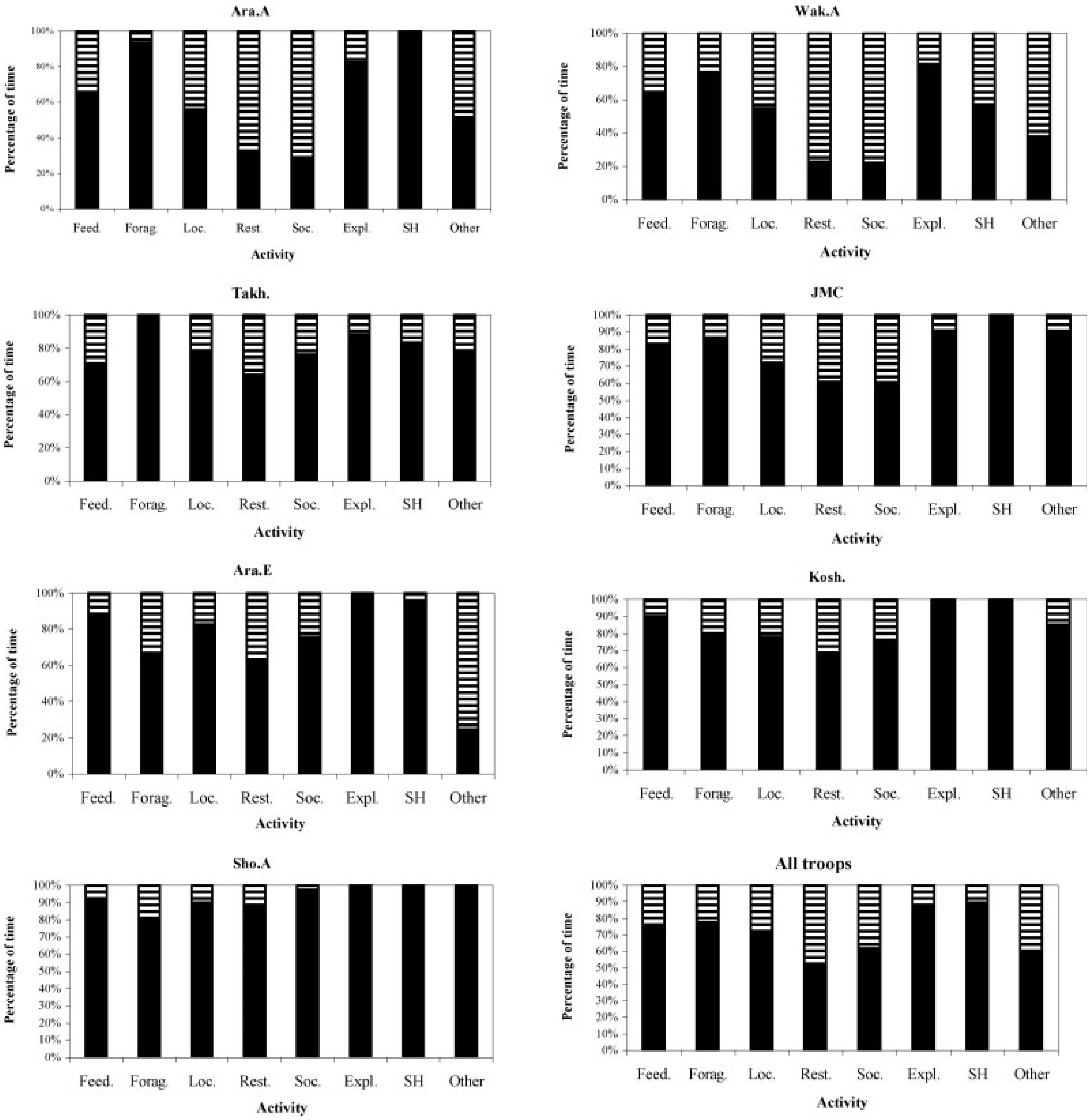

Fig. 2. Terrestriality profiles according to activity for seven separate troops and for the seven troops pooled together. The Y-axis represents complementary and mutually exclusive percentages of time namely the percentage of time spent on the ground (black areas) and the percentage on time spent off the ground (hatched areas). Expl.: Object exploring; Feed.: feeding; Forag.: foraging; Loc.: locomoting; Rest.: resting; Soc.: socializing; SH: stone handling.

ability and terrestriality. The hypotheses, predictions, and results of the tests are summarized in Table 7. First, we found that the number of stones readily available was not associated with the major intergroup differences in the occurrence of SH (namely SH frequency, prevalence, and rate of diffusion), and the general form of SH (namely duration of SH bouts and diversity of SH patterns). Moreover, the size of stones handled was not associated with the size of stones available. Because three of its major constituent predictions were rejected, we failed to accept the “stone availability hypothesis.”

Only two minor constituent predictions regarding the relationship between stone availability and some specific aspects of SH form were verified. When more stones were available in the local environment, the monkeys used more stones during SH activity and performed more SH patterns typically involving a great number of stones, such as those characteristic of a collection or gathering activity. Although the latter findings suggest that the number of stones available may influence the number of stones handled and the way to manipulate them, this was clearly insufficient to accept the “stone

TABLE 7. Hypotheses, predictions, and statistical tests results related to the ecological constraints on SH

Hypothesis	Prediction	Test result
"Stone availability hypothesis": The number and size of stones readily available in the local environment provides various SH opportunities, affecting the occurrence and form of the SH behavior	#1. Availability in stone number is positively correlated with:	
	a. The occurrence of SH (frequency, prevalence, and diffusion rate)	Not verified
	b. The persistence and diversity of SH (duration, number of phases, pattern turnover, and number of different patterns)	Not verified
	c. The number of stones used during SH bouts	Verified
	d. The frequency of SH patterns typically involving a great number of stones (e.g., gathering, scattering)	Verified
	#2. The size of stones used during SH bouts is associated with the size of stones available	Not verified
"Terrestriality hypothesis": The degree of terrestriality of individuals contributes to explain differences in the occurrence and form of SH	#3. Among all major activities, SH is the most performed on the ground	Verified
	#4. The occurrence, persistence, and diversity of SH are positively correlated with the time spent on the ground:	
	a. At the group level	Not verified
	b. At the individual level	Not verified

availability hypothesis." Second, we provided the first quantitative evidence that SH is almost exclusively a terrestrial activity. However, we showed that the relative amount of time spent on the ground by the macaques was not associated with this vertical bias at the group and individual levels. Therefore, we failed to accept the "terrestriality hypothesis."

We do not intend to infer causal relationships from measures of association between variables, mainly based on correlation and crosstabulation analyses. However, the present study undoubtedly shows that the relative stone availability and the degree of terrestriality are probably not key factors for SH innovation, subsequent diffusion, and daily occurrence in Japanese macaques. This does not imply that any dramatic local change in the availability of stones or vertical structures would not affect the chance of SH to occur in a particular troop. We believe that there are favorable environmental circumstances under which the innovation and initial diffusion of SH could be facilitated. Provisioned free-ranging troops faced atypical environmental conditions, such as the concomitant presence of novel foods (hard-coated cereal grains) and a great number of stones, sometimes artificially brought by humans as hard-packed ground for the open space of feeding areas. Wild monkeys spend more time foraging for natural foods in the forest, where climbing substrates are widespread and a substantial proportion of stones is covered by the vegetation. The former have more opportunities to encounter stones than the latter.

Failure to accept the stone availability and terrestriality hypotheses suggests that the performance of SH and the motivation to engage in this activity are both more diverse and more complex than the direct links to time spent on the ground or the number of stones readily available in the local environment. First, SH has not been reported at other sites where stones occur and several provisioned troops (e.g., Katsuyama: N. Nakamichi, pers. comm.) and all nonprovisioned troops of Japanese macaques (e.g., Kinkazan: Y. Shimooka, pers. comm.; Yakushima: G. Hanya, pers. comm.) have long been studied.

Second, once a particular stone or set of stones are involved in a SH episode, they seem to become valuable objects for the handler who pick them up and carry them to different places rather than leave them behind, and appear to trigger great interest from others who try to snatch them away from the handler as if they were the only stones available (Huffman and Quiatt, 1986). When subordinate individuals are supplanted from stones, they often wait nearby until the dominant leaves the stones behind, and they return to handle the very same stones again (Huffman, personal observation). Occasionally, human observers or tourists were threatened or even charged by a monkey while trying to take the stones it had just discarded after handling them (Leca, personal observation). These reports suggest the existence of a rudimentary form of "possession" in monkeys, already reported in chimpanzees at Bossou, Guinea, where some individuals seem to have their favorite stone tool (Matsuzawa, 1999).

Other environmental factors, such as the frequency of food provisioning, the size of the feeding site, and seasonality may influence to some extent the daily occurrence of SH, and therefore the overall opportunity for the behavior to diffuse within a troop through observational learning (Huffman and Hirata, 2003; Leca et al., submitted). Food provisioning has been performed for decades by Japanese primatologists and monkey park managers throughout Japan to help compensate for the unpredictable appearances of Japanese macaque groups and to accelerate the process of habituation. Nevertheless, food provisioning undoubtedly affects the animals' activity budget (Huffman, 1991; Huffman and Hirata, 2003; Leca et al., submitted). Attracting monkeys to the open space of feeding areas, where many stones occur, increases considerably their opportunities to encounter these objects. Feeding monkeys gives them "free" time since they can devote less time to foraging. Therefore, food provisioning is likely to enhance the chances for SH to emerge. At the other extreme, after food provisioning was stopped in the Japanese macaque troop living at Takagoyama, SH gradually disappeared (Fujita, pers. comm. cited in Huffman, 1984). By affecting the time spent to manipulate objects, food availability and especially food provisioning are environmental determinants of tool use appearance and transmission in groups of animals (Beck, 1980).

A recent longitudinal study on a captive troop of Japanese macaques showed a seasonal variation in the occurrence of SH, with a decrease in SH frequency recorded in winter (Nahallage and Huffman, submitted[2]). The visibility and availability of stones were rarely reduced during winter as snowfall was limited to a few days, but in some years and at some locations, snow may affect SH

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[2] Nahallage CAD, Huffman MA. Proximate factors associated with the occurrence of stone handling behavior in a captive troop of Japanese macaques. Submitted for publication.

to some extent. Instead, temperature was the key factor correlated with the decrease in SH activity in winter and its increase in summer. It could also be argued that food scarcity associated with winter may affect the monkeys' activity budget, forcing them to spend more time foraging in the forest, which in turn may impact on the occurrence of SH. Although the troops living at Shodoshima and Takasakiyama were solely studied during winter months (see Table 1), seasonal conditions are not likely to affect our findings for several reasons. No snowfall occurred during our observations of these troops (Leca, personal observation). Because of frequent food provisioning at these sites, the monkeys spent most of each day around the feeding sites, where stones are readily available (Leca et al., submitted). Finally, despite the cold weather, Sho.A, Sho.B, Tak.B, and Tak.C had the highest SH frequencies among the studied troops (Leca et al., in press).

When considered alone, terrestriality or stone availability often prove to be insufficient to account for all interpopulational differences in primate stone-tool use. Beck (1980) emphasized the absence of simple correlation between terrestriality and tool use behavior in primates. A closer examination of the ecological conditions of seed-cracking in the brown capuchins of the Caatinga dry forest revealed that terrestriality may not be sufficient to explain this stone-tool innovation. Moura and Lee (2004) suggested tool use is key to survive in impoverished habitats. Lee and Moura (2005) provided more support to the link between periods of food scarcity and the emergence of tool use behavior as an efficient foraging strategy that contributes to meet energy requirement.

Intersite variation in the instrumental use of stones in chimpanzees is obviously culturally based and beyond ecological determinism (Boesch et al., 1994; McGrew et al., 1997; Whiten et al., 1999). If chimpanzees at Lopé, Gabon do not use stones to crack open nuts, despite the availability and suitability of both stones and nuts, it is probably because they lack the appropriate technical knowledge to exploit this resource (McGrew et al., 1997).

To further explore the effect of the physical characteristics of stones and the sensory consequences of stone manipulation on the form of SH, additional analyses are underway to test a possible preference in the size, shape, weight, and chemical properties of stones selected by the monkeys to display SH patterns associated with particular sensory effects (e.g., auditory, olfactive, or gustative effects). Additional analyses should enable us to determine if our result on the substantial troop-specific variation in the size of stones handled may be related to the type of SH patterns preferentially performed by a particular troop (see Leca et al., 2007a, for intertroop variation in SH patterns).

Our findings urge the use of a multivariate approach when addressing the question of the evolution of behavioral traditions in nonhuman primates. In addition to ecological constraints, social factors (e.g., van Schaik, 2003; Leca et al., 2007b), and demographic influences (Lefebvre, 1995; Leca et al., in press) should be jointly considered to identify the sources of behavioral diversity in general, and variation in stone-tool use in particular. Like all stone-related behaviors in nonhuman primates, further investigation of the various factors constraining the occurrence of SH may provide new insights into the emergence of hominid material culture through stone-tool technology (cf. Foley and Lahr, 2003).

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RESEARCH ARTICLE

Food Provisioning and Stone Handling Tradition in Japanese Macaques: A Comparative Study of Ten Troops

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By addressing the influence of food provisioning on stone handling (SH), a behavioral tradition in Japanese macaques, this study contributes to the ongoing debate in cultural primatology by asking whether human intervention influences the emergence or propagation of behavioral traditions. SH is a form of object play consisting of the manipulation of stones by performing various behavioral patterns. We tested the hypothesis that the frequency of food provisioning affects the daily performance, form, and context of occurrence of SH by influencing a troop's feeding-related activity budget. We used a standardized observation procedure to investigate SH in ten troops of Japanese macaques. In troops provisioned several times a day, SH was more frequent, longer, and more prevalent during provisioning than nonprovisioning periods. These effects of provisioning were not significant in troops provisioned less frequently. SH was more frequently integrated with food-related activities in troops supplied with food several times a day than in the other troops. Food provisioning may be a key factor in the innovation and transformation phases of the SH tradition in Japanese macaques. Am. J. Primatol. 70:803–813, 2008. © 2008 Wiley-Liss, Inc.

Key words: food provisioning; stone handling; behavioral tradition; transformation phase; *Macaca fuscata*

INTRODUCTION

Culture is typically defined as a group-specific behavioral practice, persistent in several individuals over a number of years, and dependent on social means for its diffusion and maintenance [Perry & Manson, 2003]. Field studies on geographic variation in the occurrence of numerous behavioral patterns, supported by longitudinal and experimental investigations of whether and how these behaviors are socially learned, have provided extensive evidence for behavioral traditions in several primate species [e.g., Huffman & Hirata, 2003, 2004; Leca et al., 2007a; Nahallage & Huffman, 2007a; Perry et al., 2003; Whiten et al., 1999]. By addressing the influence of food provisioning on stone handling (SH), a strong candidate for a long-studied behavioral tradition in Japanese macaques (*Macaca fuscata*) [cf. Huffman, 1984, 1996; Huffman & Hirata, 2003; Huffman & Quiatt, 1986; Leca et al., 2007a], this study contributes to the ongoing debate in cultural primatology concerning how human intervention influences the innovation or propagation of behavioral traditions

Japanese macaques are known for their behavioral traditions. In this species the diffusion of several newly acquired behaviors has been investigated, such as the consumption of novel foods and novel food-processing techniques [Itani & Nishimura, 1973; Kawai et al., 1992; Leca et al., 2007b; Watanabe, 1989]. Most reported behavioral innovations in Japanese macaques occur in the artificial context of food provisioning [but see Nakamichi et al., 1998]. Provisioning has been used for decades by primatologists and monkey park managers throughout Japan to enhance visibility and habituation of the monkeys and to reduce crop-raiding. However, provisioning undoubtedly affects not only the animals' feeding habits but also their entire activity budget [Huffman, 1991; Huffman & Hirata, 2003].

SH is a form of object play consisting of the manipulation of stones by performing various behavioral patterns, socially transmitted across generations, as a behavioral tradition in Japanese macaques

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[Huffman, 1984, 1996; Huffman & Quiatt, 1986; Nahallage & Huffman, 2007a]. In recent reports, we focused on how socio-demographic factors (troop size, age structure, and observational learning) and ecological factors (stone availability and terrestriality) influenced intertroop variation in SH [Leca et al., 2007a,c, 2008]. Preliminary intertroop comparison suggests contrasting relationships between SH and provisioning [Huffman & Hirata, 2003]. To date, SH has never been reported in free-ranging, nonprovisioned troops of Japanese macaques. However, SH has not been recorded in all provisioned troops either [Huffman & Hirata, 2003]. At Takagoyama, the SH tradition gradually disappeared after food provisioning was stopped and the monkeys began to feed solely on natural vegetation [Fujita, personal communication, cited in Huffman, 1984].

Provisioning frequency varies across free-ranging and captive troops of Japanese macaques. To lure them out of the forest and make them more visible to visitors, some free-ranging troops in parks are provisioned especially frequently [Huffman, 1991]. Interestingly, there are contrasting findings regarding the temporal link between SH and feeding activities. In Arashiyama E and Takasakiyama free-ranging troops, where the emergence of the SH tradition was first documented about 25 years ago, SH is mainly observed immediately after feeding on provisioned food, which occurs several times a day [Huffman, 1984, 1996]. By contrast, the captive Takahama troop at the Primate Research Institute of Kyoto University shows SH throughout the day, regardless of feeding time, which occurs only once a day [Nahallage & Huffman, 2007b]. These reports suggest that the frequency of provisioning may somehow influence the frequency of SH. However, no systematic comparison of the relationships between SH and food provisioning across several troops of Japanese macaques has yet been conducted.

A troop's history in relation to feeding may be crucial for the transformation phase of the SH tradition, defined as the late period during which the behavior is consolidated through integration with other daily activities [Huffman & Hirata, 2003]. Increased familiarity with the properties of stones in a feeding context may expand the monkeys' SH repertoire and lead to greater stone-related behavioral diversity [Huffman & Quiatt, 1986]. This does not mean that a particular type of food provisioning is a necessary and sufficient condition for SH to appear and spread within a group. However, the occurrence of SH and its integration with other activities may vary across troops in relation to provisioning frequency.

Based on (1) earlier research on the causal links between food-related activities and object play [Mistlberger, 1994; Terlouw et al., 1993], and (2) preliminary comparisons of a few troops of Japanese macaques suggesting that provisioning frequency may influence the temporal relationship between SH and feeding activities [Huffman, 1984, 1991; Huffman & Quiatt, 1986; Nahallage & Huffman, 2007b], the goal of this study was to determine whether this pattern held true when several troops were systematically compared. We hypothesized that the frequency of provisioning affects the daily performance, form, and context of occurrence of SH in a given troop, through its influence on the feeding-related activity budget.

We tested the following three predictions: Prediction #1: In troops provisioned several times a day, SH should be more frequent, longer (at the individual level), and more prevalent (at the group level) during provisioning than during nonprovisioning periods; Prediction #2: These effects of provisioning should not hold for troops provisioned less frequently; Prediction #3: Owing to the long-term effects of provisioning on the SH tradition, the integration of SH with food-related activities (i.e., their simultaneous or interspersed performance) should be especially prevalent in troops provisioned several times a day.

To address these issues, we used a standardized observation procedure to record detailed data on the differences and similarities in the SH activity among ten troops of Japanese macaques, characterized by high variability in the frequency of food provisioning. The aim is to better understand the influence of food provisioning on the maintenance and transformation phase of the SH tradition in Japanese macaques.

METHODS

General Study Conditions

The species under study was the Japanese macaque (*M. fuscata*). We observed ten troops at six geographically isolated sites in Japan from August 2003 to February 2005 (Table I). Four troops lived in outdoor enclosures in Inuyama, Aichi Prefecture (Kyoto University Primate Research Institute: Arashiyama = Ara.A, Takahama = Takh., Wakasa = Wak.A, and Japan Monkey Centre Yakushima macaques = JMC), and six troops were free-ranging (Arashiyama, Kyoto Prefecture = Ara.E, Koshima, Miyazaki Prefecture = Kosh., Shodoshima, Kagawa Prefecture = Sho.A and Sho.B, Takasakiyama, Oita Prefecture = Tak.B and Tak.C).

The age and sex composition of all troops is described in detail elsewhere [Leca et al., 2007a,c]. Individual identities, exact age, and matrilineal membership were known for only some troops (Ara.A, Ara.E, Kosh., Takh., and Wak.A). For the other troops, every sampled subject was labeled according to its age class and sex. Observations were conducted between 7:00 and 18:00 hr. We observed captive troops from platforms located above the enclosure walls. Free-ranging troop members could be approached and observed within 3–5 m. This

TABLE I. Troops Studied, Study Periods, Number of Observers, and Total Data Sets

Troop name	Study period	Observers	TS	TOT	PFFT	OFT	PFNS	ONS	SH Bt (F)	SH Bt (CAL)	SH Nt (IAL)
Wakasa A (Wak.A)	August–November 2003	N. G.	19	224.6	18.5	156.0	84	725	59	62	224
Arashiyama A (Ara.A)	September–December 2003	N. G.	18	179.9	15.5	124.5	74	570	14	1	28
Takahama (Takh.)	September–December 2003	J.-B. L.	46	449.2	39.8	313.8	131	1462	309	28	1252
Japan Monkey Centre (JMC)	August–December 2003, March–April 2004	J.-B. L., N. G.	102	99.1	15.5	39.0	52	223	22	99	91
Koshima (Kosh.)	January–February 2004	J.-B. L., N. G.	88	339.7	18.1	197.3	84	168	9	14	7
Takasakiyama B (Tak.B)	December 2003–January 2004	J.-B. L., N. G.	438	22.8	0.0	0.0	29	29	n.a.	59	75
Takasakiyama C (Tak.C)	December 2003–January 2004	J.-B. L., N. G.	676	73.8	0.0	0.0	36	36	n.a.	182	391
Arashiyama E (Ara.E)	May-August 2004	J.-B. L., M. A. H.[a], C. N.[a]	141	431.3	94.8	65.8	302	708	317	35	579
Shodoshima A (Sho.A)	February 2005	J.-B. L., N. G., C. N.	450	77.6	11.3	5.5	40	26	30	10	27
Shodoshima B (Sho.B)	February 2005	J.-B. L., N. G., C. N.	350	51.5	1.0	0.3	12	12	4	26	67

In brackets: abbreviation of troop name. TS, troop size; TOT, total observation time in hours; PFFT, provisioning–feeding focal time (total duration in hours of focal sessions collected within 20 min after provisioning); OFT, other focal time (total duration in hours of focal sessions collected during other periods); PFNS, provisioning–feeding number of scan sessions (collected within 20 min after provisioning); ONS, other number of scan sessions (collected during other periods); SH Bt (F), number of SH bouts collected during focal sessions (n.a., not available); SH Bt (CAL), number of SH bouts collected during complete ad libitum sessions; SH Nt (IAL), number of SH notes collected during incomplete ad libitum sessions.

[a] The first two authors were the main observers (occasionally assisted by M. A. H. and Charmalie A. D. Nahallage).

TABLE II. Ranging and Food Provisioning Conditions, Grouped According to the Level of Provisioning Frequency, and Ordered According to the Frequency of Regular Provisioning

Troop	Ranging conditions	Surface of enclosure (CP) or feeding site (FR) in m^2	Level of food provisioning frequency	Regular provisioning frequency	Extra-provisioning frequency	Food supplied	Total amount of food (kg)	Average amount of food per individual (kg)	Average duration (hr) of food availability
Kosh.	FR	1,000[a]	Level-1	2/week	1/month[b]	Wh, Sp[b]	4, 10[b]	0.070, 0.175[b]	1.6±0.3
Ara.A	CP	850[c]	Level-2	1/day	3/week[b]	Pl, Sp[b]	5, 2[b]	0.278, 0.111[b]	5.2±0.8
Takh.	CP	960[c]	Level-2	1/day	3/week[b]	Pl, Sp[b]	10, 5[b]	0.217, 0.109[b]	5.4±1.5
Wak.A	CP	500[c]	Level-2	1/day	3/week[b]	Pl, Wh[b], Sp[b]	5, 2[b], 1[b]	0.263, 0.105[b], 0.053[b]	6.6±1.0
JMC	CP	4,000[d]	Level-2	2/day	All day[e]	Sp, Ap, Wh, Pl[e]	30, 10, 1, unk[e]	0.432, unk[e]	2.1±0.8
Sho.A	FR	1,200[f]	Level-3	3–4/day	1/day[b], all day[e]	Ri, Sp[b], Pn[e]	6, 15[b], unk[e]	0.020, 0.051[b], unk[e]	0.3±0.1
Sho.B	FR	1,200[f]	Level-3	3–4/day	1/day[b], all day[e]	Ri, Sp[b], Pn[e]	5, 15[b], unk[e]	0.030, 0.090[b], unk[e]	0.1±0.0
Ara.E	FR	400[f]	Level-3	4/day	All day[e]	Wh, Be (Sp, Pn, Ap)[e]	1.8, 0.8, unk[e]	0.022, unk[e]	0.2±0.0
Tak.B	FR	1,000[f]	Level-3	6/day	1/day[b]	Wh, Sp[b]	3.8, 50[b]	0.012, 0.165[b]	0.2±0.0
Tak.C	FR	1,000[f]	Level-3	12/day	1/day[b]	Wh, Sp[b]	2.8, 75[b]	0.007, 0.202[b]	0.2±0.0

CP, captive; FR, free-ranging; no superscript alphabet: regular food; Pl, commercial primate pellets; Sp, sweet potatoes; Wh, wheat grains; Ap, apples; Be, soybeans; Pn, peanuts; Ri, rice grains; unk, unknown amount of extra food supplied by visitors (highly variable depending on the presence and number of visitors); JMC, Japan Monkey Centre. The average amount of food per individual was estimated by dividing the total amount of food by the average number of feeding individuals sampled during prov.+5 min scans.

[a] Sandy beach.

[b] Extra food supplied by staff.

[c] Concrete and gravel surfaces.

[d] Grass areas and stony ground.

[e] Extra food supplied by visitors.

[f] Clay-stony ground.

research was conducted in accordance with Primate Research Institute's Guidelines for Animal Health and Welfare.

Comparative Ranging and Provisioning Conditions

Table II presents information on the troops' ranging and provisioning conditions. Captive troops were supplied regularly with commercial primate pellets, and occasionally with vegetables or fruits, scattered throughout feeding sites, i.e., specific areas inside the enclosures, either concrete and gravel surfaces or grass areas and stony ground. On a scheduled basis, free-ranging troop members gathered around feeding sites, i.e., specific areas within their home ranges where they were provisioned with cereal grains by technicians or park staff. Cereal grains were scattered throughout the feeding site, either clay-stony ground or sandy beach. At the Japan Monkey Centre, Arashiyama, and Shodoshima, visitors were allowed to give a small amount of extra food to the monkeys. Although their provisioning schedules were different, the free-ranging troops living at the same site (Sho.A/Sho.B and Tak.B/Tak.C) had overlapping home ranges. There have been no dramatic changes in the provisioning conditions of any troop for at least a decade.

The ten troops were categorized into three levels according to the frequency of regular provisioning (Table II): level-1 with the lowest frequency (twice a week), level-2 with food supplied once or twice a day, and level-3 with food distributed several times a day (3–12 times a day: 1.5–42 times more often than in the other troops). We also recorded the total amount of food supplied to each troop, and estimated the average amount of food per individual. To calculate the average duration of food availability at the feeding site, we used scan samples (see below) to measure the time elapsed between provisioning time and no food left. Overall, members of level-3 troops received a small amount of food (from 7 g per individual in Tak.C to 30 g in Sho.B) for a relatively short time (6 min in Sho.B to 18 min in Sho.A). Members of level-1 and level-2 troops received a larger amount of food (from 70 g in Kosh. to 432 g in JMC) for a longer time (96 min in Kosh. to 396 min in Wak.A).

Data Collection

The two main observational methods used were continuous focal-animal sampling and instantaneous group scan sampling, supplemented with ad libitum sampling [Altmann, 1974].

Focal sampling

We recorded every focal session with Sony digital video cameras (Sony, Tokyo, Japan). Whenever possible, the focal individual was filmed face-on and about 1-m^2 in-frame. We selected focal individuals semi-randomly [for details, see Leca et al., 2007a]. To use a nonindividually identified subject as its own control, efforts were made to sample the same individual just before and just after the provisioning time. The typical duration of a focal session was 15 min. If the focal individual performed SH during the final 2 min, the observation was extended for 5 min, or longer if SH was still in progress [see Huffman, 1996].

Scan and ad libitum samplings

Before and after each focal session, the troop was scanned and the activity of all sampled individuals was noted (feeding, foraging, SH, other). For each scan-sampled stone handler, we recorded individual identity or age and sex class, and whenever possible the SH patterns performed [for a comprehensive list, see Leca et al., 2007a]. In order to investigate whether changes in group activity were related to food provisioning, we conducted additional group scans within 10 min before provisioning time and every 5 min up to 35 min after provisioning (namely pre-prov., and from prov.+5 min to prov.+35 min, respectively). Other scan sessions were labeled nonprovisioning scans.

To supplement the data set, observers devoted an average ± standard deviation (SD) of 38.8 ± 31.8% of total observation time to collect ad libitum data on individuals performing SH. Whenever possible, ad libitum sessions were video-recorded; otherwise records were written onto a notepad. We did not conduct focal sessions for Tak.B and Tak.C troops owing to the short observation period (7 days) and the very large troop sizes (cf. Table I), which made focal follows difficult. Instead, for these troops we video-recorded ad libitum sessions after feeding, when SH is most likely to occur [see Huffman, 1996]. In some cases we recorded complete ad libitum sessions: The subject was filmed from the start (shortly after provisioning, immediately after it left the feeding site and touched stones) to the end of SH (5 min after the last stone was discarded). For SH episodes recorded on notepad or when the filmed sequence of SH was incomplete, the ad libitum session was classified as incomplete.

Data Processing

Using video-records, J.-B. L. measured the duration (in sec) of all the above-mentioned activities and each SH pattern. We distinguished two types of SH records: SH bouts collected from focal or complete ad libitum video-recorded sessions, and SH notes collected from scan sessions or incomplete ad libitum sessions. We defined an SH bout as the display of SH activity containing pauses of no longer than 120 sec [see Huffman, 1996]. If the individual paused then resumed SH within this time, this was considered as two SH episodes within a single SH bout. A resumption of SH more than 120 sec after pausing marked the start of a new SH bout.

We defined SH frequency as the average number of SH bouts per focal hour, SH duration as the mean duration of SH bouts, and SH prevalence as the mean percentage of stone handlers among individuals sampled in scan sessions. We defined SH mixed activity as the mean duration (per hour of SH bout) of performance of other activities (food-related activities, socializing, and other) ‘‘integrated’’ with SH, i.e., either performed simultaneously with SH or during pauses between SH phases. To qualify for a provisioning–feeding focal session, the subject had to feed for at least 30 sec on provisioned food.

Data Sets and Statistical Analysis

Table I summarizes the data sets for each troop in relation to provisioning. Total troop observation time included focal observation time, scan time, and time spent collecting ad libitum data. To analyze SH frequency, we used all focal sessions excluding Sho.B, Tak.B, and Tak.C troops owing to insufficient focal data, along with any focal sessions lasting less than 15 min. We used all available SH bouts to analyze SH duration and SH mixed activity, and all available SH bouts and SH notes for analyses regarding frequency of food-directed SH patterns. For captive troops, we only used scan sessions in which at least 80% of troop members were sampled. For the more widely dispersed free-ranging troops, we only considered scan sessions that sampled at least 60% of troop members. In the troops where individual identities were not known, any subjects that could be reliably recognized by morphological features on video (e.g., scars, broken finger) were used for analyses requiring independent subjects. Individuals less than 1 year old were not included in analyses. We assessed interobserver reliability between J.-B. L. and N. G. for individual identities, activities, and interactions ($k = 0.88$, 0.92, and 0.96, respectively), and intracoder reliability for J.-B. L. when transcribing the same samples of SH video-records twice, involving a total of 630 sample points ($k = 0.84$) [Martin & Bateson, 1993].

As age may affect SH frequency, we distinguished immature (up to 6 years old) from mature individuals (at least 7 years old) [cf. Leca et al., 2007c]. For most analyses, we report mean values $(X) \pm$ SD. When the assumptions of normality, independence, and homogeneity of variances were satisfied, we used parametric tests. General linear models (GLM) with repeated measures were used to assess the effect of the frequency of provisioning on SH frequency during provisioning–feeding periods and other periods. The models used the SH frequency as the dependent variable, the type of periods as the within-subject factor, the levels of provisioning frequency, the troops, and the age as the fixed factors, and the Scheffe tests for the post hoc multiple paired comparisons.

When parametric assumptions were violated, we used nonparametric tests to compare SH duration between feeding and nonfeeding individuals (Wilcoxon signed-ranks tests), and the frequency of food-directed SH patterns between level-3 troops and lower-level troops (Mann–Whitney *U* test). To assess the effect of the timing of provisioning–feeding on SH prevalence, we used χ^2 goodness-of-fit tests. To test the association between the level of provisioning frequency and SH mixed activity, we used χ^2 tests of independence. For post hoc examination of χ^2 tests, we calculated the adjusted standardized residuals, and considered *z*-scores $\geq |1.96|$ as significant. All tests were two-tailed. Statistical analyses were performed using SPSS 12.0 (SPSS Inc., Chicago). The significance level was set at $\alpha = 0.05$.

RESULTS

Effect of Provisioning Frequency on SH Occurrence (Predictions ♯1 and ♯2)

SH frequency

When analyzing whether provisioning frequency affected SH occurrence at the individual level, the main effect of provisioning frequency was significant, whereas the main effect of age and the interaction between these factors were not significant (GLM repeated measures, $N = 224$, provisioning frequency: $F_{2,218} = 72.87$, $P < 0.001$; age: $F_{1,218} = 0.12$, $P = 0.724$; provisioning frequency × age: $F_{2,218} = 1.05$, $P = 0.352$). Post hoc comparisons between provisioning frequencies showed that level-3 troops differed significantly from lower-level troops ($P < 0.001$) but level-1 and level-2 troops did not differ from each other ($P = 0.448$).

When troops instead of the levels of provisioning frequency was used as a fixed factor, the main effect of troop was significant, whereas the main effect of age and the interaction between troop and age were not significant (GLM repeated measures, $N = 224$, troop: $F_{6,210} = 22.16$, $P < 0.001$; age: $F_{1,210} = 0.79$, $P = 0.376$; troop × age: $F_{6,210} = 1.51$, $P = 0.176$). Post hoc comparisons showed that the two level-3 troops, Ara.E and Sho.A, did not differ significantly from each other ($P = 0.746$) but each of them differed from all the lower-level troops (Ara.E vs. all the lower-level troops: $P < 0.001$; Sho.A vs. Kosh.: $P = 0.010$; Sho.A vs. Ara.A: $P = 0.029$; Sho.A vs. Takh.: $P = 0.030$; Sho.A vs. Wak.A: $P = 0.027$; Sho.A vs. JMC: $P = 0.016$). All level-1 and level-2 troops did not differ significantly ($P > 0.05$). In level-3 troops, SH frequency was considerably higher during provisioning–feeding focals than other focals, and the overall SH frequency was at least two times higher than in lower-level troops (mean number of SH bouts per focal hour, Ara.E: $X_1 = X_{\text{Prov.–feeding}} = 3.1 \pm 2.1$, $X_2 = X_{\text{Other}} = 0.7 \pm 0.5$, $X_3 = X_{\text{Overall}} = 1.9 \pm 1.5$; Sho.A: $X_1 = 2.9 \pm 2.9$, $X_2 = 0.0 \pm 0.0$, $X_3 = 1.4 \pm 1.4$). In lower-level troops, there were no significant differences in SH frequency between the two periods (minimum values for all troops combined: $X_1 = 0.1 \pm 0.3$, $X_2 = 0.1 \pm 0.2$, $X_3 = 0.1 \pm 0.2$; maximum: $X_1 = 0.5 \pm 1.2$, $X_2 = 1.0 \pm 0.8$, $X_3 = 0.7 \pm 0.7$).

SH duration

To test the effect of feeding activity on SH duration, we compared the duration of SH bouts in feeding and nonfeeding individuals. In all level-3 troops, SH duration while feeding was significantly longer than when not feeding (Wilcoxon signed-ranks tests, Ara.E: $X_1 = X_{\text{Feeding}} = 229 \pm 295$, $X_2 = X_{\text{Nonfeeding}} = 40 \pm 48$, $z = -3.48$, $N = 25$, $P < 0.001$; Sho.A: $X_1 = 319 \pm 210$, $X_2 = 13 \pm 5$, $z = -2.93$, $N = 11$, $P = 0.003$; Sho.B: $X_1 = 63 \pm 74$, $X_2 = 19 \pm 10$, $z = -2.80$, $N = 10$, $P = 0.005$; Tak.B: $X_1 = 206 \pm 159$, $X_2 = 56 \pm 58$, $z = -3.18$, $N = 13$, $P = 0.001$; Tak.C: $X_1 = 158 \pm 99$, $X_2 = 20 \pm 10$, $z = -4.78$, $N = 30$, $P < 0.001$). In lower-level troops, we found no significant differences (minimum values for all troops combined: $X_1 = 11 \pm 5$, $X_2 = 17 \pm 15$; maximum: $X_1 = 103 \pm 106$, $X_2 = 122 \pm 195$, $P > 0.05$).

SH prevalence

To assess the effect of provisioning frequency on SH activity at the group level, from scan samples we compared the mean percentage of stone handlers in each troop in relation to provisioning frequency level and different periods (provisioning or not) (Fig. 1). Only in level-3 troops was SH prevalence affected by the timing of feeding on provisioned foods (χ^2 goodness-of-fit tests, $N = 7$ periods, namely nonprov., pre-prov., and from prov. + 5 min to prov. + 25 min; Ara.E: $\chi^2_6 = 26.34$, $P < 0.001$; Sho.A: $\chi^2_6 = 111.24$, $P < 0.001$; Sho.B: $\chi^2_6 = 32.02$, $P < 0.001$; Tak.B: $\chi^2_6 = 63.18$, $P < 0.001$; Tak.C: $\chi^2_6 = 117.16$, $P < 0.001$).

In all level-3 troops, provisioning resulted in more troop members SH simultaneously for about 30 min. After rapidly (9.8 ± 9.0 min) reaching a peak (24.6 ± 15.7% of stone handlers), SH activity at the group level gradually decreased to a low baseline (0.4 ± 0.3% of stone handlers) within 30 min. By contrast, the troops provisioned less frequently showed consistently low levels of SH regardless of period (χ^2 goodness-of-fit tests, Kosh.: $\chi^2_6 = 0.00$, $P > 0.05$; Ara.A: $\chi^2_6 = 0.00$, $P > 0.05$; Takh.: $\chi^2_6 = 1.60$, $P > 0.05$; Wak.A: $\chi^2_6 = 1.80$, $P > 0.05$; JMC: $\chi^2_6 = 0.60$, $P > 0.05$).

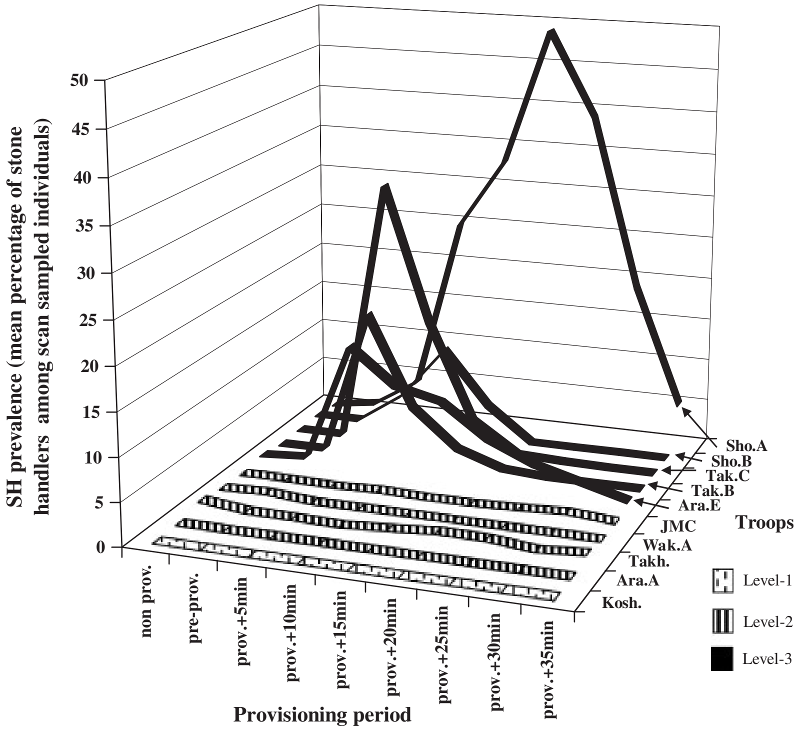

Fig. 1. Effect of provisioning on SH prevalence: intertroop comparison of the mean percentage of stone handlers among scan-sampled individuals according to the provisioning period and the level of food provisioning frequency. Nonprov., nonprovisioning scans; pre-prov., scan sessions recorded within 10 min before provisioning time; from prov.+5 min to prov.+35 min, scan sessions recorded every 5 min within 35 min after provisioning time; SH, stone handling.

Integration of SH with Food-Related Activities (Prediction ♯3)

To assess the integration of SH with feeding activity, we measured the frequency of SH while chewing food. In all level-3 troops, stone handlers simultaneously chewed food or at least had food in their cheek pouches in more than 60% of SH bouts (Ara.E: 82.7%, $N = 352$; Sho.A: 72.5%, $N = 40$; Sho.B: 63.3%, $N = 30$; Tak.B: 78.0%, $N = 46$; Tak.C: 83.5%, $N = 182$). In lower-level troops, these rates were around 50% or below (Kosh.: 52.2%, $N = 23$; Ara.A: 40.0%, $N = 15$; Takh.: 42.1%, $N = 337$; Wak.A: 21.5%, $N = 121$; JMC: 41.3%, $N = 121$).

To test whether other activities co-occurring with SH varied with provisioning frequency, we conducted a χ^2 test of independence based on a contingency table representing the duration of this form of SH mixed activity in troops belonging to the three levels and three types of simultaneous activities, namely food-related activity (food intake and foraging), socializing (allo-grooming, nursing, aggression, and social play), and other (resting, self-grooming, and object play). During most socializing or other activities, the monkey held, cuddled, or carried the stone(s) [for definitions, cf. Leca et al., 2007a]. There was a significant association between the type of activity ''integrated'' with SH and the level of provisioning frequency (Pearson χ^2 test: $N = 131$ mixed-activity bouts, $\chi^2_4 = 102.91$, $P < 0.001$). Post hoc examination of residuals showed that the integration of food-related activities with SH was significantly higher in the level-3 troops than in lower-level troops (Fig. 2a).

We conducted the same analysis to determine which of the three types of activity were interspersed with SH; that is, performed during pauses between SH phases, in relation to provisioning frequency. We found a significant association between the two variables (Pearson χ^2 test: $N = 1{,}848$ mixed-activity bouts, $\chi^2_4 = 958.17$, $P < 0.001$). Post hoc examination of residuals showed that the integration of food-related activities with SH was significantly higher in the level-3 troops than in lower-level troops, whereas other activities (resting, locomoting, vigilance, self-grooming, and object play) were more often integrated with SH in lower-level troops than in level-3 troops (Fig. 2b).

Finally, we quantified the frequency of the following food-directed SH patterns: (1) rub or clack a stone with a food item, such as a pellet or piece of sweet potato, and (2) gather, cuddle, or grasp a pile of stones mixed with supplied or natural food items, such as peanut pods or acorns. These frequencies were weighted by the total observation time for each troop and, given their rarity, plotted on a 1,000-hr scale (adjusted frequency: AF). The direct integra-

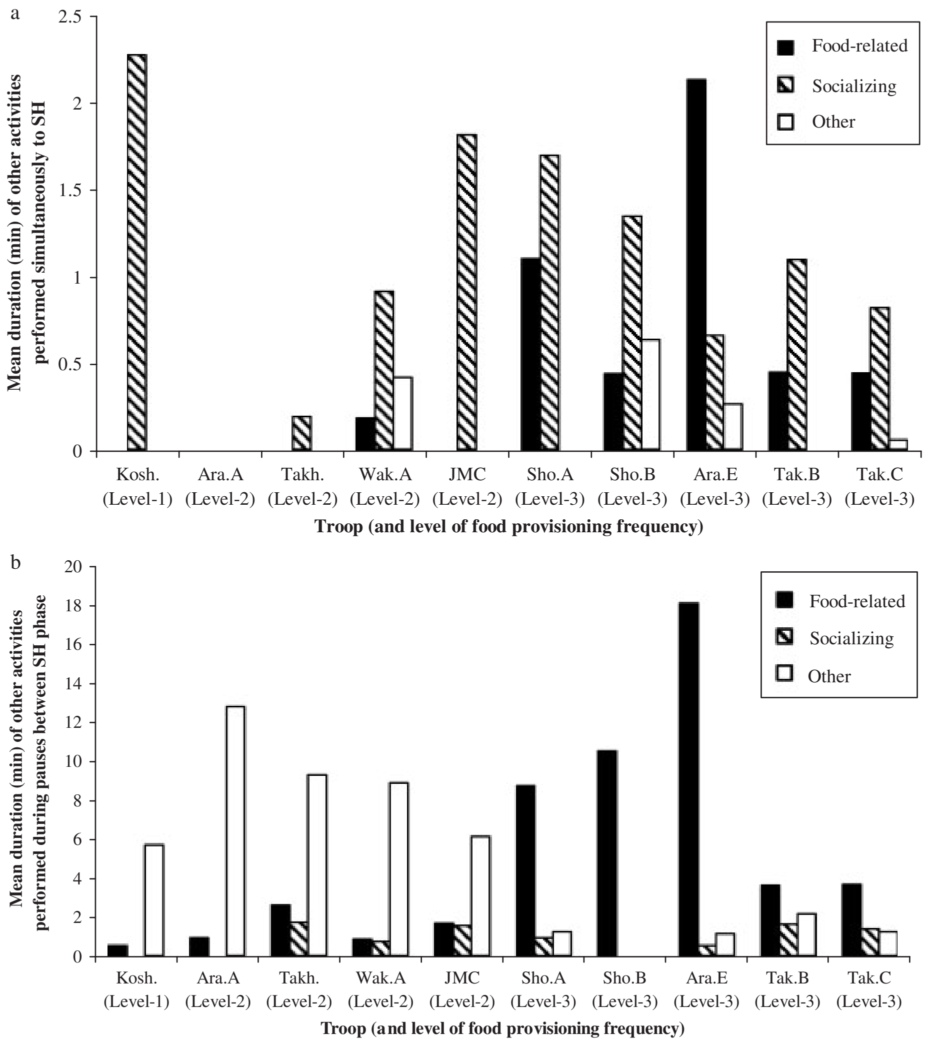

Fig. 2. SH mixed activity in terms of mean duration of other activities (food-related activities, socializing, and other) performed (in minutes per hour of SH bout) simultaneously to SH (**a**) or during pauses between SH phases (**b**). SH, stone handling.

tion of food items with SH activity was markedly more frequent in level-3 troops (Ara.E: $N = 52$, $\text{AF} = 121$; Sho.A: $N = 4$, $\text{AF} = 51$; Sho.B: $N = 2$, $\text{AF} = 39$; Tak.B: $N = 4$, $\text{AF} = 175$; Tak.C: $N = 6$, $\text{AF} = 81$) than in lower-level troops (Kosh.: $N = \text{AF} = 0$; Ara.A: $N = \text{AF} = 0$; Takh.: $N = 2$, $\text{AF} = 4$; Wak.A: $N = \text{AF} = 0$; JMC: $N = 1$, $\text{AF} = 10$) (Mann–Whitney U test: $N_{\text{level-1 and -2}} = N_{\text{level-3}} = 5$, $z = -2.64$, $P = 0.008$).

DISCUSSION

This is the first systematic investigation of the influence of food provisioning on the SH tradition in Japanese macaques. In troops provisioned several times a day, SH was significantly more frequent (regardless of age), longer, and more prevalent during provisioning than during nonprovisioning periods (Prediction ♯1). None of these effects were significant in troops provisioned less frequently (Prediction ♯2). Furthermore, integration of SH with food-related activities occurred more frequently in troops provisioned several times a day, reflecting long-term effects of provisioning on the transformation phase of the SH tradition (Prediction ♯3). The three predictions were upheld, supporting the hypothesis that provisioning frequency affects the daily performance, form, and context of occurrence of SH by influencing the feeding activity budget.

The troops provisioned several times a day received relatively small amounts of small-sized food items (e.g., cereal grains, see Table II), which were available at the feeding sites for short periods of time. Although not directly analyzed, the particular combination of food availability and size associated with frequent provisioning might give rise to unusual food-related responses. At the feeding site, most individuals rapidly fill their cheek pouches while also eating on the spot. After leaving the feeding site, they can eat in a more leisurely fashion, with few opportunities for further food-processing behaviors.

Studies suggest that the organization of food-related behaviors may be partly ''preprogramed'', so that feeding-like behavior persists for some time after provisioning [Lawrence & Terlouw, 1993]. If feeding motivation is high and food-related activities are interrupted, foraging-like behaviors might be directed at alternative objects [Haskell et al., 1996]. During all provisioning episodes in the level-3 troops studied here, cereal grains are quickly depleted at the feeding site, as is the opportunity to manipulate these small food items. Handling stones may be an extension of foraging-like behaviors, a continuation of manipulatory actions while chewing food. With provisioning repeated several times a day over long periods of time (as in level-3 troops), co-occurrence of food-related and SH activities is facilitated. This interpretation is consistent with reports of controlled feeding and persistent postfeeding foraging behaviors or object manipulation in sows [Haskell et al., 1996; Terlouw et al., 1993]. This proximate explanation builds on the argument that SH may replace other activities that are normally associated with foraging [Huffman & Hirata, 2003].

In troops provisioned less frequently but with larger food items in large amounts, some of which may still be available hours later (see Table II), postfeeding foraging-like behaviors are not interrupted; therefore, the monkeys can continue to manipulate food items while chewing. This is probably why there was no temporal connection between feeding and SH in level-1 and level-2 troops. Therefore, food provisioning constraints, including frequency, duration of food availability, and the size of food items, may strongly influence a troop's food-related activities and feeding style, which in turn could affect several aspects of SH. However, our results on the less frequently provisioned troops must be viewed with caution owing to a possible floor effect, as these troops showed few episodes of SH. Nevertheless, a recent longitudinal study on one of these troops found that SH activity occurred throughout the day, regardless of provisioning time [Nahallage & Huffman, 2007b].

These proximate explanations are in agreement with the gradual disappearance of SH at Takagoyama after provisioning was stopped [Fujita, personal communication, cited in Huffman, 1984], and with the lack of observations of SH in wild, nonprovisioned troops of Japanese macaques at other sites [e.g., Kinkazan: Shimooka, personal communication; Yakushima: Hanya, personal communication]. In nonprovisioned troops, foraging interspersed with traveling between food patches accounts for a large proportion of the daily activity budget [Hanya, 2004]; therefore, there may simply be less time available for nonsubsistence activities such as SH [see Huffman & Hirata, 2003]. The activity budget of the study troop living on Koshima island was quite similar to those of wild troops, with individuals foraging in a 33 ha forest for natural foods [see Leca et al., 2007b; Mori, 1977]. Interestingly, Kosh. is the troop provisioned least of all and the troop showing the least amount of SH both at the individual and the group level [see Leca et al., 2007c]. The original motivations underlying SH may be different from what they are today. Most monkeys observed handling stones in 2003–2005 were born into troops with well-established SH traditions. Furthermore, individuals grew up into a troop with either a strong or a weak connection between SH and provisioning. The conformity-enforcing hypothesis, which proposes that culturally nonconforming individuals may be discriminated against [cf. Lachlan et al., 2004], predicts that immature individuals should integrate the same type of connection between SH and feeding activities as most older group members.

The general behavioral predispositions of a species make behavioral innovation relatively predictable [Huffman & Hirata, 2003]. Considering the natural propensity for Japanese macaques to manipulate stones [cf. Leca et al., 2007a], and provided equivalent stone availability [cf. Leca et al., 2008], SH traditions are theoretically equally likely to emerge in all provisioned troops, although relative rate of exposure to stones does not influence the latency of infants to acquire SH [Nahallage & Huffman, 2007a]. This may account for the occurrence of SH in all the troops studied here, despite differences in its characteristics. Thus, we argue that occurrence of SH in a given troop is not directly influenced by provisioning parameters, but the context of occurrence, frequency, duration, prevalence, and form of SH are.

Anthropogenic influences can create major intertroop differences in activity budgets. Provisioning in free-ranging troops results in the daily concentration of most troop members around feeding grounds, i.e., open areas with stones. Some troop members return to the forest between provisioning periods, but most of them rest and socialize around the feeding site. This opportunity and free time may be at the origin of SH first occurring in the feeding context in frequently provisioned free-ranging troops. If the SH tradition appears in a free-ranging troop where food provisioning influences the activity budget, its long-term transformation phase is likely to include the integration of SH with food-related activities and the gradual emergence of food-directed SH patterns. This is the case for all level-3 troops, where various SH patterns combining provisioned food items were observed. However, at Arashiyama and Takasakiyama, we also observed stones gathered into piles in the forest, distant from the feeding area. This suggests that in free-ranging provisioned troops SH may occasionally be integrated with activities other than feeding on provisioned foods, such as feeding on natural foods.

Indeed, even before provisioning was started at Arashiyama in the late 1940s, monkeys were seen to handle hard, inedible fruits much as they handle stones today [Huffman, 1984].

The transformation phase of the SH tradition, revealed by the increase in contexts in which SH occurs, is all the more likely and flexible as SH appears to be a nonadaptive behavior with no obvious immediate survival value [Huffman, 1984, 1996; but see Nahallage & Huffman, 2007b], as opposed to stone-tool-use traditions for which an efficient behavioral pattern should be maintained unchanged [e.g., Boesch, 1991]. However, an eventual ''ratchet effect'' of increased complexity of SH is conceivable, possibly ultimately resulting in future use of stones as tools [Huffman & Quiatt, 1986; Leca et al., 2007a].

Although SH in Ara.E and Tak.C is now strongly linked to provisioning, the SH tradition emerged over three decades after the onset of food provisioning in these two troops. The reasons for the late appearance of SH are not fully understood. Possibly, sporadic SH appeared earlier without spreading within the troop, and without being noticed by human observers [Huffman, 1984]. However, the first individuals observed to perform SH at Arashiyama were all under 4 ears of age, emphasizing the playful nature of this behavior [Huffman, 1984]. Developmental correlates and age differences in the motivation to engage in SH should be addressed in future studies [Nahallage & Huffman, 2007b]. Changes in the local environmental conditions (e.g., provisioning style, stone availability) may also play a role [Huffman & Hirata, 2003]. Between the time when SH was first noticed, in December 1979, up to 1984 when observations were resumed by Huffman [1984, 1996], the behavior had spread within the troop. This rapid diffusion of SH may have occurred owing to construction projects when a large number of stones were left at the edge of the feeding area.

In conclusion, we demonstrated that food provisioning conditions, especially frequency of provisioning, affect the daily performance of SH. This study using data from several troops supports earlier observations suggesting that provisioning is a key factor in the innovation, diffusion, and long-term maintenance of the SH tradition in troops living in natural habitats [cf. Huffman, 1984]. The persistence of SH in food-related contexts may eventually turn into the instrumental use of stones by Japanese macaques [Huffman & Quiatt, 1986]. Evidence for relationships between SH and provisioning does not argue against a cultural interpretation of SH, as this long-enduring behavior is socially transmitted [Huffman, 1984, 1996; Nahallage & Huffman, 2007a], which some authors suggest is sufficient evidence of a behavioral tradition [e.g., Perry & Manson, 2003].

Our findings call for experimental approaches to test the strength of the connection between SH and feeding activities, to further explore the proximate causes of this behavior and its longer-term transformation. As with stone-related behaviors in nonhuman primates, a better understanding of the influence of environmental factors in the transformation of this behavioral tradition in Japanese macaques may provide new insights into the emergence of hominid material culture through stone-tool technology.

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

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A B S T R A C T

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 pattersn (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.

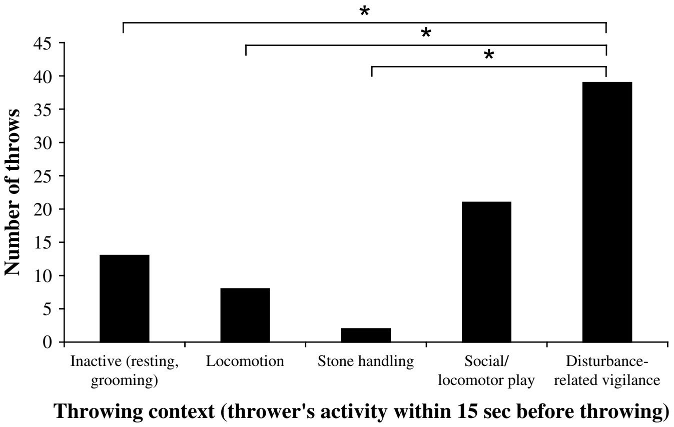

Fig. 1. Effect of the context on the number of stone-throwing events recorded in Takh. (*: $p < 0.05$).

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.).

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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Environmental and Social Factors Associated with the Occurrence of Stone-Handling Behavior in a Captive Troop of *Macaca fuscata*

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Abstract Stone-handling, a documented behavioral tradition in Japanese macaques (*Macaca fuscata*), occurs in both captive and provisioned free-ranging troops. We utilize data systematically collected as part of a broader investigation of stone-handling behavior in a captive troop to elucidate the environmental and social factors responsible for its occurrence. We analyzed contexts of stone-handling over 18 mo to determine under what conditions individuals most often perform it. There is clear seasonal variation in the occurrence of stone-handling. The lowest number and shortest duration of stone-handling bouts were in winter, gradually increasing to a peak in summer, and again decreasing toward autumn. Monkeys stone-handled more on clear sunny days than on cloudy or rainy ones. They displayed the behavior less under stressful conditions caused by human intervention or by aggression among troop members. Such stressful social conditions appeared to decrease individual motivation for stone-handling. In other words, individuals most frequently performed stone-handling under more relaxed environmental and social conditions. The findings are consistent with the hypothesis that stone-handling is a form of solitary object play behavior in macaques.

Keywords behavioral tradition · *Macaca fuscata* · object play · stone-handling

Introduction

Animals acquire new behaviors via innovation and learning. Two well-known examples of behavioral innovation are sweet-potato washing in Japanese macaques (*Macaca fuscata*: Kawai 1965) and milk bottle opening by British titmice (Fisher and Hinde 1949). The behaviors spread among other group members to become long-lived behavioral traditions. Tradition is a behavioral practice that is relatively

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long lasting, i.e., performed repeatedly over time, and is shared among members of a group in part via social learning (Perry and Manson 2003).

From the perspective of cultural primatology, it is of interest to understand the factors that influence a change in the occurrence of a behavioral tradition over time because it may inform something about the nature or function of the behavior itself. For example, after acquisition, does an individual perform the behavior at the same frequency all the time or does it vary according to the age or sex of the individual, a group's ranging condition (captive vs. wild), or different seasonal or other environmental conditions? Bernstein (1972, 1975, 1976, 1980) and Bernstein and Baker (1988) reported the influence of diurnal, temperature, and other weather conditions on the activity patterns of captive primates. Hanya (2004), Isbell and Young (1993), Maruhashi (1981), Vasey (2005), Rasoazanabary (2006), Watanuki and Nakayama (1993), and Yotsumoto (1976) conducted similar research on the variation of activity patterns under different environmental conditions of free-ranging primates. Several factors may affect an individual's performance of a behavior, which may change with time of day or season. Thus, overlooking such information by sampling a behavior for only a short duration, or looking at it from a limited age/sex/class subgroup of the population, can bias our interpretation of a behavior's function or the reason for its occurrence.

Individual or social characteristics such as age, sex, and stress caused by aggression among troop members or by human interference can contribute to changes in the frequency with which a behavior is performed. For example, in all forms of play —solitary, object, social— the frequency of occurrence changes due to age, sex, habitat, feeding conditions, season, and weather condition (Baldwin and Baldwin 1977; Fedigan 1972; Hall 1998; Kummer 1971; Nahallage and Huffman 2007a; Pellis 1991, 2002; Poirier and Smith 1974; Poirier *et al*. 1978; Starin 1990). In addition, animals experiencing stress are less likely to engage in play-related activities (Aldis 1975; McCune 1992; Poole and Fish 1975). Knowing the effects of these factors should make it easier to understand the function or proximate motivation for practicing the behavior.

We tested environmental and social factors affecting stone-handling, a form of solitary object play behavior in *Macaca fuscata* (Huffman 1984). Stone-handling is a form of object play in Candland's terminology (1978), and Fagen (1981) defines object play as "divertive interactions with an inanimate object… including exploratory manipulation" (p. 45). Stone-handling occurs in 4 captive troops and 11 provisioned free-ranging troops across Japan (Leca *et al*. 2007; Nahallage and Huffman 2007a). Stone-handling is the repetitive manipulation of stones in many ways, e.g., gather, clack, strike together, scatter, etc. (Huffman 1984, 1996). Though stone-handling has no obvious immediate survival value, primates have practiced it in Arashiyama and Takasakiyama since 1979 (Huffman 1984, 1996; Huffman and Hirata 2003) and in Takahama for *ca*. 25 yr (Nahallage 2005). There are significant group- and age-related behavioral differences in stone-handling (Huffman 1996; Leca *et al*. 2007; Nahallage and Huffman 2007a). Infants acquire the behavior from their mothers within the first 6 mo of their lives, and the presence of inter- and intratroop variations in the occurrence, frequency, prevalence, and form of stone-handling has led researchers to consider it a behavioral tradition in *Macaca fuscata* (Huffman 1996; Leca *et al*. 2007; Nahallage and Huffman 2007b).

In long-term surveys of the provisioned free-ranging Arashiyama and Takasakiyama troops, Huffman (1984, 1996) described stone-handling as object play that occurs under relaxed environmental and social conditions. Conversely, Nishie (2002) proposed that the emotional conflict between feeding and aggression avoidance at feeding time were the main proximate factors for stone-handling. However, in captive groups there is no association between feeding time and the occurrence of stone-handling (Leca *et al.* 2004; Nahallage and Huffman 2007a). Clearly, stress during feeding of provisioned food is not a consistent proximate factor inducing stone-handling by macaques.

We systematically investigated the effects of environmental and certain social factors on the occurrence of stone-handling behavior. We tested the prediction that stone-handling occurs under relaxed environmental and social conditions and not stressful ones.

Methods

Focal Group

We conducted our study at the Kyoto University, Primate Research Institute, Inuyama. We selected a captive stone-handling troop of *Macaca fuscata* for ease of detailed systematic observations. The captive Takahama troop live in a 960-m^2 outdoor enclosure. The troop comprised 48 monkeys of different age-sex classes (Table I). They ate monkey chow daily between 1000 h and 1100 h; sweet potatoes twice per week; and occasionally fruits, grains, and vegetables whenever available. They could drink water *ad libitum*. The enclosure contained climbing structures, swings, and aluminum sleeping boxes (Nahallage 2005; Nahallage and Huffman 2007a). Of the 48 subjects, 45 handled stones and we used them all in analyses (Table I).

Data Collection

We used 2 sampling methods for data collection: continuous focal individual sampling and instantaneous scan sampling (Altmann 1974). Before starting a focal observation or a scan, we noted the weather condition as sunny, cloudy, or rainy. We recorded temperature and humidity via a digital thermometer that automatically recorded the data every 30 min. We recorded each focal session for 15 min via a

Table I Age –sex distribution of Takahama group

Age-class category	Number of individuals	Number of verified stone handlers
Adult males (>10 yr)	1	1
Adult females (>7 yr)	18	15
Adolescent males (5–9 yr)	5	5
Adolescent females (5–6 yr)	0	0
Juvenile males (1–4 yr)	9	9
Juvenile females (1–4 yr)	7	7
Infant males (0–1 yr)	3	3
Infant females (0–1 yr)	5	5

digital video camera (Sony Digital Handycam). Before and after each focal session, we performed scans to record the major behavioral activities of the troop as a control for average troop activity patterns at that time of the day: prefocal and postfocal scans. We recorded resting, feeding, foraging, locomotion, grooming, playing, object handling, stone-handling, aggression, and other. We recorded all other observations *ad libitum*.

We started data collection of the troop in June 2003 and continued until November 2004. We observed all members of the group equally during all seasons (spring: March–May; summer: June–August; autumn: September–November; winter: December–February) to determine possible seasonal effects on stone-handling. The daily observation time depended on daylight length, which varied according to season (spring: 0700–1800 h, 11 focals/individual; summer: 0700–1900 h, 12 focals/individual; autumn: 0700–1800 h, 11 focals/individuals; winter: 0700–1600 h, 9 focals/individual). We divided the daily observation schedule into 1-h time blocks and sampled individuals randomly in each block. We collected equal numbers of focal samples for each individual in all time periods of the day in every month of each season to avoid sampling bias of certain age-sex classes and possible seasonal differences. We sampled each individual 43 times and obtained 878 observation hours (Nahallage 2005). Our analyses are based on 578 stone-handling bouts recorded from 45 individuals. A bout is the continuation of the behavior with pauses of ≤ 120 s, which is the duration after which further stone-handling is significantly less likely to recur (Huffman 1996). If stone-handling resumed after >120 s, we treated it as a separate bout.

Data Analysis

We analyzed video focal records of stone-handling and noted the time and day of the stone-handling bout, weather conditions, duration and frequency of stone-handling bouts, activities of a stone handler immediately before and after a stone-handling bout, and the troop activity budget during a bout. We performed 2-tailed nonparametric tests via SPSS (version 10), and set significance at $p \leq 0.05$.

Results

Effect of Season and Daily Weather Conditions

There is a significant seasonal difference in the number of stone-handling bouts performed by individuals (Friedman: $\chi^2=26.57$, df=3, $p<0.001$, $n=45$). Multiple pairwise comparisons between seasons (Siegal and Castellan 1988) show a significant difference between summer and winter ($p<0.05$), but not between autumn and spring, autumn and summer, autumn and winter, spring and summer, or spring and winter. The lowest numbers of stone -handling bouts occurred in winter and the highest in summer (Table II).

The average duration of stone-handling bouts varied across seasons (Table II). There is a statistically significant seasonal difference in the duration of bouts (Friedman: $\chi^2=26.48$, df=3, $p<0.001$, $n=45$). In winter, with the lowest average

Table II Average temperature, humidity, and stone-handling bouts in each season

	Winter	Spring	Summer	Autumn
Temperature (°C)	2.96 (–4.1–4.6)	15.19 (2.8–26.9)	27.89 (22.8–34.4)	15.73 (6.6–24.4)
Humidity	72.35 (24.6–100)	60.99 (15.4–100)	71.74 (44.2–94.2)	71.48 (23.8–100)
Total number of bouts	74	150	200	154
Frequency of bouts/h	0.69	1.11	1.34	1.14
Average time per bout (s)	90.12	116.76	138.06	103.88

temperatures (min., –4.1°C; max., 14.6°C), the number of total stone-handling bouts were the lowest and short in duration, while the number of bouts and durations were highest in summer when average temperatures were highest (min., 22.8°C; max., 34.4°C). There is a statistically significant positive correlation between the average daily temperature and the number of bouts (Spearman ρ $rS=0.150$, $p=0.037$, $n=195$).

Daily weather conditions also appear to influence directly the frequency of stone handling activity. Regardless of season, there is a statistically significant difference in the number of an individual's stone-handling bouts in different weather conditions (Friedman: $\chi^2=68.96$, df=2, $p<0.001$, $n=45$). Multiple pairwise comparisons among 3 weather conditions show a significant difference between sunny and rainy and sunny and cloudy ($p<0.05$), but not between rainy and cloudy. Individuals handled stones more frequently on sunny (84%, 487/578 bouts) than on cloudy (12%) or rainy (4%) days.

Effect of Seasonal Variation on Troop Activity Budget

When we analyzed the overall troop activity budget by seasons, there were statistically significant differences in each activity (resting/grooming: Friedman: $\chi^2=81.03$, df=3, $\rho<0.001$, $n=627$; object play: Friedman: $\chi^2=51.84$, df=3, $p<0.001$, $n=627$; locomotion: Friedman: $\chi^2=371.43$, df=3, $p<0.001$, $n=627$; aggression: Friedman: $\chi^2=25.83$, df=3, $\rho<0.001$, $n=627$; Fig. 1). Multiple pairwise comparisons for resting/grooming between the seasons show significant differences between summer and autumn, summer and winter, autumn and spring, and winter and spring ($p<0.05$), but not between summer and spring or autumn and winter. For object manipulation there is a significant difference only between summer and winter ($p<0.05$). For locomotion, there are significant differences between all 6 combinations of season (summer: autumn, summer: winter, summer: spring, autumn: winter, autumn: spring and winter: spring; $p<0.05$). In contrast, there is no significant difference for aggression between the seasons. Resting/grooming and object handling were lowest in winter and highest in summer, whereas activities such as locomotion and aggression were highest in winter and lowest in spring (Fig. 1).

Activity of Focal Stone-handling Individuals Immediately Before and After Stone-handling

We analyzed the activities each individual performed immediately before a stone-handling bout (pre-SH activity) and just after a bout (post-SH activity) to

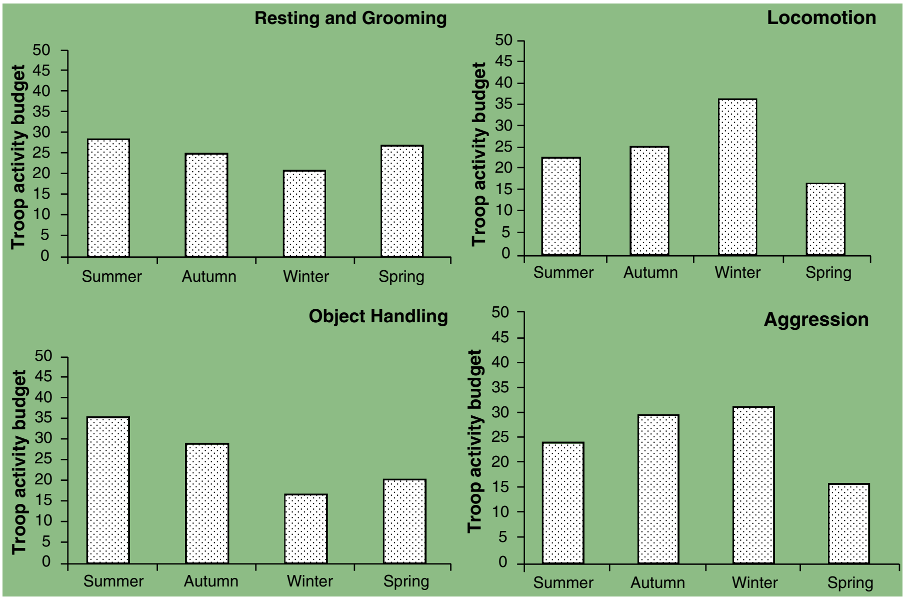
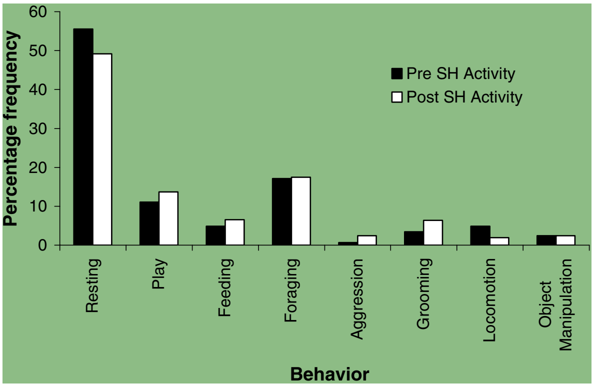


Fig. 1 Comparison of troop activity budgets in 4 seasons.

determine the possible proximate cause of stone-handling (Fig. 2). There is a significant difference between the activities individuals performed before starting a stone handling bout (Friedman: $\chi^2=172.50$, df=6, $p<0.001$, $n=45$; Fig. 2). Multiple pairwise comparisons between activities show significant differences between resting and aggression and resting and object manipulation ($p<0.05$), but not between any other activity. Resting (55%) was the most common activity in which an individual engaged just before starting a stone-handling bout. The other most common activities displayed were foraging (17%) and social play (11%). The least common activity was aggression (0.6%; Fig. 2). Resting (49%) was again the most common activity that an individual displayed immediately after stone-handling and foraging (17%), and playing (14%) followed resting (Fig. 2).

Fig. 2 Activity an individual performed before and immediately after a stone-handling bout.



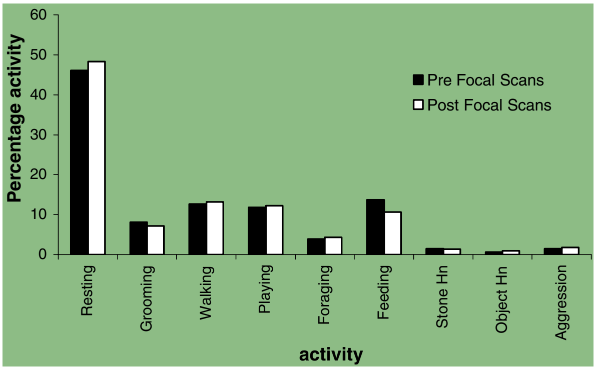


Fig. 3 Troop activity budget during focal stone-handling bout based on prefocal and postfocal scans of the troop.

Effect of Other Troop Members and External Disturbances

We used prefocal and postfocal scans to describe the overall activity of troop members when a focal individual was handling stones (Fig. 3). Stone-handling occurred most often when >50% of the other troop members were resting (Fig. 3). The 2 other most common behaviors at the time were grooming (9%) and feeding (10%). Aggressive encounters among other troop members in prefocal scans were also relatively infrequent versus other activities (15%, 351/2361 total focal observations of stone handlers). There is no statistically significant relationship between prefocal scan troop aggression and the occurrence of stone-handling in subsequent focal observations (χ^2 with Yates correction = 2.6887, 2 sided; p=0.1011).

Conversely, drastic external disturbances such as the capture of the whole troop for their annual health checkup had a profound effect on stone-handling. We calculated the percentage of occurrence of stone-handling over total focal sessions per week after the October 2003 medical checkup. A return to normal stone-handling level is gradual, starting with a nearly total absence of stone-handling in the first week after capture and release on October 7. The percentage frequencies of stone-handling for the 3 wk after a medical examination are: wk 1: 8% (October 8–14); wk 2: 25% (October 15–21); wk 3: 45% (October 22–30).

Discussion

Environmental and social factors are associated with variation in the occurrence of stone-handling in Takahama troop. Individuals tended to handle stones more under milder climatic and less under stressful social conditions. Our findings are consistent with previous reports from less systematic, albeit long-term surveys of stone-handling in 2 free-ranging troops at Arashiyama and Takasakiyama (Huffman 1984, 1996).

Environmental factors can be important determinants of when and how frequently stone-handling occurs. Monkeys handled stones more in summer, when the temperature was warmer, than in winter; thus, the significant positive correlation between daily temperature and number of bouts further supports our results. Similarly, the frequency of stone-handling in our study troop was lowest on rainy days and more frequent in sunny weather conditions. Therefore, our results support previous studies of object manipulation by Bernstein, who revealed that object manipulation rates were higher in hot than in cold weather (geladas; monkeys: Bernstein 1975; stumptailed macaques: Bernstein 1980; mangabeys: Bernstein 1976; pig-tailed macaques: Bernstein 1972). Likewise, the studies also noted that in wet or rainy weather conditions, individual proximity to others and inactivity increased while object manipulation rate decreased noticeably (Bernstein 1975; Bernstein and Baker 1988). Other activities also show clear seasonal variation, suggesting that not only object manipulation is affected by season and weather conditions. For example, resting was highest in summer and lowest in winter, indicating that they become less active in hot weather conditions, which is supported by the low rates of locomotion in summer (Fig. 1). Bernstein (1972, 1980) reported a similar pattern for captive stump-tailed and pig- tailed macaques. In our focal troops, aggression was high in both winter and autumn, and low in summer and spring. Low aggression during summer could partly be a result of inactivity during hot weather conditions. In Takahama troop, like the Arashiyama and Takasakiyama troops, the mating season starts in November and continues until the end of January when many aggressive encounters occur in the troop, undoubtedly increasing tension among its members. Social aggression during autumn and winter could also influence the low rates of object manipulation and high rates of locomotion in the troop (Fig. 1). Environmental factors, in combination with social factors, clearly can play a key role in when and how frequently individual macaques handle stones.

Takahama troop's overall activity budget while individuals displayed stone-handling, and the activities that individuals performed just before starting a stone-handling bout, indicate that they handle stones under relaxed social conditions and not as a result of aggressive encounters with others or because of other stress-related conditions. The activity monkeys performed most before stone-handling was resting, with aggression occurring at very low levels. A gradual increase in stone–handling each week after the annual medical examination, which entails capture and anesthesia to record body mass and to collect blood samples, further supports the idea that individuals display the behavior less under stressful conditions. It takes a few weeks for behavioral normality to return, during which individuals are sensitive to the slightest sounds caused by human activities outside their enclosure. Whenever they hear such a sound, they stop what they are doing and walk together around the edge of the enclosure.

Our results are in sharp contrast to conclusions based on the analysis of 21 focal sessions (30 min each) on 21 adult females at Arashiyama during 2.5 mo in the fall and winter of 2000–2001 (Nishie 2002). Of the 21 focal adult females, 13 handled stones and 8 did not. Based on analyses of feeding time, aggression directed to others, self-scratching, and the subjects' relative rank, Nishie (2002) suggested emotional conflict between feeding and aggression avoidance by lower-ranking females as the main proximate factors for the occurrence of stone-handling. However, there are limits to the inferences that one can draw from that study because there was a highly skewed age-sex class in subjects (adult females), restricted seasonal data collection (mating season, colder fall and winter months), a small focal sample size (1 focal observation/individual), and an inflated data base using 5 s of stone-handling inactivity instead of the standardized 120 s used in all other systematic studies of stone-handling to quantify bouts (Huffman 1996; Leca et al. 2007; Nahallage and Huffman 2007a). Clearly the factors lead to potential biases that one cannot ignore and limit the potential of any conclusion derived therefrom to explain proximate factors responsible for stone-handling in general from the data. Our data are not directly compatible with those of Nishie, making a direct test of his hypothesis from the results of our study impossible. Nonetheless in 578 stone-handling bouts, we found no relationship between feeding or aggression and the occurrence of stone-handling. In addition, the fact that in both Arashiyama and Takahama, >85% and 93% of troop members, respectively, perform stone-handling (Huffman 1996; Nahallage and Huffman 2007a; Huffman and Quiatt 1986), and that all infants acquire the behavior within the first 6 mo postpartum (Huffman 1996; Nahallage and Huffman 2007b) contradicts the suggestion that lower-ranking individuals perform it (Nishie 2002).

A short 5-d study (38 h, 52 focal individuals) in Takasakiyama troop examining the duration of stone-handling by individuals receiving aggression during feeding showed that they do not handle stones or do so (do not handle stones, $n=2/23$; handle stones, $n=21/23$) for statistically significantly shorter durations (56 s±39.82, range 0–144 s) than nonaggressed stone handlers did ($n=29$, 165 s±117.42, range 0–422 s) (Nahallage, *unpub. data*). Further, the latency period before starting stone-handling was significantly greater in aggressed (105 s±100.55, range 7–421 s) versus nonaggressed (21 s±31.36, range 1–149 s) stone-handlers (Nahallage, *unpub. data*). The negative impact of aggression on duration and latency of stone-handling in the Takasakiyama free-ranging troop and the lack of a relationship between feeding and aggression on stone-handling in our captive in the Takahama troop strongly support the idea that such object play is most likely to occur under nonstressful conditions.

There are differences in the occurrence of stone-handling between captive and provisioned free-ranging troops. In captive troops, stone-handling occurs throughout the day (Nahallage 2005; Nahallage and Huffman 2007a), and in provisioned free-ranging troops it occurs soon after provisioning (Huffman 1984, 1996; Leca *et al.* 2007; Nahallage 2005). For provisioned free-ranging troops, one could reason that due to a large troop size and less food availability per individual at regular time intervals, a monkey's main concern is to gather as much food as possible into its cheek pouches over the short period it remains in the feeding ground. Once monkeys gather enough food, they move away from the provisioning ground to start chewing on the food and to handle stones. No doubt the provisioning situation is stressful, but it is not proof that individuals handle stones because they are stressed, only that the behavior occurs more often in provisioned troops after they have obtained food. In natural situations, when monkeys feed or forage they simultaneously use both their hands and mouth. However, provisioned free-ranging troops first gather food into the cheek pouches because of competition and later chew slowly, for which they use only their mouth. Therefore, they may want to engage in some form of activity with their hands while they chew. This is one interpretation for why macaques continue to handle stones until they finish the food in their cheek pouches (Huffman and Quiatt 1986), but does not explain the situation for captive troops because there is no relationship with feeding. An alternative explanation for the occurrence of stone-handling in adults of free-ranging troops, which is consistent with results of both free-ranging (Huffman 1984, 1996) and captive troops (Nahallage and Huffman 2007a; this study), is that under the daily routine of gathering food in the restricted space of the provisioning grounds, once they have filled their cheek pouches, monkeys disassociate themselves from feeding competition and move away to a quieter place. The relaxed state could heighten their motivation to handle stones, while they finish the food in their cheek pouches before moving on to forage on natural vegetation or to socialize with other individuals.

Overall, one can interpret our results as an indication that monkeys perform stone-handling most often under climatically favorable and socially relaxed conditions, as expected for any form of play behavior. We found no evidence that stone-handling occurs as a result of stressful conditions alone. In troops where stone-handling is closely linked to provisioning of food, it is important to investigate systematically and in detail the possible effects of provisioning frequency and food type on the occurrence and form of stone-handling (Leca et al. in press). Stone–handling occurs at 11 sites across Japan, in both captive and provisioned free-ranging troops, and further extensive investigation and comparison of all factors likely to affect stone-handling is needed that would further clarify the function and nature of stone-handling and the effects of different ecological and social factors responsible for intersite variation in this and other behavioral traditions.

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Research Article

Comparison of Stone Handling Behavior in Two Macaque Species: Implications for the Role of Phylogeny and Environment in Primate Cultural Variation

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This study describes the stone handling (SH) behavior of captive rhesus macaques and compares it with that of a captive troop of Japanese macaques with reference to the relative contributions of phylogeny-driven behavioral propensities, environmental differences and socially facilitated learning to the formation of culture. These systematically collected data demonstrate for the first time that two closely related macaque species might share a common cultural behavior, SH. The rhesus troop displayed SH behavioral patterns that was already described in Japanese macaque troops. The one exception was a new pattern not yet seen in any Japanese macaque troop. Differences in the physical environment of the two study enclosures may be responsible for some of the variation in observed SH behavioral patterns in these two troops. These data support the idea that environmental factors can be important for the formation of cultural variation, when the key materials needed to perform the behavior are present in both habitats (stones). Our results are consistent with the prediction made by Huffman and Hirata [The biology of tradition: Models and evidence. Cambridge: Cambridge University Press. p 267–296] that an interactive triad of phylogenetic, environmental and social factors can be responsible for the formation of cultural variation in primates. Am. J. Primatol. 70:1124–1132, 2008. © 2008 Wiley-Liss, Inc.

Key words: *M. fuscata*; *M. mulatta*; behavioral predisposition; object play; environment

INTRODUCTION

Many studies have used inter-population behavioral variation within a species and between subspecies to search for culture in primates [e.g. Galef, 2003; Hohmann & Fruth, 2003; Itani, 1958; Leca et al., 2007a; McGrew, 1992; Perry et al., 2003; van Schaik et al., 2003; Whiten et al., 1999, 2001]. Some emphasize that inter-troop cultural differences in behavior are based solely on social processes [Janson & Smith, 2003; McGrew, 1992; van Schaik et al., 2003; Whiten et al., 1999, 2001]. It is often difficult, however, to demonstrate the contribution of social learning in wild populations to the acquisition and transmission of a specific behavior across generations. In the absence of clear evidence for social learning in most field studies, caution about attributing culture to behavioral variation has been voiced, noting that ecological influences (i.e. absence of conditions for the behavior to occur), genetics or individual trial and error learning are more parsimonious explanations for observed variation [Galef, 1992; Janik, 2001; Laland & Janik, 2006; Tomasello, 1994]. Perry and Manson [2003] state that the influence of ecological and genetic factors need not be completely eliminated for behavioral patterns to be defined as culture, as long as social influences can be demonstrated in the acquisition of the behavior. Others too have discussed the biological and ecological foundations of culture. Based on the studies of self-medication in the African great apes and stone handling (SH) in Japanese macaques, Huffman and Hirata [2003] predicted that cultural behaviors could be ‘‘shared’’ by different populations, between which cultural transmission is not physically possible, regardless of whether they are the same species, different subspecies or even closely related species. They argued that if there is evidence for social learning in the acquisition and diffusion of a particular behavior within a group (or species), and that behavior is present across groups of the same or closely related species, then phylogeny-driven behavioral propensities and environmental factors (habitat structure, season) could have a positive role in the occurrence of cultural variation in that behavior.

Very few studies, however, have looked at putative cultural behaviors shared by two different

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but phylogenetically close primate species [Hohmann & Fruth, 2003: bonobo-chimpanzees; Huffman and Hirata, 2003: African great apes, Japanese and long-tailed macaques]. To date, no systematic behavioral study has compared a putative cultural behavior present in two species to appraise these predictions. Here, we evaluate this prediction with SH, a known cultural behavior in Japanese macaques.

SH is one of the best-studied cultural behaviors in Japanese macaques [Huffman, 1984, 1996; Huffman & Hirata, 2003; Huffman & Quiatt, 1986; Leca et al., 2007a,b; Nahallage & Huffman, 2007a,b, 2008]. SH is a solitary object play behavior consisting of the manipulation of stones in different ways, e.g. gather, clack, strike together and scatter [Huffman, 1984, 1996]. Appearance of SH, its initial transmission among other troop members and long-term diffusion across generations spanning three decades are well documented for the Arashiyama troop, where the behavior was first observed in 1979 [Huffman, 1996]. SH consists of a suite of behavioral patterns that has significant individual as well as inter-group level variation [Leca et al., 2007a; Nahallage & Huffman, 2007a]. To date, 45 behavioral patterns of SH have been recorded from ten different populations. Troops that live in close proximity to each other displayed similar SH patterns compared with the troops that live apart, indicating the existence of cultural zones in populations living in close proximity [Leca et al., 2007a]. Furthermore, no major difference was found in the occurrence and form of SH between the two Japanese macaque subspecies (*Macaca fuscata fuscata* and *Macaca fuscata yakui*) [Leca et al., 2007a].

Socially biased learning plays an important role in the initial acquisition of SH by infants in both free-ranging and captive troops [Huffman, 1996; Nahallage & Huffman, 2007b]. In a systematic 18-month study in the captive Takahama troop at the Primate Research Institute, Kyoto University, the timing of acquisition of SH by infants was shown to depend on the level of proximity to the mother, the frequency of SH performed by the mother and the prior attention paid to the mother's SH [Nahallage & Huffman, 2007b]. If the mother did not display SH, the infant only began to do so after proximity to SH peers increased from around 4–5 months of age [Nahallage & Huffman, 2007b]. Together, the above-mentioned studies of SH in Japanese macaques support Huffman and Hirata's [2003] predictions about the interplay of phylogeny, environmental and social factors.

In this article, we analyze for the first time SH behavior in rhesus macaques and compare it with the Takahama troop of Japanese macaques. We investigated whether there were similarities in the type of behavioral patterns displayed by the individuals of these two species and investigate the possible role of environment for group-level behavioral variation.

METHODS

Subjects and Housing Conditions

Our study was conducted at Kyoto University's Primate Research Institute, Inuyama. This research was approved by and conducted in accordance with the Primate Research Institute's Rules and Guidelines for Animal Health and Welfare. The Takahama captive Japanese macaque troop was housed in a 960 m^2 outdoor enclosure. This troop consisted of 48 monkeys of different age–sex classes; the oldest individual was 30 years of age (Fig. 1). Out of these 48 monkeys, 45 were observed to stone handle and these were all used in our analyses [Nahallage & Huffman, 2007a]. The captive rhesus troop was housed in a 680 m^2 outdoor enclosure. The troop consisted of 29 monkeys of different age–sex classes, the oldest individual was 11 years of age and the troop consists of relatively young individuals compared with the Japanese macaque troop (Fig. 1). Except for four adult monkeys, all rhesus troop members' stone handled during their focal sessions and were used for the analysis. The four adults not included were rare stone handlers. We had ad libitum recordings only to verify that they exhibited SH. We define young as individuals from newborn to up to 4 years of age and adult as individuals over 5 years of age [Nahallage & Huffman, 2007a].

The Japanese macaque enclosure was equipped with metal climbing structures, swings and aluminum sleeping boxes (Fig. 2). Total climbing structure area was 82.56 m^2 (9% of the enclosure) consisting of 118 metal pipes (diameter 5 cm, length −3 to 4 m) constructed about 30 cm above the ground. The climbing structures of the rhesus enclosure consisted of wide flat wooden walking structures and logs built 2 m above the ground and connected by bolts and joints (Fig. 2). Total climbing structure area for the rhesus enclosure was 406.88 m^2 (60% of the enclosure), consisting of 267 wooden logs (diameter 18–25 cm, length 4–5 m) and 42 flat wooden planks (height × width −5 cm × 12 cm, length −3 to 5 m). Monkeys used these pathways for locomotion, playing, resting, feeding, SH, etc. The ground of the Japanese macaque enclosure had three flat terrace areas at different elevations separated by two cement slopes. Stones could only be found on the flat areas (ranging $8 \times 10 \times 7$ mm to $92 \times 62 \times 41$ mm in size) [Nahallage & Huffman, 2007b]. Although for safety reasons we did not enter the rhesus enclosure, visual inspection from outside allowed us to conclude that there was no obvious difference in stone size or availability between the two study enclosures.

We out rule the possibility of inter-species observation of SH between these two groups, because they were located on the opposite sides of the institute campus. The possibility that the rhesus macaques observed other neighboring groups of SH Japanese macaques cannot be completely out ruled.

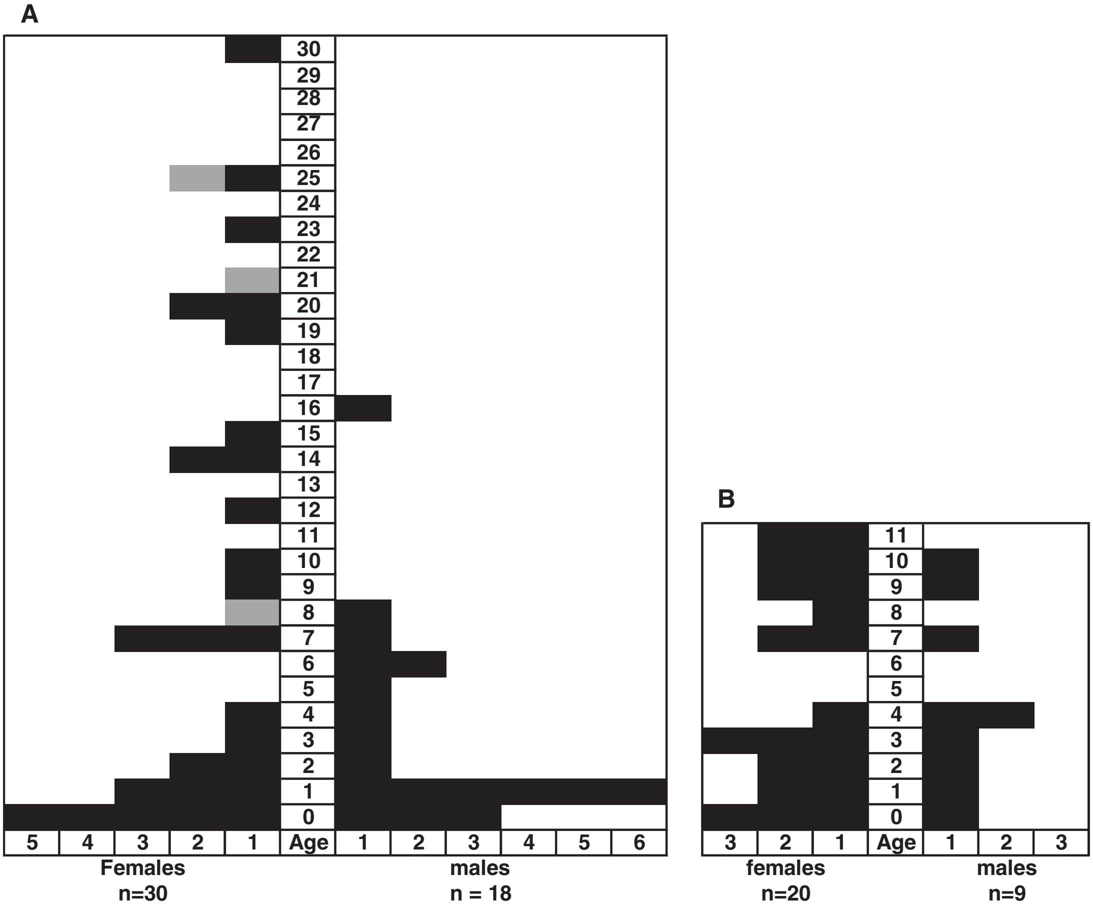

Fig. 1. Histogram of the age sex distribution of the two troops; (A) Japanese macaque troop; (B) rhesus macaque troop (black: verified stone handlers, gray: verified nonstone handler.

However, the nearest SH Japanese macaque enclosure is about 5 m away, and the high walls of the enclosures make direct observations of SH in other neighboring Japanese macaques unlikely. Furthermore, the appearance of SH in the rhesus group has been suggested by primate care staff Mr. Kiyonori Kumazaki as coinciding after the construction of the enclosure's pond in 1998 when stones used in its construction were left in the enclosure (personal communication).

Data Collection

We used continuous focal animal sampling for data collection [Altmann, 1974]. Each focal session was video recorded for 15 min using a digital video camera (Sony Digital Handycam, China). The focal session was extended if SH was still in progress or started toward the end of the session. The session was continued for 5 min after the last contact with stones and terminated thereafter, if there was no further contact with stones [Huffman, 1996].

We collected data on the Takahama troop from June 2003 through November 2004. An equal number of observations were made on all members of the group in all seasons of the year (spring: March–May; summer: June–August; autumn: September–November; winter: December–February). Each individual was sampled 43 times, and a total of 878 observation hours were obtained [Nahallage & Huffman, 2007a]. The analyses presented below for Japanese macaques are based on a total of 578 SH bouts recorded from 45 individuals. A SH bout is defined as the occurrence of the behavior with pauses of no longer than 120 sec, the duration after which further SH is significantly less likely to resume [Huffman, 1996]. If SH resumed after more than 120 sec, it was treated as a separate bout.

Data collection of the rhesus group was conducted from December 2003 to August 2004. We collected data for three seasons (excluding autumn, owing to the disturbance caused by construction work on the adjacent enclosure). Each individual was sampled 30 times on average (SD = 1.43) and a total of 363 observation hours were obtained. The analyses presented below for rhesus macaques are based on a total of 103 SH bouts recorded from 25 individuals.

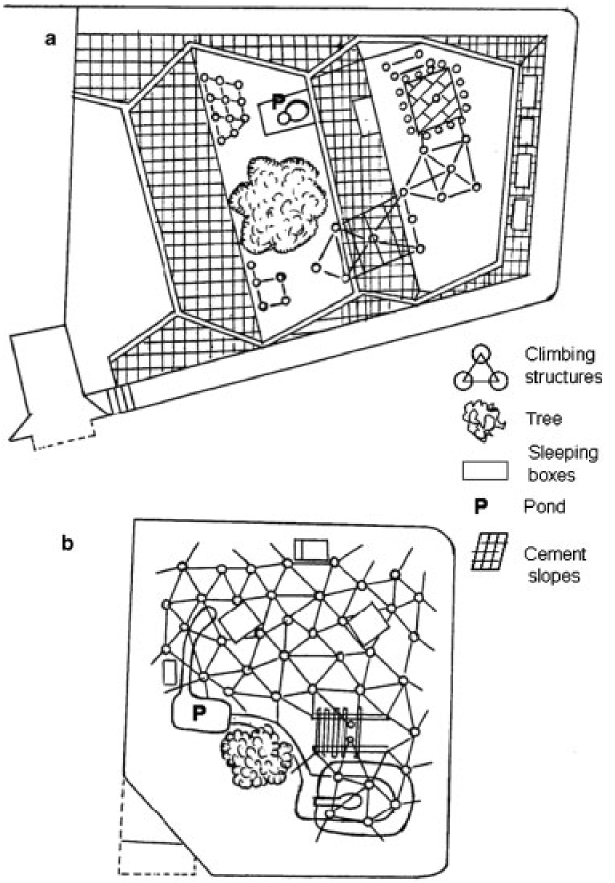

Fig. 2. Two enclosure structures; (a) Takahama Japanese macaque enclosure (b) rhesus macaque enclosure.

Data Analysis

From video focal records we calculated the duration and frequency of SH bouts, frequency of behavioral patterns in each bout, whether SH was a solitary or communal activity (sitting within 1–2 m to a another stone handler or within that individuals visibility range) and whether it occurred on or off ground. We grouped the SH behaviors into five categories according to their basic motor pattern: (i) investigatory, (ii) locomotion, (iii) collecting/gathering (iv) sound production and (v) combine with objects and other complex behaviors [Nahallage & Huffman, 2007a]. For the purpose of comparison, we grouped investigatory, locomotion and collecting/gathering as simple activities, and sound production and other complex patterns as complex activities [see also Leca et al., 2007a]. To assess behavioral variants of SH in each group, we adopted and modified the definitions used by Whiten et al. [1999, 2001] and Leca et al. [2007a]. The definitions of occurrence were (1) ''customary'' if exhibited by more than 70% of group members, (2) ''habitual'' if exhibited by 50–70% of group members, (3) ''present'' if exhibited by 25–50% of members, (4) ''rare'' when exhibited by less than 25% but more than 0% of the group members and (5) ''absent'' instead of ''unknown'', for 0%, considering that we spent 878 and 368 hr observing Takahama and rhesus groups, respectively. For statistical analysis, we performed two-tailed nonparametric tests using SPSS (version 10), and α was set at $P \leq 0.05$.

RESULTS

Comparison of Behavioral Patterns Between Species

There was a difference in the total number of SH behavioral patterns displayed by the two species. The rhesus macaque troop displayed 23 patterns, whereas the Japanese macaque troop displayed 45 patterns. All but one of the 23 rhesus SH behaviors were displayed by the Japanese macaques (Table I). In addition, the rhesus macaques had a statistically significant lower SH rate in relation to Japanese macaques (Mann–Whitney, $U = 304.00$, $N1 = 45$, $N2 = 25$, $P = 0.002$). Mean SH rate for rhesus and Japanese macaques is 0.57 ± 0.44 bouts/hr and 1.18 ± 0.78 bouts/hr, respectively.

Rhesus macaques displayed a behavioral variant that has not been observed in any of the ten Japanese macaque troops studied so far. We called this behavioral pattern ''insert into a cavity'' (IC); where a monkey repeatedly inserts and takes out a stone from a cavity or the open end of a pipe. Only five individuals were observed to exhibit this behavior.

When we grouped the 46 behavioral patterns displayed by one or both macaque species according to the frequency of occurrence, Japanese macaques had seven customary behavioral patterns (pick, hold, bite, grasp walk, carry, rub on surface and roll in hand) and five habitual ones (lick, sniff, cuddle, put in mouth, scatter) (Table I). In rhesus macaques three behavioral patterns were customary (hold, carry and rub on surface) and five were habitual (pick, bite, lick, put in mouth and grasp walk) (Table I). As the total number of behavioral patterns displayed was different for each species, we compared the proportions of behaviors displayed. The proportion of customary behaviors displayed by Japanese and rhesus species were 13.04 and 15.55%, respectively. The proportion of habitual behaviors displayed by Japanese and rhesus species were 21.74 and 24.44%, respectively (Table I). Even though the behaviors ''hold,'' ''carry'' and ''rub on surface'' were customary in both species, expressed as the mean percentage of behaviors performed by each troop, they were more common in the rhesus macaques (rhesus: 23, 11 and 25%, respectively, Japanese macaques: 15, 3 and 12%, respectively) (Fig. 3(a)). One of the most conspicuous differences between the two troops was the high percentage of ''rub on surface'' behavior displayed by both young and adult rhesus macaques (Fig. 3(a, c)).

TABLE I. Frequency of Occurrence of the Stone Handling Behaviors According to Two Species and Age-class. C: Customary, H: Habitual, P: Present, R: Rare, (–): Absent

Behavioral pattern	*Macaca mulata*	*Macaca fuscata*	Adult (M.m)	Adult (M.f)	Young (M.m)	Young (M.f)
Investigative						
Pick (PI)	H	C	P	C	C	C
Hold (H)	C	C	C	C	C	C
Bite (B)	H	C	P	C	C	C
Lick (L)	P	H	H	H	P	H
Sniff (SN)	H	H	H	H	H	H
Cuddle (CD)	R	H	–	R	R	C
Put in mouth (PIM)	H	H	P	H	H	C
Move in mouth (MIM)	R	P	R	P	R	R
Locomotive						
Move and push (MP)	R	R	–	–	P	P
Grasp walk (GW)	H	C	P	H	H	C
Carry (CA)	C	C	P	P	C	C
Carry in mouth (CIM)	P	P	R	P	P	H
Toss walk (TW)	R	P	–	R	R	P
Collecting/gathering						
Insert into cavity (IC)	R	–	R	–	R	–
Gathering (GA)	–	P	–	P	–	P
Pick up (PU)	–	R	–	P	–	R
Pick up small stones (PUS)	R	R	–	R	R	R
Pick up and drop (PUD)	R	R	–	R	R	R
Grasp with hands (GH)	–	R	–	R	–	–
Sound producing activities						
Rub on surface (ROS)	C	C	H	H	C	C
Roll in hands (RIH)	R	C	R	H	P	C
Rub together (RT)	R	R	R	R	P	P
Scatter (SC)	R	H	R	P	R	H
Clacking (CL)	R	R	–	R	R	P
Rub with hands (RWH)	–	R	–	P	–	R
Pound on surface (POS)	–	R	–	R	–	R
Slapping (SL)	–	R	–	R	–	R
Rub with mouth (RWM)	–	R	–	–	–	R
Rub in mouth (RIM)	R	R	R	–	R	R
Tap in mouth (TIM)	–	R	–	R	–	R
Flinting (FL)	–	R	–	P	–	P
Flip (F)	–	R	–	R	–	R
Swiping (SW)	–	R	–	R	–	–
Flint in mouth (FIM)	–	R	–	R	–	–
Combination with other objects and complex activities						
Put in water (PIM)	–	R	–	–	–	R
Wrap in leaves (WIL)	–	R	–	–	–	R
Rub on fur (ROF)	–	R	–	–	–	R
Combine with objects (COO)	R	R	–	R	R	P
Throw (TH)	–	R	–	–	–	R
Stone groom (SGR)	–	R	–	–	–	R
Shake in hand (SIH)	–	R	–	R	–	R
Wash (W)	–	R	–	R	–	R
Spin (SP)	–	R	–	R	–	–
Throw and sway (TS)	–	R	–	R	–	–
Jump and throw (JT)	–	R	–	R	–	R
Run and throw (RAT)	–	R	–	R	–	–
Total number	23	45	16	37	23	39
No. of simple behaviors	16	18	11	17	16	17
No. of complex behaviors	7	27	5	20	7	22

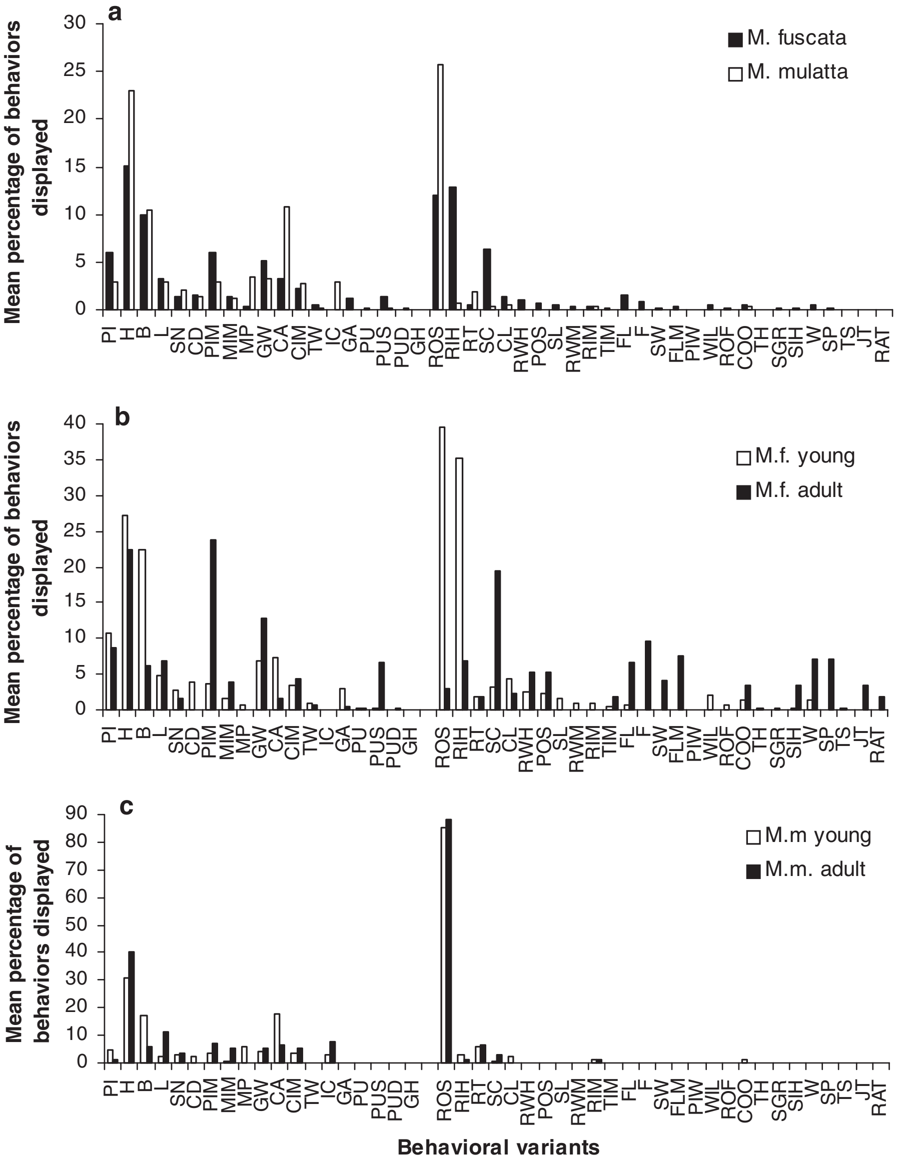

Fig. 3. Mean percentage of stone handling behaviors displayed by (a) two macaque species; (b) adults and young of Japanese macaques; (c) adults and young of rhesus macaques.

Simple and Complex Behavioral Patterns

This analysis was done to find out how demographic factors might affect SH. There were 19 simple behaviors and 27 complex behaviors in the SH repertoire of macaques (Table I). When we calculate the percentage of complex behaviors over the sum of complex and simple behaviors for each individual, Japanese macaques displayed more complex behaviors than rhesus macaques (Mann–Whitney, $U = 250.00$, $N1 = 45$, $N2 = 25$, $P < 0.001$). The numbers of simple and complex behaviors performed by rhesus macaques were 16 and 7, respectively, and for Japanese macaques 18 and 27, respectively. As the oldest rhesus were 11 years of age, we also compared the rhesus SH patterns with those of Japanese macaques below 11 years of age. The outcome was similar: Japanese macaques displayed significantly more complex behaviors than rhesus macaques (25 complex behaviors; Mann–Whitney, $U = 179.50$, $N1 = 34$, $N2 = 25$, $P < 0.001$).

When we exclude the two most common complex behaviors (“rub on surface” and “roll in hand”) displayed by adults and young, there is a significant difference between the frequency of complex behaviors displayed by young and adult Japanese macaques (Mann–Whitney, $U = 159.50$, $N1 = 25$, $N2 = 20$, $P = 0.038$), with adults displaying complex behaviors more frequently (Fig. 3(b)).

SH Activity on the Ground, Above the Ground, and Solitary Vs. Communal

Concerning the percentage of individuals' SH time spent above the ground, there was a significant difference between troops (Mann–Whitney, $U = 125.50$, $N1 = 45$, $N2 = 25$, $P < 0.001$). Rhesus macaques spent more SH time above the ground, on the climbing structure, than Japanese macaques. Japanese monkeys spent 85% of time SH on the ground and 15% on the climbing structures above the ground. Rhesus monkeys spent 67% SH on the wooden structures compared with 33% on the ground. Furthermore, rhesus macaques displayed more communal SH than Japanese macaques (Mann–Whitney, $U = 333.50$, $N1 = 45$, $N2 = 25$, $P = 0.004$).

DISCUSSION

Shared Behavioral Propensity for SH

The occurrence of SH behavior in rhesus macaques confirms the prediction that these two closely related macaque species share a behavioral propensity for SH. There is no compelling evidence to suggest that observed differences are owing to the inherent species differences. With the exception of one behavior, ''insert into cavity,'' all behaviors displayed by the rhesus macaques are typical SH behavioral patterns of Japanese macaques. It should be noted that among all Japanese macaques troops studied to date, Takahama troop exhibits the greatest number of SH behaviors, in fact all the behaviors known for Japanese macaques. Even though the rhesus macaque troop exhibited a lower SH rate and displayed fewer SH patterns than the Takahama troop, both rate of occurrence and patterns exhibited fall within the recorded range observed in Japanese macaque troops [Leca et al., 2007a]. The SH rate for ten captive and free-ranging Japanese macaque troops ranged from 0.1 to 5.9 per hour and the overall number of SH patterns exhibited per troop ranged from 17 to 45 [Leca et al., 2007a]. The rhesus macaque troop falls above the captive PRI Arashiyama troop and the free-ranging Koshima troop in both SH rate and the number of behaviors displayed (Arashiyama: SH rate 0.2/hr, 17 behaviors; Koshima: SH rate 0.1/hr, 16 behaviors; Leca et al., 2007a).

Interestingly, a similar trend was reported for tool use behavior in chimpanzees and bonobos. Hohmann and Fruth [2003] stated that the extent of tool use by bonobos appears to be at the lower end of the range for chimpanzees, resembling that of the chimpanzee populations of Kibale and Budongo. This was attributed to the differences in the evolution of material culture in these two *Pan* species [Hohmann & Fruth, 2003]. Bonobos' lack of need to engage in tool use for food acquisition is another possibility [McGrew et al., 1997]. In the case of SH, however, stones are readily available for all troops [Leca et al., 2008], ruling out an ecological difference.

All customary behaviors and some of the habitual SH behaviors displayed by the rhesus and Japanese macaques studied here are common object manipulative behaviors of many Old-World Monkeys [Torigoe, 1985]. SH behavior has also been observed in a few troops of *M. fascicularis* (Florida Monkey Jungle—A. Zeller; Ubud, Bali-Indonesia—A. Fuentes; Thailand—K. Bauer, Myanmar—Aye Mi San personal communication). All of these troops were captive or provisioned free ranging. It has not yet been reported in *M. cyclopis* another member of this species group. This may reflect the paucity of research on captive or provisioned troops of this species. So far, no other macaque taxonomic groups, i.e. *sylvana*, *silenus*, *sinica* or *arctoides* have been reported to SH. It will be of interest to see just how widely SH occurs among other macaque species.

Socio-Demographic Factors Influencing Behavioral Variation of SH

Demographic structure and the duration for which these cultures have been present in each troop may also contribute to the quantitative differences between SH in the rhesus and Japanese macaque troops. In Japanese macaques, a troop's SH repertoire increases over time, and the newly emerging behavioral patterns become more specialized. At Arashiyama in 1983, 5 years after the behavior's innovation, the troop displayed eight SH behavioral patterns. By 1989–1990, Arashiyama and Takasakiyama troops displayed 17 and 16 behavioral patterns, respectively [Huffman, 1984, 1996]. In 2004, almost 21 years later, the SH repertoire had increased in number to 32 and 31, respectively [Leca et al., 2007a].

Infant Japanese macaques start SH with a few basic patterns, then the number and complexity of behaviors gradually increases with age, peaking at 3–4 years [Nahallage & Huffman, 2007b]. In the Takahama troop most of the complex behaviors were displayed by the individuals over 15 years of age [Nahallage & Huffman, 2007a]. The absence of older adults may therefore be one reason for the lack of more complex behaviors in the PRI rhesus troop's repertoire.

SH first begun in the rhesus troop about 10 years ago in 1998 (see Methods), much more recently than in the Takahama troop, which is thought to have started SH around 25–30 years ago [Nahallage & Huffman, 2007a]. The rhesus macaque troop's current demography, behavioral profile (mostly simple, nonspecialized behaviors) and the small number of SH patterns displayed are all consistent with this relatively recent emergence of SH.

It has recently been demonstrated that social learning plays a key role in the acquisition of SH behavior by infant Japanese macaques [Nahallage & Huffman 2007b]. The age of acquisition of SH varied from infant to infant (6–31 weeks) and was closely related to the frequency of SH exhibited by an infant's mother. When we started our observation on the rhesus macaque troop the infants that year were already older than six months and they were all observed to SH. Our comparison with Japanese macaques leads us to conclude that SH can be considered a cultural behavior in rhesus macaques. We assume that this troop has at least reached the tradition phase, at which the behavior is now passed down from mother to offspring and/or other multigenerational lines.

Environmental Factors Influencing Cultural Behavioral Variation

Another possible reason for the behavioral variation between two troops is the physical environment of their enclosures, especially the climbing structure areas. These structures constitute 60% of the rhesus macaques and only 9% of Japanese macaques' enclosures. The rhesus often rub stones on the metal bolts of the climbing structures, presumably for the sound it produces. The loud sound that results appears to draw others attention to the behavior. Several individuals, irrespective of age, may then pick up a stone(s) and carry it (them) on to the wooden walkways and start rubbing them against the iron bolts. The bolted junctures of these walkways are close together, bringing SH individuals into close proximity with each other. The synchronization of SH in rhesus macaques could thus be explained by the contagious nature of play behavior [Huffman, 1984; Leca et al., 2007b].

As a direct consequence of these environmental factors, rhesus macaques displayed the ''rub on surface'' pattern more, and SH more on these wooden structures, above the ground. This also explains the high percentage of communal SH in rhesus compared with Japanese macaques. The Japanese macaque enclosure does not have wooden walkways. When they perform ''rub on surface'' they do so on the ground on the cement passageway, and the sound produced does not appear to stimulate SH in other troop members. They perform more solitary SH bouts, mainly on the ground, and the frequency of ''rub on surface'' is lower than in the rhesus troop.

All the above factors support the view that SH in the two species studied is owing to the combination of shared phylogenetic behavioral propensities, and environmental and social factors. Other factors may also contribute to the cultural variation seen in other behavioral contexts. Further studies of inter-species cultural variation in animals within the framework of the predictions evaluated here are encouraged. Such work promises to provide insight into the interface of phylogenetic and ecological factors influencing the processes and mechanisms of a cultural behavior.

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11. CULTURED JAPANESE MACAQUES - A MULTI-DISCIPLINARY APPROACH TO STONE HANDLING BEHAVIOR AND ITS IMPLICATIONS FOR THE EVOLUTION OF BEHAVIORAL TRADITIONS IN NON-HUMAN PRIMATES

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11.1. Abstract

Japanese primatologists have paid attention to cultural phenomena in non-human primates since its earliest stage. The most famous example of behavioral traditions in Japanese macaques is probably sweet potato washing behavior. After being innovated by a young female on Koshima Islet, this behavior was socially transmitted from the innovator to most other group members. More recently, stone handling (SH) behavior, a form of solitary object play, also became a well-known example of culture in this species. A longitudinal study allowed following the appearance, subsequent transmission, and transformation processes over 30 years and across multiple generations in a provisioned group at Arashiyama, Kyoto. Also under more controlled conditions of captivity, we assessed how the individual acquisition, expression, and possible functional aspects of SH behavior may be influenced by specific environmental factors, access to demonstrators by naïve individuals (typically within mother-infant dyads), and neuro-motor developmental constraints. Finally, a 10 troop inter-site comparison of this behavior was carried out to investigate the genetic, ecological, and socio-demographic factors that may affect the innovation, spread, and maintenance of the SH culture. This research on SH is the most extensive and systematic survey focused on the intra- and inter-group variability of a single type of behavior in monkeys to date.

11.2 Introduction

The concept of culture (also referred to as behavioral tradition) in animals was first proposed in 1952 by the founder of primatology in Japan, Kinji Imanishi, who predicted that culture should be present in all socially living animals. By the early 1950s, provisioning and individual recognition of all members of several Japanese macaque (*Macaca fuscata*) troops across Japan were accomplished, including Koshima, Takasakiyama, Arashiyama, and Minoo. Thus started the practice of long-term comparative and collaborative research, one of the many early contributions by Japanese scientists to the field of primatology (Huffman 1991; Yamagiwa and Hill 1998; Takahata et al. 1999). Provisioning provided the first outdoor laboratory situation for recording the process of behavioral innovation and diffusion of behaviors in a novel environment and research at these sites has contributed much to our understanding of the patterns of diffusion of innovative behavior in primates (reviewed in Itani and Nishimura 1973; Nishida 1987; Thierry 1994; Huffman and Hirata 2003).

Perhaps the most widely cited evidence for culture in animals is the innovation and transmission of sweet potato washing behavior in the Japanese macaques on Koshima Island, Miyazaki Prefecture, Kyushu (Kawai 1965). More recent work in Japanese macaques has focused specifically on the innovation and diffusion of new behaviors across individuals and the establishment of group-specific behavioral traditions in free-ranging provisioned troops (Huffman 1984, 1996; Huffman and Quiatt 1986; Watanabe 1994; Leca et al. 2007a). Extensive collaborative field studies of socially learned behaviors among the great apes, have also documented complex behavioral traditions in chimpanzees (Tomasello 1990; Whiten et al. 1999) and orangutans (van Schaik et al. 2003a).

Evidence for socially mediated learning and culture in many species now exists, including the great apes, New World monkeys, rats, cetaceans, birds and fish (see Fragaszy and Perry 2003). These examples range from the opening of milk bottle caps by British tit birds (Fisher and Hinde 1950, 1952) and pinecone stripping by Israeli black rats (Aisner and Terkel 1992; Terkel 1996) to examples including transmission of behaviors sometimes leading to social traditions as diverse as mate choice in guppies (Dugatkin 1996), new vocalizations in ravens (Enggist-Dueblin and Pfister 2002), feeding techniques of Tonkean macaques (Drapier and Thierry 2002), abnormal behaviors of captive rhesus macaques (Hook et al. 2002) and prey capture by killer whales (Rendell and Whitehead 2001). All of these studies have looked at determinants of cultural behavior, including innovation, transmission, acquisition, developmental constraints thereof, long-term maintenance and inter-group variation. However, none have considered the role of all of these factors into an integrated framework of social learning.

There are two basic approaches to the study of social learning, the underpinnings of culture. The first focuses on underlying mechanisms, i.e. 'how' the information is transferred between two individuals. Under a controlled experimental setting, a naïve subject, faced with a problem solving task, is given the opportunity to observe an experienced subject and learn from its behavioral strategies (Custance et al. 1999). The second focuses on the pathway of behavioral diffusion under natural conditions in a stable social group, i.e. from 'whom' the information is transferred (Biro et al. 2003). Inter-individual tolerance allowing spatial proximity, frequency of the behavior performed, and the attention paid to the behavior are essential factors to predict the speed of diffusion of a novel behavior and the pathway of transmission (Coussi-Korbel and Fragaszy 1995; Huffman and Hirata 2003; van Schaik et al. 2003a). However, not only social, but also environmental, demographic, and developmental constraints can affect the efficiency and speed of acquisition and diffusion of a particular behavior (Huffman and Hirata 2003). Thus far, only the study of stone handling (SH) behavior in Japanese macaques has embraced all of these determinants into the understanding of a single cultural behavior.

Our long-term study supports the idea of SH culture and provides insights into the nature of social learning, its role in the spread of behavioral innovations, the factors influencing inter-group behavioral variation, the emergence and transformation of culture, and the potential importance of culture in the process of biological evolution.

11.3 Stone handling behavior

SH is a seemingly non-adaptive solitary object play activity (Huffman 1984, 1996; but see Nahallage and Huffman 2007a and section 11.6.8 below). SH consists of manipulation of stones in various ways including rubbing or clacking them together, pounding them onto other hard surfaces, picking up and rolling them together in the hands, cuddling, carrying, pushing or throwing them (Fig. 11.1; Table 11.1). Currently 45 different behavioral patterns are documented in Japanese macaques (Leca et al. 2007a).

SH is reported to occur in four captive troops and six provisioned free-ranging troops across Japan, and still other sites are known but have not yet been systematically investigated. This behavior has been followed for 30 years across multiple generations in the Arashiyama troop, Kyoto, Japan beginning from its innovation (Huffman 1984, 1996; Leca et al. 2007a). Unlike potato washing, SH was first transmitted horizontally among playmates. Transmission began to occur vertically from elder to younger individuals around 1984. Since then, SH has been acquired by every infant in the group, but never by individuals over five years of age.

11.4 Long-term observation of the Arashiyama troop

11.4.1 Innovation

Japanese macaques have been studied at Arashiyama since 1954, after monkeys were enticed to narrow down their wide seasonal ranging patterns when provisioning was successfully initiated at the Iwatayama Monkey Park (Huffman 1991). In spite of the intense history of research at the site by many scientists in succession, SH was not noted until December 7, 1979 (Huffman 1984). The first individual recognized to perform this behaviors was the three-year-old, middle ranking female Glance-6476 (Fig. 11.2). She had brought several flat stones from the forest and was gathering them together and scattering them about with the palms of her hands on the open ground of the provisioning site. This was the first and the last time that SH was observed by Huffman during a 14-month study lasting up to September 1980.

11.4.2 Transmission

In October 1983, when Huffman returned again to Arashiyama to resume research, SH had already diffused to many members of the troop and had become a daily occurrence. SH was classified into 8 basic behavioral patterns: gathering, pick up, scatter, roll in hands, rubbing stones, clacking, carry and cuddle (Huffman 1984). By 1985, an additional 9 behavioral patterns were also recognized, with 6 of those patterns being variations of the original 8 (pick up and drop, rub of surface, flinting, pick up small stones, rub with hands, and grasp with hands). The 3 new behaviors were toss walk, move and push, and grasp walk, all behaviors considered to reflect an increasing familiarity with stones in general as the practice of SH spread and became a substantial part of the individual and the troop daily activity.

In June of 1984, 49% (115/236) of the troop exhibited SH and by June of 1985, 60% (142/236) of the troop members born before June 1984 were verified to be new SH handlers. Eighty percent (92/115) of the individuals observed were born between 1980 and 1983, after the first record of SH was made in 1979. The remaining 20% were young adult males (N= 6, 4.5 – 8.5 years old), young adult females (N= 6, 4 years old), and adult females (N= 11, 5 plus years old).

The evidence strongly suggests that SH originated from the Glance kin group, given that other than Glance-6476, the first female observed to SH in 1979, the only older individuals noted to SH were her two female cousins, Glance-6775 and Glance 6774, and a lower ranking female Blanche-596475. Unlike potato washing and wheat washing behavior, two of the earliest examples of cultural traditions in Japanese macaques, no individuals have ever been noted to acquire SH behavior after they reached the age of 5 years. This supports our observations that SH was not likely innovated earlier than 1978 or 1979, otherwise we should expect to have found older stone handlers during these early surveys. Eleven years on into the study in 1991, every individual under the age of 10 was observed to SH. Thus, unlike other examples of cultural behavior reported in Japanese macaques, SH first spread laterally among young individuals of the same age, and only began to be transmitted from adults to offspring, when the first female stone handlers began to have offspring of their own.

The route of transmission of a novel behavior is in part determined by the nature of the behavior and the social networks in which it normally occurs. Those most likely to be together while engaging in a particular kind of behavior, whether it be play, foraging, grooming or sleeping, should be more likely to learn variants of these behaviors from one another (Huffman 1996).

11.5 Environmental versus social influences of a demonstrator, and the role of developmental constraints in the acquisition and expression of stone handling

The long-term study at Arashiyama allowed us to determine the general pathways of diffusion of SH and evaluate the factors that may have contributed to the spread of SH within the group. One the one hand, mothers were presumed to be the primary source of an infant's early exposure to SH (Huffman 1984, 1996). On the other hand, we believe that there are atypical environmental conditions, such as the concomitant presence of provisioned foods and numerous stones, sometimes artificially brought by humans around the open space of feeding areas, under which the innovation and initial diffusion of SH could be facilitated (Huffman 1996; Leca et al. 2008a; Nahallage and Huffman 2008a,b).

However, only through controlled captive conditions, are we able to systematically evaluate the possible contributions of environmental, social and developmental factors to behavioral acquisition. Nahallage and Huffman (2007b) studied the SH behavior of a captive group of 48 Japanese macaques at the Primate Research Institute, Kyoto University, for 24 months spanning two breeding seasons between 2003-2005, during which 14 infants were born.

11.5.1 Environmental factors

Based on a detailed analysis on the exposure of infants to specific areas of an outdoor enclosure with varying stone availability, we failed to validate the environmental stimuli hypothesis, stating that the total time spent in areas with high stone availability and, therefore, exposure to more stones, increases the likelihood that an infant acquires SH behavior. We found no significant correlations between the age of SH acquisition and the rate of stones encountered from birth to acquisition.

11.5.2 Access to demonstrators by naïve individuals and the acquisition of behaviors

We investigated the effect of pivotal individuals as demonstrators on the initial acquisition and development of SH behavior by focusing on inter-individual interactions, in particular mother-infant dyads. In the 14 mother-infant dyads born during the study, all but one infant started SH within the first 6 months after birth. There was great variability among them in the age SH was first displayed (6-31 weeks). During their first three months of life, infants spent 75% of the time within one-meter of their mother, significantly more than they spent with other individuals. This high level of proximity to the mother had a significant impact on the age at which SH was acquired. Infants of mothers with higher SH frequencies exhibit the behavior earlier than infants of less frequent SH mothers. Two infants, born in consecutive years, to the same non-SH mother were the last to acquire the behavior. These results suggest that the acquisition of SH behavior in infants was strongly influenced by the amount of time spent in proximity to a stone handler and the frequency of the behavior displayed by that model (Nahallage and Huffman 2007b). Infants of frequent SH mothers spent proportionally twice as much time (83%) watching their mothers when she was SH than did infants whose mother showed low SH frequency (42%). The former tried to take stones away from their mothers in 75% of the SH bouts whereas the latter tried to do so in only 33% of these bouts, resulting in a difference in the amount of time an infant took part in its mother's activity. Differences in mothers' SH frequency could affect their infant's exposure to SH, opportunities to handle stones, and practice SH.

11.5.3 Constraints of neuro-motor development on the expression of SH behaviors

Few longitudinal studies have been conducted on the ontogeny of specific cultural behaviors, but rather most tend to deduce development from cross-sectional observations (Lonsdorf 2005). Furthermore, neuro-motor development has rarely been considered as a constraint in the expression of matched behavioral patterns between experienced and naïve individuals. Our study showed that though mothers had a strong influence on the initial acquisition of SH behavior in infants, infants did not perform the same behavioral patterns as adults mainly because of developmental constraints in the kinds of behaviors they could perform (Nahallage and Huffman 2007b). There was a gradual increase in the number and complexity of SH patterns displayed by infants, which revealed a neuro-motor developmental phase of this behavior. The infants we studied acquired the basic SH behaviors at around 2-3 months. Common to other behavioral traits observed during the early stages of infant development in macaques, stone manipulation patterns were quite simple actions, mainly pick up, cuddle, lick or bite a stone and typically short in duration. Infants did not perform any complex manipulative action with stones during this time. The average number of patterns performed by an individual up to 6 months of age was 3.75 ± 1.90. At around 6 months, individuals started to perform more complex stone-directed actions such as clacking or rubbing two stones together or on a substrate. On average they displayed 8.85 ± 2.26 patterns from six to 12 months of age. According to neuromotor studies on macaques, the earliest sign of relative independent finger movement (RIFM) occurred at 2-3 months, with mature patterns occurring at 7-8 months (Bortoff and Strick 1993). Galea and Darian-Smith (1995) reported that performance on a reach and grasp test by a group of young macaques approached adult levels by 6 months. This agrees with our study showing infants starting the behavior between 2 to 3 months and performing activities that require firm grasp of the stones around 6 months. Even though the motoneuronal projections responsible for finger movement develop rapidly in the first neonatal months, they do not mature until the second year of life. This explains the increase in the number of SH patterns up to 3-4 years of age. Older juveniles displayed the highest number of patterns among all age classes (18.14 ± 5.38), whereas the number of patterns displayed decreased into adulthood, which might reveal the appearance of individual preferences or behavioral routines over the years (Nahallage and Huffman 2007b).

We concluded that at the time of acquisition, infants acquired a rudimentary form of SH, but were constrained from matching specific behaviors from the demonstrator due to their level of neuro-motor development. Our findings support developmental theories on juvenile primates (Pereira and Fairbanks 1993). Later on however, this kind of matching did occur, and was particularly noticeable for rare behaviors displayed by the mother, which were then being seen to diffuse among offspring and others. A good example for this is the throw and run behavior displayed by the alpha female of the troop. Her son first started throwing stones when he was one and half years old but was not able to perform the run and throwing together, but by around 3 years of age he was seen performing the throw and run behavior just like his mother. They were the only individuals who displayed this behavior in the troop (Nahallage and Huffman 2007b; Leca et al. 2008c).

11.6 Exploring and explaining inter-group behavioral differences

11.6.1 The method of elimination

Recently, primatologists have found evidence of inter-group behavioral variation in several non-human primate taxa including capuchins, macaques, and great apes (Whiten et al. 1999; Huffman and Hirata 2003; Perry et al. 2003; van Schaik et al. 2003b; Leca et al. 2007a). The ‘method of elimination’ is a multi-step decision procedure that may be used to assess whether a geographically variable behavior is or is not traditional or cultural (van Schaik 2003; see also Boesch 1996). First a patchy geographical distribution of the behavior must be demonstrated. Within the same (sub)species, a given behavioral pattern can be customary or at least habitual in some groups and rare or even absent in others although it is ecologically possible. Like some ethnographic research in human social sciences or like the powerful comparative method used in ethology, this group-contrast approach to cultural primatology has been widely used by field primatologists as a first step to identify candidates for cultural behaviors, particularly in primate stone-tool cultures (e.g., Whiten et al. 1999).

Second, inter-group behavioral differences are typically attributed to genetic, environmental or cultural factors (Goldberg and Wrangham 1997; Whiten et al. 1999; Yamakoshi 2001). By elimination, when obvious genetic and ecological causations can be ruled out, or at least when the effects of genetic and ecological factors are likely to be minimal, then inter-group behavioral variation is largely considered cultural. Third, the behavior should meet a set of criteria, such as being observed in at least two members of one group, showing pathways of diffusion within age structures, affiliated networks, or along matrilineages, being largely dependent on social means for its diffusion and maintenance, and being persistent across generations, or at least over a number of years (Fragaszy and Perry 2003). As more elements congruent with the concept of tradition are provided, the likelihood of alternative interpretations decreases (van Schaik 2003). Accordingly, if a behavior shows a geographically patchy distribution unlikely attributed to genetic or ecological differences between sites, and if it is long-lasting and socially-transmitted, then a cultural phenomenon can be inferred (McGrew 2003).

11.6.2 Exploring genetic, ecological, demographic and social factors

To better understand how the SH tradition in Japanese macaques may appear, spread, and be maintained within the group over generations, we used the method of elimination to investigate the roles of genetic, ecological, demographic, and social factors in explaining inter-group similarities and differences in SH (Leca et al. 2007a,b, 2008a,b,c). Our main goal was to test several hypotheses proposing that SH variability reflects more demographic and social constraints than genetic and ecological factors. Our specific objectives were: 1) to establish the comprehensive repertoire of SH local variants in Japanese macaques; 2) to provide a systematic and broad inter-group comparison of the frequency, form, and context of occurrence of SH; 3) to address the possible role of genetic determinants in SH variation, through a comparison of the behavior in the two subspecies of

Japanese macaques, *Macaca fuscata fuscata*, widely distributed in the Japanese archipelago, and *M. f. yakui* endemic to Yakushima, a small island at the southern limit of distribution of the species (cf. Fooden and Aimi 2005); 4) to evaluate three major environmentally-based hypotheses invoked to account for inter-group differences in SH; 5) to consider the influence of various socio-demographic constraints on the appearance, diffusion, and maintenance of SH; 6) to test the association between geographic proximity and cultural similarity, as a way to infer a phenomenon of cultural zone; 7) to explore the transformation over time in the form of SH from the perspective of stone-tool use in non-human primates.

We conducted a systematic comparison of SH in ten troops of Japanese macaques. Nine troops belonged to the *M. f. fuscata* subspecies and one troop was *M. f. yakui*. Four captive troops were housed in large outdoor enclosures at the Kyoto University Primate Research Institute, and Japan Monkey Centre, Inuyama, and six free-ranging provisioned troops lived at four geographically isolated sites in Japan, namely Arashiyama, Takasakiyama, Koshima, and Shodoshima (Fig. 11.3). The comparison represented a total of 2,328 individuals and included two long-term studied troops at Arashiyama and Takasakiyama. We used the same observation procedure in all troops studied: continuous focal-animal sampling interspersed with instantaneous group scan sampling, and occasionally supplemented with ad libitum sampling (Altmann 1974). We analyzed a total of 1,950 hours of observation, including 1,280 video-recorded SH bouts (Leca et al. 2007a). We provided a rigorous documentation of the local environmental context of SH occurrence, such as site-specific stone availability and the conditions of food provisioning (Leca et al. 2008a,b).

11.6.3 Inter-group variation in SH

We listed a total of 45 different behavioral patterns in the SH repertoire of Japanese macaques (Leca et al. 2007a; Nahallage and Huffman 2007a). By taking a group-contrast approach to chart inter-group diversity in SH, Leca et al. (2007a) showed substantial variability in the frequency of occurrence and form of SH among the ten study troops. We found major inter-group differences in the frequency of occurrence and the prevalence of most of the 45 SH patterns, with local variants being customary in some troops, and rare or even absent in others although they were ecologically possible, and performed by a majority of individuals in some troops, or only idiosyncratically in others (Leca et al. 2007a,b; see Table 11.2 for definitions).

The frequency of occurrence of SH patterns were highly variable according to the pattern and troop in question. Very few patterns were unique to any troop, as most were shared between two or more troops. Even though most simple SH patterns (corresponding to investigative, locomotion, and collection activities) could be observed in most study troops, their frequency of occurrence varied from being present or to being a customary practice. The frequent occurrence of more complex SH patterns (*flint*, *combine with object*), corresponding to percussive, rubbing and other complex manipulative activities was even more restricted to particular troops, but again highly variable depending on the pattern. Finally, a few complex SH patterns were specific to one troop, such as *tap in mouth*, *spin*, and *wrap in leaf* in the Takahama troop, and *stone groom* in the Shodoshima A troop.

Following Whiten (2005), we defined a ‘tradition’ as a local behavioral variant, showing different frequencies of occurrence across the study sites, i.e. being customary or habitual in at least one site, but absent elsewhere. We defined a ‘culture’ as a package of multiple related traditions, and ‘cultures’ as distinctive arrays of clustered traditions. Almost all SH patterns showed geographically patchy distributions, i.e. had different profiles of frequency of occurrence across the study sites, and were referred to as local variants or SH traditions. In terms of behavioral complexity, we found three levels of SH culture, each level being defined by troop-dependent clusters of SH traditions (Leca et al. 2007a).

In summary, our results revealed a significant inter-troop variability in the form of SH, consistent with the extensive and multiple inter-site behavioral differences recorded in chimpanzees, and interpreted as cultural variation (cf. Whiten et al. 1999).

11.6.4 No major evidence for genetic determinants in SH variation

First, our comparative study revealed that *M. f. yakui* did not notably differ from *M. f. fuscata* in the SH repertoire, as well as the occurrence, form, and context of SH. We found that SH patterns varied as much between seven troops of the same subspecies (*M. f. fuscata* in Wak.A, Takh., Ara.E, Sho.A, Sho.B, Tak.B, and Tak.C) as between subspecies themselves (*M. f. fuscata* versus *M. f. yakui*) (Leca et al. 2007a).

Second, the occurrence of SH behavior in rhesus macaques (*Macaca mulatta*) and long-tailed macaques (*M. fascicularis*) confirmed the prediction that closely related macaque species shared a behavioral propensity for SH (Huffman and Hirata, 2003; Nahallage and Huffman 2008a). With the exception of one variant, all the SH patterns displayed by the rhesus macaques were typical of Japanese macaques. We found no compelling evidence to suggest that the observed differences could be attributed to differences inherent to these two species (Nahallage and Huffman 2008a). Therefore, we can assume that most SH patterns are macaque ‘universals’. All the basic motor actions involved in every SH pattern are shared behavioral predispositions, i.e. they are already present in the repertoire of the genus *Macaca* (Huffman and Hirata 2003; Nahallage and Huffman 2008a).

Third, Fooden and Aimi (2005) provided information about the geographic distribution of extant populations of Japanese macaques, including continuities and discontinuities, migration, and genetic variability. There was evidence for geographic variation in mitochondrial DNA of Japanese macaques (Hayasaka et al. 1991). Although it is acknowledged that genes determine the occurrence of general behavioral categories within a given species, such as the ability to handle stones or use tools, we suggest that intraspecific genetic differences are negligible in terms of possible implications for local behavioral variants, such as the manual dexterity to clack rather than rub stones together.

In sum, based on comparative analyses at the subspecies and species levels, common behavioral predispositions in phylogenetically close taxa, and knowledge of genetic determinism, it is reasonable to consider that genetic and phylogenetic factors may not be key to explaining the observed inter-troop variability in the form of SH in macaques (Leca et al. 2007a; Nahallage and Huffman 2008a).

11.6.5 Role of ecological factors in SH variation between troops

SH is a behavior particularly well-suited for the method of elimination. Its apparent lack of direct adaptive consequences and the arbitrariness of its behavioral variants make it easier to rule out ecological factors as potential causes of inter-group variation (Leca et al. 2008b). Among the most obvious ecological differences which could affect SH, we addressed site-specific availability in stone number and size, the degree of terrestriality of individuals, and food provisioning constraints.

11.6.5.1 Stone availability and terrestriality

Although we demonstrated that SH is almost exclusively a terrestrial activity, our comparative analyses showed that the number of stones readily available and the relative amount of time spent on the ground by the macaques were not significantly associated with the inter-troop differences in the occurrence of SH. Moreover, the size of stones handled was not associated with the size of stones available (Leca et al. 2008b). The absence of evidence supporting the stone availability and terrestriality hypotheses suggests that the performance of SH and the motivation to engage in this activity are both more diverse and more complex than the direct links to time spent on the ground or the number of stones readily available in the local environment.

However, this does not imply that any dramatic local change in the availability of stones or substrates (such as vertical structures) would not affect the chance of SH to occur or the form of SH in a particular troop. We believe that there are favorable environmental circumstances under which the innovation and initial diffusion of SH could be facilitated (Leca et al. 2008a; Nahallage and Huffman 2008a,b).

11.6.5.2 Food provisioning

Food provisioning undoubtedly affects the animals’ activity budget (Huffman 1991; Huffman and Hirata 2003; Leca et al. 2008a; Jaman and Huffman 2008). Feeding monkeys gives them ‘free’ time since they can devote less time to foraging. Moreover, attracting monkeys to the open space of feeding areas, where stones occur and many individuals can gather and observe each other, may result in increased behavioral coordination at the group-level and contagion-like processes. In this context, the occurrence of an individual starting to manipulate stones could enhance the probability for a neighboring group member to exhibit SH. In turn, the latter stone handler could enhance the probability for another neighboring group member to exhibit SH, and so on. Therefore, food provisioning is likely to increase the chances for SH to emerge and diffuse, or at least to be expressed.

We found that food provisioning constraints, including provisioning frequency, duration of food availability, and the size of food items considerably influenced a troop’s food-related activities and feeding style, which in turn could affect several aspects of SH. In troops provisioned several times a day, SH was more frequent, longer, and more prevalent during provisioning than non-provisioning periods. These effects of provisioning were not significant in troops provisioned less frequently. Moreover, SH was more frequently integrated with food-related activities in troops supplied with food several times a day than in the other troops. Thus, we argued that the context of occurrence, frequency, and form of SH in a given troop were directly influenced by provisioning parameters (Leca et al. 2008a). Food provisioning may be a key factor in the innovation and transformation phases of the SH tradition in Japanese macaques. However, evidence for relationships between SH and food provisioning does not argue against a cultural interpretation of SH, since this long-enduring behavior is socially transmitted (Huffman 1984, 1996; Nahallage and Huffman 2007b), which some authors suggest is sufficient evidence of a behavioral tradition (Perry and Manson 2003).

11.6.6 Demographic constraints on the emergence, transmission, and maintenance of SH

By both facilitating and limiting the expression of particular behaviors, demographic factors may influence the likelihood of individual innovation, the subsequent diffusion of a novel behavior within a group, and its long-term maintenance (Huffman and Hirata 2003). Group size and composition can be regarded as major constraints to the appearance, spread, and transformations over time of traditional behaviors. Here, we evaluated how group size, the age structure of the group may account for the substantial inter-troop variations in SH reported in Japanese macaques. The ten study troops varied greatly both in size and proportion of individuals belonging to the different age classes (Leca et al. 2007b).

11.6.6.1 Group size

We found that troop size was positively correlated with the percentage of troop members exhibiting SH simultaneously. The larger the group, the higher the proportion of individuals performing SH at the same time (Leca et al. 2007b). The effect of troop size on the synchronized performance of SH may reveal the contagious nature of play. Seeing group members playing is a reliable cue for more individuals that the current environmental conditions are safe enough to engage in play. The sight of nearby stone handlers and even the loud noise generated by percussive patterns may increase the individual probability to start handling stones. This stimulation effect may be amplified by an increasing number of troop members and eventually result in a form of “hysterical contagion”. This may help to explain the increase in number of SH individuals (synchronized occurrence) around feeding time in free-ranging provisioned troops, as this is the only time when most troop members are all together in the same location.

11.6.6.2 Age structure

Another demographic factor, age class composition of the group may also affect the diffusion and maintenance of SH. We verified that a group with abnormal age structure (e.g., missing age classes) showed lower proportion of stone handlers and lower frequency of SH than more normally age structured groups. The very low occurrence and frequency of SH in the captive Arashiyama A troop, with no subadults and young adults, strongly supported the view that a group’s age structure might affect the diffusion and maintenance of SH behavior. We suggested that the age gap in the Arashiyama A troop might have constrained the diffusion of SH from the young to the older group members (Leca et al. 2007b). The restricted practice of SH by young individuals and only very occasional practice by older troop members may not be sufficient to maintain the behavior in this troop in the long-term.

These findings are consistent with long-term field observations conducted at Arashiyama and described above, suggesting that 1) after initial innovation by youngsters, SH behavior first spreads among young individuals, probably peer playmates, 2) there is a critical period after which SH cannot be acquired by an individual (> 5 years), and 3) when a behavioral practice is restricted to a particular class of group members, its propagation should be slow and its maintenance may be jeopardized (Huffman 1996; Leca et al. 2007b,c, in review).

In sum, the present findings supported the hypothesis that patterns of variation in SH across troops reflected variability in group size and composition in age classes.

11.6.7 Social influences and observational learning in SH

11.6.7.1 Cultural zones

We found a positive correlation between geographic proximity and cultural similarity in SH between troops. In other words, there were significantly greater similarities in SH patterns in the troops living at the same site, compared to other troops. The numbers of patterns showing the same occurrence in the two troops living at Shodoshima (Sho.A and Sho.B) and in the two troops living at Takasakiyama (Tak.B and Tak.C) were 26 and 25, out of 33 respectively. These neighboring troops had similar sets of SH patterns and their total numbers of patterns observed were close (23 and 22 at Shodoshima, and 27 and 31 at Takasakiyama; Leca et al. 2007a).

The geographic distribution of clear troop-dependent clusters of SH variants and the similarities in the SH repertoires between the free-ranging troops living at the same site were suggestive of the phenomenon of cultural zones, since any alternative explanation is hard to imagine. Although food provisioning schedules were different, neighboring troops had overlapping home ranges and came into occasional contact around the provisioning site, where SH activity most often occurs.

The notion of cultural zones is based on the possibility of 1) inter-troop observation when monkeys come into occasional contact around the feeding sites where most SH activity occurs and 2) males transferring

SH patterns when migrating from one troop to another. When such inter-troop social influences do not exist (e.g., troops separated by substantial geographic distance in natural situations or by artificial barriers like concrete walls in captive conditions), the troops showed more differences in their SH repertoires: their mean number of behaviors showing the same frequency of occurrence was only 12.1 ± 7.3. Inter-troop cultural transmission in wild chimpanzees has been inferred from the geographical distribution of certain tool-using behaviors and social conventions (Boesch et al. 1994; McGrew et al. 1997, 2001), and suggested from field experiments (Biro et al. 2003).

In Japanese macaques, food provisioning provokes several times a day the gathering of most troop members around feeding sites. Attracting monkeys to the open space of feeding areas, where small-sized foods (cereal grains) are scattered on the ground among stones, increases considerably their chances to encounter these objects, and spatial proximity among individuals represents opportunities to observe others handling stones. Although SH is a primarily solitary activity, non-SH individuals are very likely to observe performances of SH by other group members, and often show close interest in others' stones (Huffman and Quiatt 1986; Quiatt and Huffman 1993; Leca et al. 2008b).

11.6.7.2 Social tolerance and spatial cohesion

To test the hypothesis that SH will be more prevalent in more cohesive groups, we calculated, for the 10 study troops, a group-level index of social tolerance, defined as the mean percentage of group members within 1 m of each other. This typical index of group-level social tolerance was not significantly correlated with the frequency and rate of diffusion of SH (Leca, unpublished data). In other words, the troops showing higher levels of positive social interactions (such as grooming and playing) were not necessarily the troops with more frequent episodes of SH and higher percentages of stone handlers. Instead, group size and group spatial cohesion after food provisioning was positively correlated with the prevalence of SH. Larger troops characterized by closer physical proximity among individuals feeding on provisioned food also showed higher percentages of troop members exhibiting SH simultaneously (Leca et al. 2007b).

Therefore, inter-group differences in SH prevalence and cultural similarity in SH between neighboring troops were better explained by inter-group transfers, as well as opportunities for observational learning and behavioral coordination both within and between troops rather than intra-group social tolerance alone.

11.6.7.3 Transformation of the SH tradition

The transformation phase of the SH tradition is defined as the late period in which long-enduring practice and acquired familiarity with the behavior and the stones are gained through the integration of SH with other daily activities (Huffman and Quiatt 1986; Huffman and Hirata 2003). By using similar methods of data collection for about 15 years of continued observation at Arashiyama and Takasakiyama, we found that the monkeys have almost doubled the size of their SH repertoire and largely diversified the contexts in which SH activity was practiced (Leca et al. 2007a).

The late emergence of SH patterns not recorded before involved complex manipulative actions, such as *combine with object*, *rub/put on fur*, *stone groom*, and *wash* revealed an increased diversity in the combination of stones with other objects or substrates. The appearance of variants combining the use of hands and mouth (e.g., *carry in mouth*, *move inside mouth*, *bite*, and *lick*) suggested that SH had become more integrated with foraging and feeding activities. The integration of SH with food-related activities and the emergence of food-directed SH patterns were more frequent in free-ranging troops where food provisioning strongly influenced the activity budget.

In human material culture, the "ratchet effect" is referred to as the cumulative modifications and incremental improvements resulting in increasingly elaborate technologies (Tomasello 1999). Our longitudinal data suggested that the long-term cultural transformation of SH might result in a generational ratchet effect, defined as an increase in the diversity and complexity of SH patterns compared to earlier generations of stone handlers.

From a functional viewpoint, almost all the 45 SH patterns currently observed in Japanese macaques are regarded as a non-instrumental manipulation of stones, with no obvious survival value (Huffman 1984; Leca et al. 2007a; but see Nahallage and Huffman 2007a for a possible ultimate function of SH). When combined with other objects, the stones handled by Japanese macaques were never used as tools to achieve an overt goal.

However, when practiced on a daily basis and by most members of a group, the non-instrumental manipulation of stones could be considered as a behavioral precursor to the possible use of stones as tools (Huffman and Quiatt 1986; Huffman 1996; Leca et al. 2008a). The gradual transformation of the SH tradition, associated with a generational 'ratchet effect' could ultimately result in future stone-tool use, as stone-related behaviors become more deeply ingrained into the behavioral landscape of these monkeys at the population level.

For example, the persistence of SH in food-related contexts may eventually turn into the instrumental use of stones as foraging tools by Japanese macaques (Huffman and Quiatt 1986; Leca et al. 2008a).

This prediction was eventually verified. Until recently, there was no optimal SH pattern and no local survival advantage in performing a particular SH pattern rather than another. However in 2004, we witnessed the emergence of the first example of a possible adaptive transformation in the spontaneous practice of SH. Unlike all other SH patterns performed by Japanese macaques, unaimed stone-throwing exclusively observed in the captive Takahama troop during periods of disturbance and in conjunction with agonistic signals typical of this species could be regarded as a spontaneous tool-using behavior (Leca et al. 2008c). Based on the analysis of the contexts that may elicit the behavior, we inferred that stone-throwing might serve to augment the effect of agonistic displays. The Takahama troop was the only one to show a complexity level-3 SH culture. This troop also exhibited the most diverse SH repertoire (44 patterns out of a total of 45), and showed the highest frequencies of occurrence in SH patterns (28 habitual or customary patterns) among all troops. These findings suggest that, although SH was observed in the ten studied troops, the transformation of SH into an adaptive behavior is more likely in troops where SH is a well established behavioral tradition showing diverse and complex patterns performed in various contexts.

This study of stone-throwing also supports the view that tool-use evolves in stages from initially non-functional behaviors, such as object play (Beck 1980; Huffman and Quiatt 1986; Leca et al. 2008c), 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 provided particular environmental circumstances exist. As an unselected but eventually beneficial trait, the SH tradition would be an exaptation (cf. Gould and Vrba 1982).

11.6.8 Possible functions of stone handling behavior

While not every socially learned behavior needs to be adaptive, the propensity to learn and adopt new behaviors certainly is. In the immediate sense, SH appears to be rewarding in itself, rather than the means to an end (Huffman 1996). Why the behavior persists in troops over many generations, despite the lack of any obvious direct adaptive value or function to those who practice SH, has long been an elusive question.

Two hypotheses regarding the occurrence of other types of object play in animals are the misdirected foraging behavior hypothesis and the motor training hypothesis. According to the misdirected foraging hypothesis, play in captive or domesticated animals is motivationally directed to objects as if they were food (Hall 1998; Pellis 1991; Pellis et al. 1998). However, SH as described here is not consistent with the misdirected foraging behavior hypothesis (pseudo-feeding behavior) proposed by Pellis (1991). Even in provisioned free-ranging troops, SH occurs predominantly after feeding, not before. Thereby we conclude that this behavior is not elicited by the anticipation of food as described for captive otters and other zoo animals (Hediger 1964; Pellis 1991).

Though many theories have been proposed for the function of play behavior (Smith 1978), no single one can be applied across the board to all play behaviors in all species. Indeed, there are differences of play activities exhibited by the same species living under different environmental conditions (Ramsey and McGrew 2005). SH is no exception, as evidenced by the contrasts and similarities of the behavior between free-ranging and captive provisioned troops, and age class differences within the same troop reported here.

The underlying function of play is expected to vary according to the content of the behavior itself, potential motivational differences brought about by differences in the social and natural environment, and by species' level characteristics. This is confirmed for Takahama macaques also, in that the frequency of SH is significantly greater on clear sunny days versus cloudy or rainy days as well as during warmer seasons of the year than in the colder months, and that monkeys suppress SH for days following periods of externally induced intense stress, i.e. capturing the entire troop for annual check-ups, moving a group temporarily into a new enclosure (Nahallage and Huffman 2008b).

When we compare age-class differences in SH, the possible motivations for performing the behavior appear to be different for young and adults (Nahallage and Huffman 2007a). This is of particular interest to us, given that the behavior is only acquired by individuals when young. This leads us to speculate that unlike other play behaviors that disappear from the repertoire of most primates when they reach adulthood, presumably because they no longer serve a function, biological and cultural selective forces may be acting on individuals who have acquired SH, to maintain the practice throughout life.

The immediate motivation for young to handle stones, like any other form of object play, is most likely to be that it is intrinsically an enjoyable activity (Hall 1998). They are naturally curious about what others are doing and have the desire to play with an object made 'popular' by others' use of it (Huffman 1984). At the functional level, playing with stones allows them to develop and practice the interactive use of motor and perceptual skills supportive of physical and neurophysiological development. In macaques, a surge of synaptogenesis occurs roughly 2 months before birth and continues up to 3 years of age (Rakic et al. 1986; Bourgeois et al. 1994). The overall trend in the increasing complexity of SH behaviors (pattern and number of behaviors) over time from infancy into the juvenile period is consistent with this increase in neural-motor developmental activity. These findings are consistent with Fairbanks' (2000) model describing the heightened frequency of object manipulation in correlation with synaptic development in juvenile vervets and rhesus macaques (Rakic et al. 1986). We feel that this model is the best functional explanation for SH in young Japanese macaques.

For adults, the immediate motivation to SH appears to be different from that of young. With age, adults exhibit fewer bouts of longer duration, involving relatively more complex behavioral patterns than young (Nahallage and Huffman 2007a). They concentrate on these more demanding manipulative activities, with seemingly intense concentration. They carry stones to their individually preferred locations to stone handle in an unhurried, seemingly 'leisurely', manner. Sometimes older individuals sit nearby their preferred location, waiting for others to leave, before going there to SH and performed the behavior most often in the afternoon. We suggest that SH may allow adults to temporarily divert their attention away from the social interactive network of associations with others by concentrating on this solitary activity. Since adults have already acquired the necessary motor skills during early life, we propose that the ultimate function of SH is also different from that of young. However, an equally important neurophysiological benefit may be gained by them from its practice. As macaques grow older, a decline in memory and cognitive impairment and associated pathology (senile plaque, synapse loss) of the prefrontal cortex occurs (Hof and Duan 2001 for a review). Recently, a number of clinical studies have shown the benefits for elderly humans in significantly reducing the risk of acquiring such disease through regular leisure activities involving concentrated mental activity (reading, playing board games, cards and musical instruments) (e.g. Verghese et al. 2003). It has been suggested that the mental exercise of such leisure activities may stimulate new neural growth around damaged parts of the brain caused by aging (Coyle 2003). A shift in the role of SH activity from neural-motor development when young to basic maintenance in adults and re-generation of neurophysiological pathways in aging adults may be the prominent functions behind the sustained practice of this seemingly non-adaptive behavior in macaques.

11.7 Conclusions and future directions

In Japanese macaques, the individual acquisition and expression of SH behavior, the appearance, diffusion, and maintenance of the SH culture, as well as inter-troop variation in the frequency, form, and context of occurrence of SH were better explained by neuro-motor developmental constraints, socio-demographic factors (namely group size, age structure, inter-group transfers, opportunities for observational learning in mother-infant dyads and among peer-playmates, and behavioral coordination at the group level), and environmental factors that were not stone-related (food provisioning) than by genetic differences, stone availability, or terrestriality. We presented what may be the most extensive and systematic survey focused on the intra- and inter-group variability of a single type of behavior in monkeys to date. Through the combination of the method of elimination, cross-sectional and longitudinal analyses, evidence for social transmission and durability of SH, and the view of behavioral predispositions, we drew an overall picture of rich cultural diversity in a particular type of object play behavior in Japanese macaques. Amongst the rare non-adaptive proposed traditional behaviors (see also 'leaf-pile pulling' in chimpanzees: Nishida and Wallauer 2003), SH is the most thoroughly documented.

To further explore the proximate causes of SH and the constraints on its propagation and long-term transformation, our findings call for experimental approaches 1) to test the strength of the connection between SH and feeding activities, 2) to assess the influence of the physical characteristics of the stones on stone selectivity, 3) to examine the effect of the contagion process on the synchronized performance of SH, 4) to investigate how visual and auditory stimulus enhancement may help trigger SH behavior at the individual level, and 5) to evaluate the distinct effects of various social learning processes, such as social enhancement, social facilitation, or imitation on the individual acquisition of SH. Such experiments could involve respectively: 1) the manipulation of food provisioning schedule, 2) the introduction into the environment of new stones varying in size, shape, weight, and chemical properties, 3) the manipulation of size of subgroups from a social group held in captive conditions, 4) the setting up of particular stone arrangements, such as piles of stones, to simulate SH by-products and the playback of sounds produced during SH activity, and 5) the introduction of stones to semi-isolated individuals or into caged-groups under the controlled conditions of captive settings.

Field studies on geographic variation in the occurrence of numerous behavioral patterns, supported by longitudinal and experimental investigations of whether and how these behaviors are socially learned, can provide extensive evidence for behavioral traditions in several primate species (Huffman et al. 2008).

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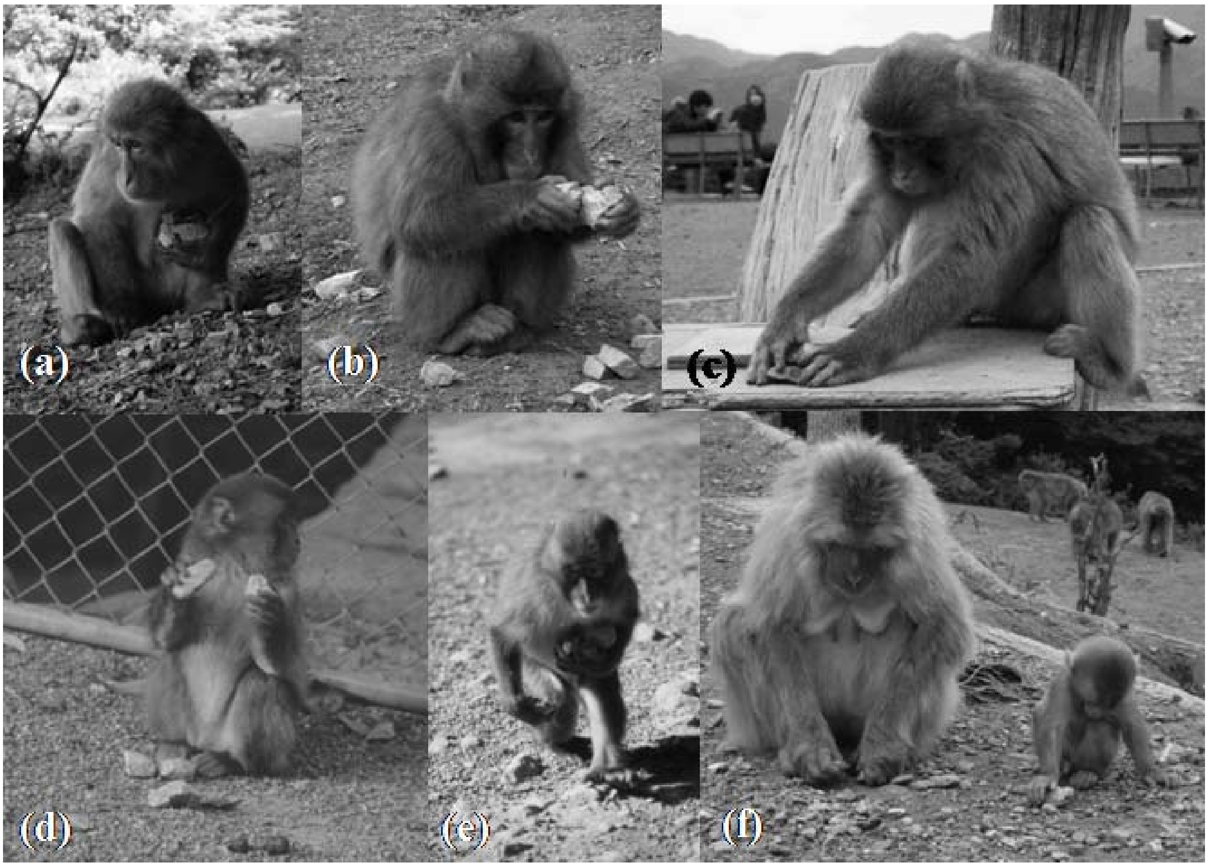

Fig. 11.1. Five SH patterns. (a) cuddle, (b) rub together, (c) rub on surface, (d) clack, (e) carry, and (f) a mother-infant dyad performing SH simultaneously. Credit: photos (a), (c), and (f) by JB Leca, photo (b) by N Gunst, and photos (d) and (e) by MA Huffman.

Fig. 11.2. Glance-6476 (three-year-old, middle ranking female): First individual recognized to perform SH on December 7, 1979.

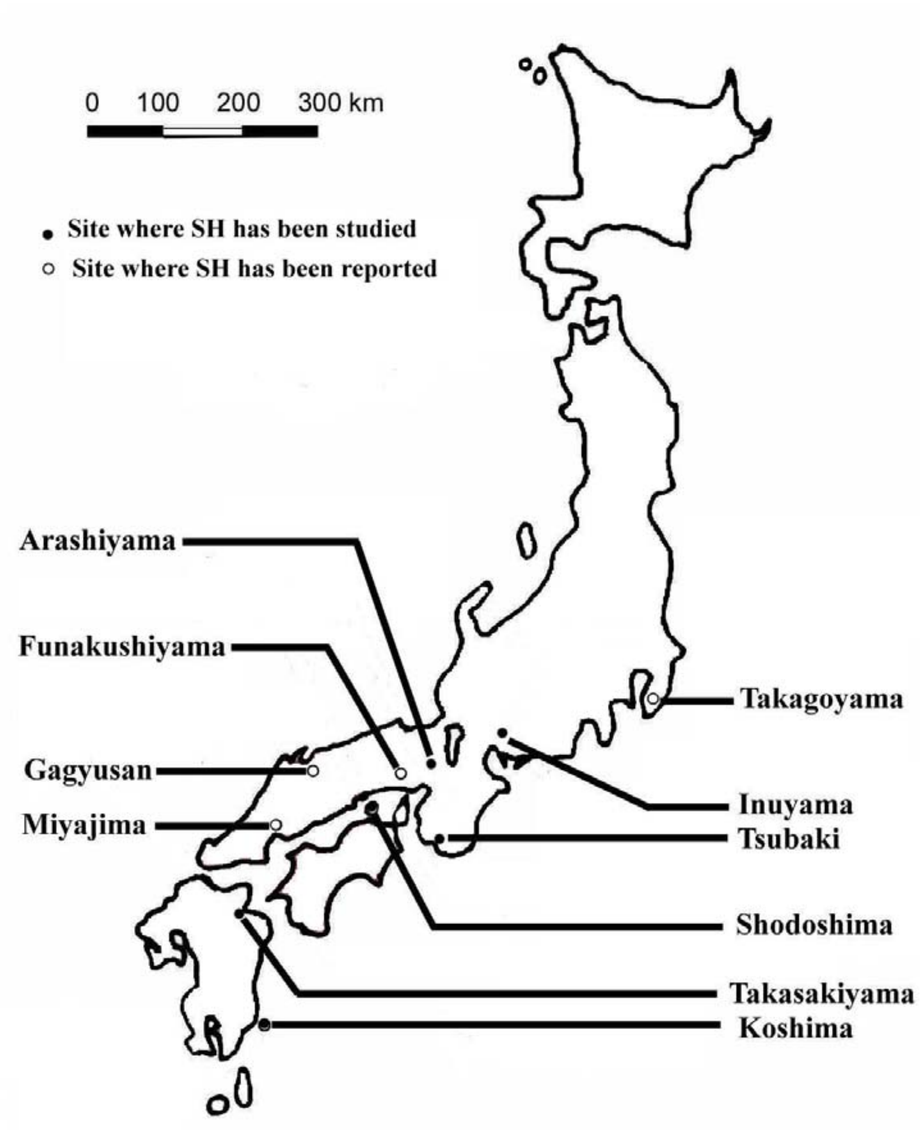

Fig. 11.3. Map of the sites in Japan where SH has been studied or reported. Sources: Arashiyama, Funakoshiyama, Gagyusan, Takagoyama, Takasakiyama, Yakushima (Huffman & Hirata, 2003), Arashiyama, Inuyama (Primate Research Institute and Japan Monkey Centre), Koshima, Shodoshima, Takasakiyama (Leca et al., 2007a), Tsubaki (Leca, unpublished data), Miyajima (Watanabe, pers. comm.).

Category	Name	Definition
Investigative activities		
	Bite	Bite a stone
	Hold	Pick up a stone in one's hand and hold on to it, away from the body
	Lick	Lick a stone
	Move inside mouth	Make a stone move inside one's mouth with tongue or hands
	Pick	Pick up a stone
	Put in mouth	Put a stone in one's mouth and keep it sometime
	Sniff	Sniff a stone
Locomotion activities		
	Carry	Carry a stone cuddled in hand from one place to another
	Carry in mouth	Carry a stone in mouth while locomoting
	Grasp walk	Walk with one or more stones in the palm of one or both hands
	Move and push/pull	Push/pull a stone with one or both hands while walking forward/backward
	Toss walk	Toss a stone ahead (repeatedly) and pick it up while walking
Collection or gathering activities		
	Cuddle	Take hold of, grab or cradle a stone against the chest
	Gather	Gather stones into a pile in front of oneself
	Grasp with hands	Clutch a stone or a pile of stones gathered and placed in front of oneself
	Pick up	Pick up a stone and place it into one's hand
	Pick and drop	Pick up a stone and drop it repeatedly
	Pick up small stones	Pick up small stones and hold them between fingertips (like the picking up of wheat grains)
Percussive or rubbing sound producing activities		
	Clack	Clack stones together (both hands moving in a clapping gesture)
	Combine with object	Combine (rub or strike) a stone with an object different from a stone (food item, piece of wood, metal, etc.)
	Flint	Strike a stone against another held stationary
	Flint in mouth	Strike a stone against another held in mouth
	Pound on surface	Pound a stone on a substrate
	Rub in mouth	Rub a stone against another held in mouth
	Rub/roll on surface	Rub or roll a stone on a substrate
	Rub stones together	Rub stones together
	Rub with mouth	Rub a surface with a stone held in mouth
	Scatter	Scatter stones about, on a substrate, in front of oneself
	Shake in hands	Take stones in one's open palm hand and shake the stones with the hand moving back and forth
	Slap	Slap, tap or pound a stone with one’s fingertips or palm of hand
	Swipe	Swipe stones together (both hands moving in a sweeping gesture)
	Tap in mouth	Tap a stone held in mouth with fingertips or palm of hand
Other complex manipulative activities		
	Flip	Turn a stone over with both hands
	Put in water	Put a stone in water
	Roll in hands	Roll a stone in one's hands
	Rub/put on fur	Rub or put a stone on one’s fur while self-grooming
	Rub with hands	Hold a stone in one hand and rub it with the other (like potato-washing)
	Spin	Spin a stone around on the ground using two fingers of one hand or both hands (one moving forward and the other backward)
	Stone-groom	Allo-groom with a stone
	Throw	Throw a stone without jumping or running
	Throw and jump	Throw a stone and jump (or vice versa)
	Throw and run	Throw a stone and run (or vice versa)
	Throw and sway	Throw a stone and sway (or vice versa)
	Wash	Put a stone in water or pick up a stone from water and rub it with hands
	Wrap in leaf	Wrap a stone in a leaf (or wrap a leaf around a stone)

Table 1. Forty five SH patterns performed by Japanese macaques and categorized according to general activity patterns (after Leca et al., 2007a).

	Captive troops				Free-ranging troops					
SH pattern	Ara.A	Wak.A	Takh.	JMC*	Kosh.	Ara.E	Sho.A	Sho.B	Tak.B	Tak.C
Investigative activities										
Lick	P	H	C	P	P	P	(-)	(-)	P	P
Move inside mouth	-	H	H	P	-	P	(-)	(-)	P	P
Pick	C	P	P	P	P	P	P	(-)	(-)	P
Put in mouth	P	H	H	P	-	P	H	P	P	P
Locomotion activities										
Carry	-	C	H	H	P	C	H	H	H	H
Carry in mouth	-	H	C	P	-	P	P	P	P	P
Move and push/pull	-	C	H	P	P	H	P	P	P	P
Toss walk	P	P	C	P	-	H	(-)	(-)	P	P
Collection (gathering) activities										
Pick and drop	-	-	P	-	-	P	P	(-)	P	H
Pick up small stones	-	-	H	-	-	H	(-)	(-)	P	P
Percussive or rubbing sound producing activities										
Clack	P	P	H	H	-	-	P	P	P	P
Combine with object	-	P	C	P	-	H	(-)	P	(-)	P
Flint	-	H	C	P	-	P	P	P	P	H
Flint in mouth	-	P	P	-	-	-	(-)	(-)	(-)	P
Pound on surface	-	P	H	H	-	P	P	(-)	(-)	H
Rub in mouth	-	P	P	-	-	-	(-)	(-)	(-)	P
Rub stones together	-	H	C	P	-	C	P	P	H	H
Rub with mouth	-	P	P	-	-	-	(-)	(-)	(-)	(-)
Shake in hands	-	-	P	P	-	P	(-)	P	P	P
Slap	-	-	H	P	-	-	(-)	(-)	(-)	(-)
Swipe	-	P	P	-	-	P	(-)	(-)	P	H
Tap in mouth	-	-	P	-	-	-	(-)	(-)	(-)	(-)
Other complex manipulative activities										
Flip	-	P	H	-	-	P	(-)	(-)	P	(-)
Put in water	-	-	P	-	-	P	(-)	(-)	(-)	(-)
Rub/put on fur	-	H	P	P	-	P	(-)	P	(-)	(-)
Spin	-	-	P	-	-	-	(-)	(-)	(-)	(-)
Stone groom	-	-	-	-	-	-	P	(-)	(-)	(-)
Throw	-	P	P	P	-	-	(-)	(-)	(-)	(-)
Throw and jump	-	-	H	-	-	-	(-)	(-)	(-)	(-)
Throw and run	-	-	P	P	-	-	(-)	(-)	(-)	(-)
Throw and sway	-	-	P	-	-	-	(-)	(-)	(-)	(-)
Wash	-	-	P	P	-	H	(-)	(-)	(-)	(-)
Wrap in leaf	-	-	H	-	-	-	(-)	(-)	(-)	(-)
No. pattern occurrence	5	20	32	19	4	20	11	10	15	19

Table 2. Frequency of occurrence of the 33 SH patterns that are not observed in all the ten studied troops of Japanese macaques, four captive (PRI Arashiyama = Ara.A, Wakasa = Wak.A, Takahama = Takh., and Japan Monkey Center = JMC) and six free-ranging troops (Koshima = Kosh., Arashiyama E = Ara.E, Shodoshima = Sho.A and Sho.B, Takasakiyama = Tak.B and Tak.C); No asterisks: *Macaca fuscata fuscata* troops, asterisk: *M. f. yakui* troop; C: Customary: Exhibited by at least 90% of the sampled individuals in at least one age class, or at least 70% of the sampled individuals in at least two age classes, H: Habitual: Not customary but observed at least three times in several individuals, consistent with some degree of social transmission, P: Present: Not customary or habitual, but observed at least once, -: Absent: Not observed despite sufficient observation time (at least 90 hours of total observation time), (-): Unknown: Not observed but absence uncertain because of insufficient observation time (less than 90 hours of total observation time); No. pattern occurrence: Number of SH patterns scoring at least the Present status; Neighboring troops living at the same site (respectively two troops at Shodoshima and two troops at Takasakiyama) are represented inside a dotted-line frame.

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ORIGINAL ARTICLE

The first case of dental flossing by a Japanese macaque (*Macaca fuscata*): implications for the determinants of behavioral innovation and the constraints on social transmission

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Abstract We report the first case of dental flossing behavior by a Japanese macaque. We used cross-sectional data to assess the presence of this novel tool-use behavior at the group-level. Although this behavior was performed frequently by a central middle-ranking middle-aged female during her grooming interactions, and appeared at least four years ago, it remained idiosyncratic to its innovator, and until now has not spread to other group members. We examined the factors that may have favored this innovation, including the environmental context, the individual characteristics of the innovator, and the structural and functional aspects of the behavior. Group size, kinship, and dominance are socio-demographic factors that are likely to limit the opportunities for any group member to observe the innovator, and thus constrain the diffusion of this potential candidate as a new behavioral tradition. This is one of the rare studies to document the spontaneous appearance of tool-use behavior in primates under natural conditions. Identifying the determinants of innovations and the constraints on their diffusion within social groups of non-human primates is of special interest to understanding cultural evolution.

Keywords Behavioral variant · Constraint · Innovation · Tradition · Tool-use

Introduction

Innovation is defined as the discovery of novel information, the emergence of new behavioral patterns, or the performance of existing behaviors in a novel context (Reader and Laland 2003). When a novel behavioral practice, initially invented by an individual—the innovator—spreads to other group members, and is dependent on social means for its diffusion and maintenance, it becomes a tradition (Fragaszy and Perry 2003). Various factors may enhance or limit the likelihood of innovation and subsequent propagation within a group, including individual attributes (age, sex, social rank, personality), social relationships (dominance, affiliation, kinship), group size and cohesiveness, and structural, contextual, and functional aspects of the new behavior (Huffman and Hirata 2003).

Innovations and traditions can be found in various animal taxa (reviewed by Laland and Hoppitt 2003). Identifying the determinants of the spontaneous appearance of new behavioral patterns and the constraints on their diffusion within social groups of non-human primates is of special interest to understanding cultural evolution in hominids (McGrew 1992). On the one hand, there are numerous examples of socially-transmitted behavioral innovations in several non-human primate species (Huffman 1996; Whiten et al. 1999; Perry et al. 2003; van Schaik et al. 2003). However, little is known about the initial process by which novel behavioral patterns emerge spontaneously and the various factors influencing the rate, speed, and route of their subsequent transmission within a group (but see Kummer and Goodall 1985; Tanaka 1998; Huffman and Hirata 2003;

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Bonnie and de Waal 2006; Leca et al. 2007a; for a few notable exceptions).

On the other hand, only a subset of innovations becomes traditions. Many new behaviors have been reported to appear in primate troops, but were either idiosyncratic, or independently adopted by very few individuals, or their performance was restricted to a small class of the population, and for some reason, they never spread widely within the group by social means. Wild chimpanzees (*Pan troglodytes*) show a variety of spontaneous tool-use innovations (sensu Beck 1980) peculiar to one individual and bound to disappear after the death of their unique performers (reviewed by Nishida et al. 2009). Health maintenance, a sub-division of self-medicative behavior (sic Huffman 2007), in the form of the use of twigs as "toothpicks" by one or very few individuals has been reported in great apes, including chimpanzees (McGrew and Tutin 1972, 1973), bonobos, *Pan paniscus* (Ingmanson 1996), and orang-utans, *Pongo pygmaeus* (Russon et al. 2009). Although macaques are not frequent tool-users (Beck 1980; but see Malaivijitnond et al. 2007; Leca et al. 2008a), dental flossing behavior has been reported in long-tailed macaques, *Macaca fascicularis* (Watanabe et al. 2007). The spontaneous and idiosyncratic use of tools in hygiene contexts, such as stones in allo-grooming and sticks as vaginal probes have been occasionally reported in this genus (Weinberg and Candland 1981; Sinha 1997).

The role of the importance of these behaviors to the performers themselves in the likelihood to innovate has received little attention (Kummer and Goodall 1985). Surprisingly, few attempts have been made to address the factors that would constrain or even impede the spread of certain novel behavioral patterns (Reader and Laland 2003). As Huffman (1996) pointed out, it is critical to know the history of a behavioral innovation in order to assess how environmental factors and social influences may enhance or limit its propagation within a group.

In an effort to encourage the compilation of relevant data on the determinants of behavioral innovations in non-human primates and stimulate general interest in the constraints on their diffusion within social groups, we report the first case of dental flossing (DF) behavior in a free-ranging group of Japanese macaques (*Macaca fuscata*). We systematically documented the frequent use, by an adult female, of hair as dental floss to remove food remains stuck between her teeth. We used cross-sectional data to assess the presence of this novel tool-use behavior at the group-level. We examined the initial conditions that may have favored this innovation and evaluated the various constraints that may account for the lack of diffusion within the group of this potential candidate for a new behavioral tradition in Japanese macaques.

Methods

Study group

The following observations were made on the free-ranging Arashiyama E troop of Japanese macaques at the Iwatayama Monkey Park, Arashiyama, Kyoto Prefecture, Japan. Japanese macaques have been provisioned and studied since 1954 at Arashiyama (Huffman 1991; see Leca et al. 2008b for details on provisioning conditions). All group members were individually identified, and their ages and kin relations through maternal lineages were known. The study group contained 145 individuals of 15 separate matrilines. All age/sex classes were present, including 56 old adults, aged 16 years and more (52 females and four males), 25 middle-aged adults, between 11 and 15 years old (21 females and four males), 15 young adults, between 7 and 10 years old (14 females and one male), 22 subadults, between 4 and 6 years old (14 females and eight males), 13 juveniles, between 2 and 3 years old (six females and 7 males), and 14 yearlings and infants (six females and eight males) (Leca et al. 2007b).

Data collection

To garner detailed data on the DF behavior performed by the innovator, JBL collected 15-min video-recorded focal-animal samples (Altmann 1974) of subject Chonpe-69-85-94 with a Sony DCR-HC48 digital camera. This focal subject was sampled independently of its activity, throughout the day, but not twice in the same hour-block. The typical duration of a focal session was 15 min. If the focal subject performed DF during the final 2 min, the observation was extended for 5 min, or longer if DF was still in progress. A DF event (or DF behavior) was considered to occur any time an individual:

1. stretched one or a few pieces of its own hair or another individual's hair, by either grasping the tip(s) of the hair with one or both hands, or by clutching its lips from the basal to the distal end of the hair; and
2. inserted the hair between the upper or lower front teeth (incisors or canines) by performing repeated teeth-chattering to remove food remains stuck between the teeth.

Subjects were never encouraged to floss for the purpose of this study (by providing them with hair, for example: cf. Watanabe et al. 2007), but instead observations were made on spontaneous DF behaviors. Because DF may serve to remove food remains stuck between the teeth, we tested the effect of feeding activity on DF by sampling the innovator within 1 h after provisioning time (post-feeding focals) and any other time throughout the day (non-feeding focals).

To assess the DF prevalence at the group-level (percentage of individuals performing the DF behavior), JBL and NG collected continuous 15 min pen-and-paper focal-animal samples on the other group members (Altmann 1974). We selected the focal individual independently of its activity and by using a semi-random procedure (Leca et al. 2007b, c, 2008a, b, c). However, preliminary analysis on the context of occurrence of DF in Chonpe-69-85-94 showed that all DF behaviors were performed during grooming activity. Therefore, during the last 10 days of the study period, and in order to supplement the data set and reach a threshold of 30 min of grooming patterns in a maximum number of group members, we also collected a series of 2-min pen-and-paper focal-animal samples in an ordered list of temporarily undersampled subjects. In this series, an individual was eligible as the next focal subject if it was engaged in self-grooming activity or involved as participant in an allo-grooming interaction, and the subject with least cumulative data was given priority. We recorded the following activities: self-grooming, allo-grooming, dental flossing, feeding, foraging, locomoting, resting, agonistic interaction (avoidance or aggression), and other. We defined grooming as the activity consisting of combing and/or picking through its own or another individual's hair (self-grooming and allo-grooming, respectively) with the hands or mouth. Given the potential risk of being aggressed by dominant flossing recipients, we established the dominance hierarchy within the group by recording ad libitum data (Altmann 1974) on the direction of dyadic agonistic interactions.

Visibility was excellent. The observers could approach and sample the subjects within 2–5 m. The following observations were made between 0800 and 1600 hours, from June 10 to July 31 and from September 9 to October 30, 2008.

Data analysis

We collected a total of 170.7 h of focal data, including 17.8 h on Chonpe-69-85-94 and 152.9 h on 113 other group members. These data comprised 5.8 and 64.4 h of grooming activity, respectively. From the video samples, NG recorded:

1. the duration of the same activities as for paper-and-paper samples;
2. the identity of the focal subject's grooming partners;
3. the number and duration of the DF events;
4. from which body part the hair was used to floss (head/neck, chest, belly, back, ano-genital region, arm, and legs);
5. whether the focal subject used the same or different hair in the successive DF events within a DF bout; and
6. whether or not the focal subject licked off the food remains mixed with saliva and attached to the hair after each DF event.

As for the DF patterns, we distinguished three different variants or DF techniques. First, the "stretching with mouth" technique was a behavioral sequence lasting around 5 s and consisting of stretching its own hair or another individual's hair (typically several long hairpieces) by clenching its lips on to the basal part of the hair, inserting the hair between the front teeth by slightly pulling its head downwards, and pulling the head backwards while gradually moving the lips to the distal end of the hair and performing repeated teeth-chattering (Fig. 1a). Second, the "stretching with hand" technique consisted of stretching its own hair or another individual's hair by grasping and pulling the tip(s) of the hair between the thumb and forefinger of one hand, moving the mouth to the hair, and inserting the hair between the front teeth by performing repeated teeth-chattering (Fig. 1b). Third, the "plucking" technique consisted of pulling out its own hair with one hand, holding the hair horizontally by grasping and pulling the tips of the hair between the thumb and forefinger of both hands, taking the hair to the mouth, and inserting the hair between the front teeth by performing repeated teeth-chattering (Fig. 1c).

We arbitrarily defined a DF bout as the display of DF activity with possible pauses of no longer than 120 s. If the individual resumed DF within 120 s after pausing, then the two DF episodes were considered as a single DF bout. If DF was resumed more than 120 s after pausing, this would mark the start of a new DF bout. A DF bout could consist of several DF events interspersed with pauses of no longer than 120 s.

To assess the prevalence of DF, we ascribed each group member to one of three DF categories: verified flosser, verified non-flosser, or non-verified individual. An individual was labeled a verified flosser if at least one DF event had been recorded during its total focal time. We labeled an individual as a verified non-flosser if it was sufficiently sampled during grooming activity (at least 30 min of focal data) but was never observed performing DF. When an individual was not observed performing DF, but was insufficiently sampled during grooming activity (between 6 and 30 min of focal data), it was labeled as non-verified individual. Because individuals aged one year and less seldom groom, they were not included in the analyses. Of the 17 non-sampled group members (with no focal data), 15 were peripheral males and two were peripheral females.

We verified the linearity of the dominance hierarchy for 87 adult females, including the innovator Chonpe-69-85-94 ($h' = 0.25$, directional consistency index $= 0.96$, $p < 0.001$; cf. de Vries 1995). We distinguished three

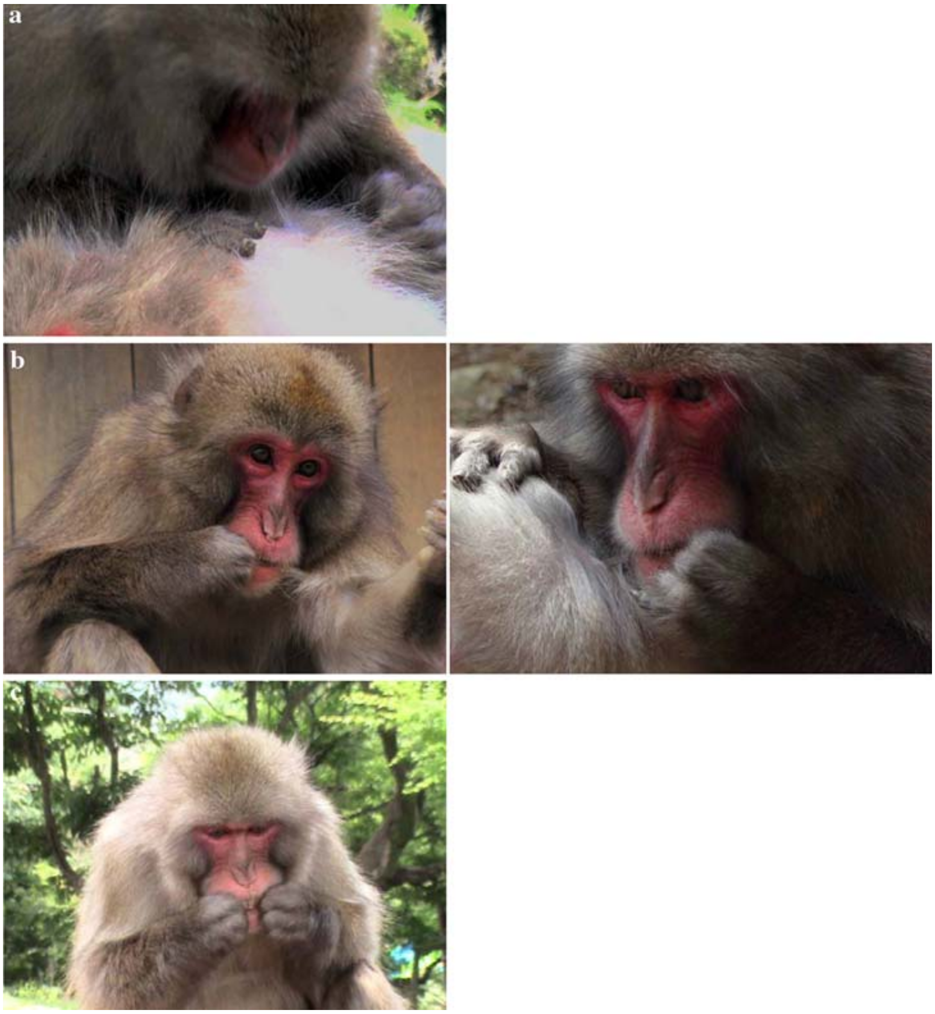

Fig. 1 **a** "Stretching with mouth" technique. **b** "Stretching with hand" technique during self-grooming (*left*) and during allo-grooming (*right*). **c** "Plucking" technique

classes of individuals according to their dominance rank: high-ranking, middle-ranking, and low-ranking individuals ($N = 29$ for each dominance class). Inter-observer reliability kappa coefficients were $k = 0.89$ for individual identities and 0.94 for all activities and behaviors including DF. Intra-coder reliability kappa coefficient was $k = 0.87$ (cf. Martin and Bateson 1993).

We reported percentages on number of events or durations and mean values ± the standard deviation (SD). To compare the observed frequencies of the two categories of dichotomous variables (e.g., use of same hair vs. use of different hair) to the frequencies expected under a binomial distribution with a probability parameter of 0.5, we used two-tailed binomial tests. To test the effect of dominance on the choice of flossing recipients, we used a two-tailed Mann–Whitney U test to compare the cumulative durations of DF events on lower-ranking and higher-ranking recipients. Statistical analyses were performed using the SPSS 13.0 analytical program. Significance levels were set at $\alpha = 0.05$.

Results

Social profile of the innovator: status, kinship, and partners

The innovator Chonpe-69-85-94 was a central-troop (cf. Leca et al. 2007b) middle-aged (14 year-old) female. She was middle-ranking, and ranked 42 out of 87 adult females. She had no offspring and only two close kin: her mother (Chonpe-69-85) and her younger brother (Chonpe-69-85-06). The 12 other living members of the Chonpe matriline were distant kin (Leca, unpublished data).

Out of 130 potentially available grooming partners, Chonpe-69-85-94 had grooming interactions with 11 individuals. She devoted 71.9% of her grooming to her two close kin, including 43.1% to her mother and 28.8% to her younger brother. The nine other grooming partners totaled 28.1% of grooming interactions, ranging from 0.4 to 5.3%. Among them, five individuals were dominant over Chonpe-69-85-94. The next results relate to Chonpe-69-85-94 only.

The dental flossing innovation

Frequency and duration of DF activity and DF behavior

The DF behavior occurred in 41 out of 70 focal samples (58.6%) collected on Chonpe-69-85-94. We recorded 63 DF bouts in 17.8 h of focal samples. Thus the DF frequency was 3.5 bouts per hour. The mean duration of DF bouts was 2.1 ± 3.0 min, ranging from 0.1 to 11.8 min. The mean number of DF events per bout was 9.3 ± 16.0, ranging from 1 to 81. The mean duration of DF events was 5.0 ± 2.4 s and the DF activity represented 4.6% of the total activity budget of Chonpe-69-85-94.

Context of occurrence of the DF behavior

The DF behavior was always associated with grooming activity, either starting the grooming sequence (9.5%), ending it (15.9%), or being interspersed within (74.6%). Out of 589 DF events, 167 (28.4%) were recorded during self-grooming activity with a frequency of 1.3 events per minute, whereas 422 (71.6%) occurred during allo-grooming interactions, with a frequency of 1.9 events per minute. Out of 63 DF bouts, 27 (42.9%) were associated with self-grooming activity at a frequency of 0.2 bout per minute, whereas 36 (57.1%) occurred during allo-grooming interactions, with a frequency of 0.2 bouts per minute.

Overall, there were 1.7 DF events and 0.2 DF bouts per minute devoted to grooming activity. In terms of time budget, the DF activity represented 10.8% of time spent self-grooming, 15.6% of time spent allo-grooming, and 13.9% of time devoted to grooming in general. There was no significant difference in the occurrence of DF behavior between post-feeding and non-feeding focals ($N_{\text{with DF}} = 20$ and 21, $N_{\text{without DF}} = 15$ and 14, respectively, $\chi^2 = 0.06$, $df = 1$, $p = 0.808$).

Form and recipients of the DF behavior

In 100% of DF events, Chonpe-69-85-94 used hair to floss her teeth and never used any other object or her fingers alone. Among the 589 DF events, the "stretching with hand" technique was the most frequently performed (65.4%), followed by the "stretching with mouth" technique (28.7%), and the "plucking" technique (5.9%). For the "stretching with mouth" and "stretching with hand" techniques, most of DF events were performed during allo-grooming (62.1 and 82.3%, respectively), whereas the opposite occurred for the "plucking" technique, with 35 DF events recorded during self-grooming and none during allo-grooming interactions (Fig. 2).

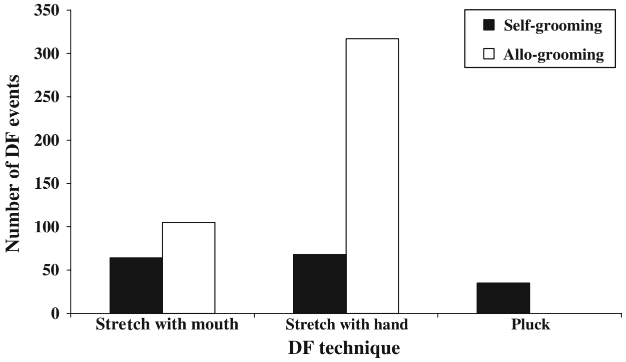

Fig. 2 Distribution of DF events according to the three DF techniques and the type of grooming activity

In almost all the DF events where the "plucking" technique was performed (90.9%), the flosser spent a few seconds selecting and removing several hairpieces from the first tuft clutched before using the remaining ones to floss. Such patterns to select the number and/or types of hair was less frequent when the "stretching with mouth" and the "stretching with hand" techniques were performed (31.8 and 59.3%, respectively). Overall, video close-ups showed that the number of pieces of hair used as floss ranged from one to about five or six pieces. In the successive DF events within a DF bout, the focal subject used significantly more different hairs than the same hairs (210 vs. 142 events, respectively; two-tailed binomial test (0.5), $p < 0.001$). After flossing, the focal subject very occasionally discarded the hair immediately; usually, however, she almost systematically looked at the hair and then licked off saliva (presumably mixed with food remains) attached to the hair before discarding it (18 vs. 571 events, respectively; two-tailed binomial test (0.5), $p < 0.001$). Although there were preferred flossing sites on the flossing recipient's body, the hair used to floss came from every body part (back 221 events, chest 96 events, arm 83 events, belly 79 events, leg 74 events, ano-genital region 25 events, and head/neck 11 events).

When DF was associated with allo-grooming, Chonpe-69-85-94 had flossing interactions with 7 of her 11 grooming partners. She devoted 88.9% of her flossing interactions to her two close kin, including 74.9% to her mother and 14.0% to her younger brother. We found a significant effect of dominance on the choice of flossing recipients among the grooming partners: after excluding the two close kin from the analysis, the duration of DF events on higher-ranking recipients was significantly lower than on lower-ranking recipients (Mann–Whitney U test: $N_{\text{lower-ranking}} = 4$, $N_{\text{higher-ranking}} = 5$; $z = -2.56$; $p = 0.011$). In other words, the flosser spent less time flossing on dominant than on subordinate individuals. It should also be noted that during the three cases of DF bouts ending with aggression directed from the flossing recipients to the flosser (having its hair stretched is presumably painful), the former were dominant over the latter.

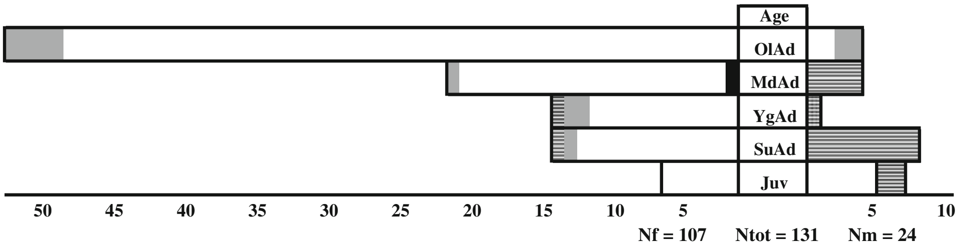

Fig. 3 Age and sex distribution of verified flosser (observed performing DF at least once: *black areas*), verified non-flossers (sampled at least 30 min during grooming activity and in which DF was not observed: *white areas*), non-verified individuals (in which DF was not observed, but individuals were undersampled—less than 30 min—during grooming activity: *grey areas*), and non-sampled individuals (*horizontal lines*) according to age and sex classes. *Juv* juvenile, *SuAd* subadult, *YgAd* young adult, *MdAd* middle-aged adult, *OlAd* old adult. The *left part* of the distribution represents the number of females (N_f), and the *right part* represents the number of males (N_m), N_{tot}: total number of individuals

Current prevalence of the DF behavior at the group-level

From 152.9 h of this focal data on 113 other central group members, we obtained 103 verified non-flossers and ten non-verified individuals. Therefore, the DF behavior was reasonably declared absent from the rest of the group and the prevalence of DF at the group-level was one verified flosser out of 113 central-troop individuals, i.e. around 0.01% (Fig. 3).

Discussion

Determinants of the DF innovation

Environmental opportunities to start flossing one's teeth

Because they are provisioned with food several times a day, Arashiyama E troop members have "free time on their hands", and this opportunity could lead them to further explore various objects and incorporate them into feeding activities (Huffman and Quiatt 1986; Leca et al. 2008b). These artificial conditions are likely to enhance the appearance of food-related tool-use, such as the use of dental floss. Provisioning has relaxed selective pressures on foraging, and created favorable environmental conditions under which various behavioral innovations by Japanese macaques may occur (Leca et al. 2007a, 2008c).

Likewise, Watanabe et al. (2007) suggested that the DF behavior exhibited by a troop of long-tailed macaques living around a Buddhist temple in Thailand, probably originated from special anthropogenic circumstances: because the shrine visitors worshiped the monkeys, they allowed them to climb up their shoulders and pull out some hair from their heads to use as dental floss.

Individual characteristics of the DF innovator

Because DF is always grooming-related, the behavior is more likely to appear in frequent groomers, i.e. central group members, than in individuals less involved in grooming interactions, i.e. peripheral group members (cf. Nakamichi and Shizawa 2003). Thus, it is not surprising that the innovator was a central individual. We could not assess whether the social status of the innovator—middle-ranking—was consistent with other findings, because most reports broadly classified innovators as either high or low-ranking, with no intermediate dominance rank (Reader and Laland 2001).

As an adult female, the current age of the innovator was consistent with most studies, whereas the sex was not. It has been found that innovators were more frequently males and adults than females and non-adults (reviewed by Reader and Laland 2001). However, the innovator may have been younger when she first performed the DF behavior. This is consistent with previous research showing that most Japanese macaque innovators are juvenile females (Kawai 1965; Itani and Nishimura 1973; Huffman 1984; Kawai et al. 1992).

Finally, Chonpe-69-85-94 might have temperamental traits that made her prone to behavioral innovation. Despite extensive observation of most troop members in a study of stone handling behavior, she was the only individual observed repeatedly rolling small stones on the palm of her hand while intensively grooming her palm and presumably trying to remove a spine stuck in it (Leca, personal observation). This first report of Japanese macaques seeming to attempt to use stones in a health-maintenance context is suggestive of a generally inventive temperament. Sinha (2005) suggested the role of temperament in bipedal begging innovation by bonnet macaques (*Macaca radiata*).

How and why inventing DF?

Because chance may account for a good number of behavioral innovations (Reader and Laland 2003), and DF was always associated with grooming activity, we suggest that the DF innovation is an accidental by-product of grooming. Thus, the following is a reasonable scenario: during regular grooming episodes, Japanese macaques sometimes bite into hair or pull it through their mouths to remove external parasites, such as louse eggs (Tanaka and Takefushi 1993). Because of particular anatomical constraints such as diastema (i.e. gaps between incisors), pieces of hair may accidentally have stuck between Chonpe-69-85-94's teeth, and as she drew them out, she may have noticed the presence of food remains attached to them. The immediate reward of licking the food remains off the hair may have encouraged her to repeat the behavior for the same effect in the future, by actively inserting the hair between her teeth.

Therefore, the DF innovation could be a transformation of grooming patterns via the running of hair between the teeth to remove louse eggs. These scenarios are consistent with the "perception–action" perspective on the development of tool-use and foraging competence in monkeys, apes, and humans, postulating that skilled actions are acquired through the routine generation of species-typical exploratory actions, coupled with learning about the outcomes and affordances of each action that generates directly perceptible information (Lockman 2000; Gunst 2008).

Besides possible proximate causes, the problem arises about why the DF behavior has been maintained by its innovator for several years. A first parsimonious explanation of this behavior is that the flosser may simply enjoy the interaction between the hair and its teeth, and apparent pleasurable feedback potentially gained from the activity may be an immediate reinforcement (cf. Leca et al. 2007d). Second, DF could alleviate the possible physical annoyance caused by a piece of food stuck between the teeth. A third beneficial consequence of DF could be an improvement in the teeth condition. Flossing one's teeth is a form of health maintenance regarded as self-medication (Huffman 2007). Because all self-medicative behaviors are driven by some quest for comfort, these interpretations are congruent with the classification of the tooth-pick behavior in orangutans as a "comfort innovation" (Russon et al. 2009). Because DF was not more frequent in post-feeding than non-feeding periods, we doubt that the DF innovation had significant, or even any, survival value, through the very small amount of extra food the flosser can obtain from its behavior.

Emergence of new DF variants

Although these data did not allow us to accurately determine the order of appearance of the different DF techniques, past observations and comparative analysis of the behavioral patterns support the view that the "plucking" technique was acquired later than the two other DF variants. First, previous long-term behavioral observations of this group showed that Chonpe-69-85-94 had been using the "stretching with hand" and the "stretching with mouth" techniques for at least four years (Leca, unpublished data; Vasey, personal communication). Although the "plucking" technique was not noticed before 2008, its absence remains speculative. Second, several elements show a higher level of complexity in the "plucking" technique than in the two other variants:

1. the former consists in manipulation of a detached object (plucked hair) whereas hair is attached to the skin in the latter;
2. the former requires both hands to be used whereas only one hand is used in the latter;
3. hair selection was more frequent in the former than in the latter; and
4. since the former necessitates hair to be pulled out, it is more invasive than the latter.

Likewise, the "stretching with hand" technique, that requires the use of hand and mouth can be considered more complex, in terms of sequence of actions, than the "stretching with mouth" technique, in which only the mouth is used. Although we cannot determine the exact timeline, we propose the following order in the emergence of DF techniques: first the "stretching with mouth" technique, then the "stretching with hand" technique, and last the "plucking" technique. In long-tailed macaques, there was a generalization of the DF behavior with hair to the use of coconut shell fibers for the same purpose (Watanabe et al. 2007). In Japanese macaques, even non-instrumental object manipulation can undergo a major "transformation" process over time, with an increase in the diversity and complexity of the behavioral patterns exhibited (Leca et al. 2007c, 2008a).

Constraints on the diffusion of the DF innovation

The first individual to display a novel behavior may do so repeatedly and sometimes for long periods of time before it starts diffusing within the group (Nishida et al. 2009). However, it took less than four years for most behavioral innovations reported in Japanese macaques to be transmitted to at least a second group member (Kawai 1965; Itani and Nishimura 1973; Huffman 1984; Watanabe 1989; Nakamichi et al. 1998). Therefore, it is reasonable to consider the DF innovation as being not particularly prone to diffusion.

Socio-demographic features at the group level

Group size and number of grooming partners available With 145 individuals, the Arashiyama E troop is a large troop of Japanese macaques. However, the innovator had grooming interactions with relatively few partners (11 individuals), and among them a large proportion of grooming time (71.9%) was allocated to two individuals. This is consistent with findings from another group of Japanese macaques, comparable in terms of number of adult females, maternal kin-groups, and environmental conditions (both are free-ranging provisioned troops), showing that in large groups, most females had grooming interactions with a small subset of females (Nakamichi and Shizawa 2003). Because DF was grooming-related, the small grooming network of the innovator may constrain the diffusion of the behavior. Large-sized groups comprise many uninformed bystanders who could slow down the diffusion (Lefebvre and Giraldeau 1994). Not only group size but also group composition in age classes may affect the diffusion and performance of some behaviors in this species, like stone handling (Leca et al. 2007b).

Kinship The innovator had only two close kin: her mother and only one sibling, a 2 year-old brother. She had no offspring. Since the pathways of diffusion of most behavioral innovations by Japanese macaques involve at some point the spread among siblings and the downward vertical transmission from mother to offspring (Huffman 1984; Nahallage and Huffman 2007), this paucity in individuals closely related to the innovator may limit opportunities for diffusion of DF. Long-tailed macaque mothers exaggerated their DF actions in the presence of their offspring, which could facilitate the learning of the behavior by infants (Masataka et al. 2009). Another channel of diffusion of innovations in this species is the upward vertical transmission from offspring to mother (Huffman 1984). However, the nature of the behavior (see below) may explain the lack of transmission of DF from the innovator to her mother, despite their close social proximity.

Dominance Among the few non-related grooming partners of the innovator, most were higher-ranking. In despotic macaque species, for example Japanese macaques, grooming is mainly directed up a hierarchy (Koyama 1991). Our data suggest that when associated with allo-grooming interactions, the DF behavior is not risk-free. Stretching others' hair to make it suitable for flossing is likely to be more painful for others than regular allo-grooming patterns, thereby exposing the flosser to aggressive reactions from flossing recipients. The risk of being aggressed by dominant flossing recipients may account for the innovator spending less time flossing on higher-ranking than lower-ranking partners. If the expression of the DF innovation is restricted by dominance relationships, it may limit its chance of spread to group members of all social status. In dominance-structured groups, social status may constrain behavioral innovations, their subsequent propagation, and long-term maintenance (Leca et al. 2007a).

Structural and functional aspects of the DF behavior

Depending on their form, function, or context of performance, some types of behavior may be more or less prone to spread within a group (Tanaka 1998).

Form First, the innovator's dependence on object use was shown by the fact that in all DF episodes she used hair to floss her teeth and never used her fingers alone. However, as opposed to feeding innovations whose propagation can be constrained by access to and monopolization of the novel food source (cf. Leca et al. 2007a), the lack of diffusion of the DF innovation cannot be explained by the opportunity to get access to the flossing tool—the number of hairs on its own body or on others' bodies is countless. Second, mathematical models predict that the expected proportion of naive individuals learning the new skill will decrease as skill complexity increases (Cavalli-Sforza and Feldman 1981). This explanation may not hold for DF either. The behavioral patterns involved in the performance of the three DF techniques (e.g., stretching with hand, plucking, holding, repeated teeth-chattering) are simple enough to be exhibited by all but the very young individuals in Japanese macaques, a species also known for complex object manipulation (cf. Leca et al. 2007c).

A third possibility could be that individuals are not able to make the discrimination between the novel behavior (i.e. using hair as dental floss) and regular grooming patterns. In their form, the "stretching with mouth" and "stretching with hand" techniques are close to some grooming variants such as "combing" and "pinching" (cf. Tanaka 1998). As for the "plucking" technique, which differs from regular grooming, it was only performed during self-grooming activity, thereby limiting the opportunity for social influence, and its frequency could be too low to make this variant noticeable by others. In other words, the DF behavior, as currently practiced by its innovator, would not be conspicuous enough to be reliably noticed and learnt by naive group members. The anthropogenic circumstances of DF innovation in long-tailed macaques (see above) could make the behavior more attractive to naive individuals and could account for the spread of this innovation within the group (Watanabe et al. 2007).

Context, innovation-related risk, and function The more specialized the context and function of the behavior, the more limited will be the subgroup of individuals that will acquire it (Huffman and Hirata 2003). In Japanese macaques, DF behavior occurs mainly during allo-grooming, a social interaction involving a certain amount of risk to one or both protagonists (cf. Zahavi 1977). Aversive flossing recipients' reaction to harmful behaviors may explain why the "plucking" technique was not observed during allo-grooming interactions. The social transmission of certain behavioral variants may be constrained by the risk of aggression (cf. Tanaka 1998). In a group of long-tailed macaques where DF has spread widely, the behavior was self-directed and performed solitarily (Watanabe et al. 2007). Observing each other at a distance with a lower risk of aggression may have facilitated the diffusion of the behavior.

The low adaptive value of the DF innovation may also partly account for the lack of propagation. Such object manipulation may not spread simply because of the narrow window of its applicability (cf. Sinha 2005; but see Huffman 1984). Comfort innovations may also be less likely to diffuse than those that are related to subsistence or socio-sexual communication (van Schaik et al. 2006).

Conclusions and future directions

This is one of the rare studies to document the spontaneous appearance of tool-use behavior in Japanese macaques under natural conditions (see also Leca et al. 2008a). The lack of report on DF in other troops of Japanese macaques and the idiosyncratic presence of the behavior in this troop may reflect possible intra-troop and inter-troop variations in:

1. the likelihood of behavioral innovation;
2. the social constraints on the early dissemination and long-term maintenance of such inventions; and
3. appropriate social and/or environmental reinforcement for the emergence, propagation, and continued practice of this behavior.

When a behavior is restricted to one or very few group members, it is likely to disappear at the group level (Leca et al. 2007a; Nishida et al. 2009). Further investigation, including experimentally-elicited DF, may help to determine more accurately the conditions of appearance of this novel behavior, and to elucidate why it has not spread within the group (cf. Watanabe et al. 2007; Leca et al. 2008a).

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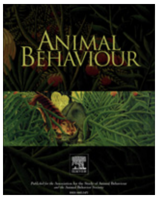

Indirect social influence in the maintenance of the stone-handling tradition in Japanese macaques, *Macaca fuscata*

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Comparative and longitudinal studies have shown that stone-handling (SH) behaviour, defined as the noninstrumental manipulation of stones by performing various behavioural patterns, is socially transmitted across generations as a cultural behaviour in Japanese macaques. We investigated experimentally how stimulus/local enhancement, a form of indirect social influence through the physical traces typically left in the environment by previous stone handlers, might trigger SH behaviour at the individual level, and thus could contribute to the maintenance of the SH tradition at the group level. Through the semicontrolled conditions of field experiments, conducted in the free-ranging provisioned Arashiyama E troop, in which the SH tradition has been well established for nearly three decades, our results supported the stimulus/local enhancement hypothesis. Most group members preferentially directed their SH behaviour towards typical physical traces of SH activity (piles of stones) over randomly scattered stones. Encountering SH artefacts enhanced the use of these particular stones for performing SH in that particular part of the environment. The common occurrence of such 'play stations' may favour the frequent reuse of the same stones over time and explain the transport of stones between and around SH artefacts. We provided evidence for the role of indirect social inputs on the long-term persistence of the SH tradition in Japanese macaques, through SH by-products, the stimulating effect of which can be delayed in time and separate in space from others. We discuss our findings from the perspective of socially mediated behaviours, conformity-enforcing responses and niche construction.

In the quest for cultural versus alternative explanations of behavioural variation within and between groups of the same animal species, there has been a heated conceptual and methodological debate among field and laboratory researchers. Before such behavioural variability can be regarded as cultural, it is acknowledged that the effects of genetic and ecological factors should be minimal. However, depending on the environmental conditions of the study, the species' attributes and the behavioural domain under investigation, the questions addressed and the methods used to answer them vary considerably. Three major approaches have been taken to assess whether intra- and intergroup behavioural diversity in a given species can be considered evidence for culture (often labelled 'behavioural tradition' by ethologists; reviewed in Caldwell & Whiten 2007).

First, the 'group contrast' approach (see Fragaszy & Perry 2003a) consists of examining variation in the frequency of behavioural variants between groups (often sampled from geographically separate populations; Whiten et al. 1999; Rendell & Whitehead 2001; Hunt & Gray 2003; Perry et al. 2003; Leca et al. 2007a). Second, the longitudinal approach relies on the social context of diffusion and maintenance over time of a novel behaviour within a group, as a way to assess whether social or individual learning is more likely to be involved (Coussi-Korbel & Fragaszy 1995; Lefebvre 1995).

However, from a conceptual viewpoint, the very notion of culture is debatable until there is empirical evidence that the transmission and maintenance of the novel behaviour within the group are socially mediated (Fragaszy & Perry 2003b; Galef 2004). Therefore, the third approach consists of conducting experimental studies to determine whether 'socially biased learning' processes (Fragaszy & Visalberghi 2001, 2004) could support the putative cultural behaviours observed in the wild. Social learning is any form of learning influenced by the presence of, observation of or interaction with another individual (typically a conspecific) or its products (Galef 1988). The various 'social influences supporting the learning of novel behaviours' (Fragaszy & Visalberghi 2004, page

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27) or the performance of species-specific behaviours can thus be divided into two broad categories, namely direct social influences and indirect social influences (Galef 1988; Tomasello et al. 1993; Whiten 2000; Visalberghi & Fragaszy 2002).

Among the forms of direct social influences, the probability of an individual performing a behaviour may increase in the presence of a conspecific performing the behaviour, which is already in the observer's behavioural repertoire (social facilitation), or in the mere presence of a conspecific resulting in a behavioural disinhibition by reduction of isolation-induced fear (social enhancement). An individual's behaviour may also be triggered by the synchronized performance of a similar behaviour by several conspecifics, as part of an amplification process (contagion). Finally, an individual may learn to copy some part of the form of the behaviour performed by a demonstrator or may learn from a model the goal to pursue (imitation/emulation). Most studies on social-learning processes have focused on direct social influence through the necessary presence of other group members (reviewed in Zentall & Galef 1988; Fragaszy & Perry 2003a).

By contrast, indirect social influence assumes that an individual's behaviour may result from directing its attention to a 'limited aspect of the total stimulus situation to which the response is to be made' (Spence 1937, page 821), without necessarily interacting directly with a conspecific. If stimulus/local enhancement is involved in the acquisition, transmission or maintenance of a habit, then individuals should tend to focus their attention on, or aim their responses towards, particular objects or places in the environment after observing conspecifics' actions in conjunction with those objects or at that place (Thorpe 1963; Byrne & Russon 1998). Through the stimulating effect of the physical traces (or artefacts) left behind by previous individuals, indirect social influences are delayed in time and separate in space from others. For example, residual olfactory cues left on foraging trails by ants and rodents affect the selection of feeding sites (Hölldobler & Wilson 1991; Galef & Buckley 1996). As opposed to some of the complex learning processes mentioned above, the role of stimulus/local enhancement offers a more parsimonious explanation for the acquisition of foraging techniques by immatures in various taxa such as birds, rodents and primates (Denny et al. 1988; Tomasello et al. 1993; Huber et al. 2001; Gunst et al. 2008). However, to date, indirect social influence on the acquisition, performance or long-term maintenance of behaviours has not received the formal attention it deserves.

One reason for this could be the lack of experimental data obtained from the spontaneous behaviours in free-ranging and socially living groups of animals. Most experimental studies of social learning have used artificial tasks and were conducted in the unnatural social conditions of laboratory settings (reviewed in Galef & Laland 2005). Recent criticisms about the ecological validity of these studies has led to recommendations for field experiments using biologically relevant tasks and allowing individuals to interact spontaneously with each other and with test stimuli, with no human-imposed outcomes for the successful completion of the task (Matsuzawa 1994; Galef 2004; Huffman et al. 2008; Watson & Caldwell 2009).

Here, we took a field experimental approach to test the indirect social influence of lithic artefacts on the enduring performance of stone-handling (SH) behaviour in Japanese macaques. The SH activity is the noninstrumental and seemingly playful manipulation of stones, such as repeatedly pounding a stone on a substrate, clacking two stones together, or gathering several stones into a pile (Huffman 1984). SH is the longest studied and best-documented cultural behaviour in monkeys to date (reviewed in Huffman et al. 2008). Research on SH has already benefited from a comparative approach revealing substantial variation in SH between troops of Japanese macaques, and from long-term observational studies conducted at several points in time over a 30-year period to address the influence of environmental, sociodemographic and developmental constraints on the emergence, diffusion and maintenance of the SH tradition (Huffman 1984, 1996; Huffman & Quiatt 1986; Huffman & Hirata 2003; Leca et al. 2007a, b, 2008a, b, in press a). For example, the continuous study of mothers and infants during the first 6 months of life, in the semicontrolled conditions of an outdoor enclosure, showed that (1) the mother was the primary source of an infant's early exposure to SH, (2) the acquisition of SH behaviour by young individuals may involve direct social influences (social facilitation) through the observation by naïve infants of their mothers as SH demonstrators, and (3) some intragroup variability in the performance of SH patterns could be interpreted from the viewpoint of developmental constraints (Nahallage & Huffman 2007a, b).

However, the maintenance of the SH tradition across generations may involve not only direct social influences but also indirect social inputs through the stimulating effect of SH artefacts (Quiatt & Huffman 1993). Through the enduring practice of SH behaviour, acquired familiarity with the stones and occasional integration of SH with other daily activities, Japanese macaques often carry stones about and leave them behind when engaging in another activity. As a result of these regular transports, small piles of stones are conspicuously deposited on grassy patches, stone slabs or at the base of large trees (Huffman & Quiatt 1986). The common occurrence of such SH artefacts or 'play stations' around the feeding ground, and sometimes in the forest, may favour the frequent reuse of the same stones over time (Quiatt & Huffman 1993). However, the hypothesis that encountering physical traces of previous SH activity affects subsequent SH activity has not yet been tested.

The present work is the first to use a field experimental approach to examine the environmental and social conditions, at least partially reconstructed, under which the SH tradition may be maintained within troops of Japanese macaques. We studied the free-ranging provisioned Arashiyama E troop, in which the SH tradition has been well established for nearly three decades (Huffman 1984, 1996; Leca et al. 2008b). Therefore, it is beyond the scope of this study to address the social-learning processes involved in the initial establishment of the SH tradition. Our main goal was to investigate experimentally how the physical traces typically left in the environment by previous stone handlers might help, through a stimulus enhancement process, trigger SH behaviour in individuals on a daily basis, and thus contribute to the long-term maintenance of the SH tradition at the group level.

We tested the 'stimulus/local enhancement hypothesis' on the performance of SH, proposing that individuals should preferentially direct their SH activity towards the places where previous stone handlers left conspicuous physical traces of their SH activity, and more specifically towards piles of stones. Our specific objective was to test two predictions derived from the 'stimulus/local enhancement hypothesis'. Prediction 1 stated that the frequency and duration of SH behaviour should be significantly higher when directed to a pile of stones than when directed to randomly scattered stones for all individuals entering the experimental area, including the first one to do so, that is, when any possible direct social influence had been removed. Prediction 2 stated that if the location of the piles of stones changed during consecutive visits to the same area, a given stone handler should be more attracted to the new locations (where the piles of stones are) than the previous locations. Rejection of the 'stimulus/local enhancement hypothesis' could suggest that the persistence of the SH tradition and the motivation to engage in this activity are better explained by direct social influences such as social facilitation or social enhancement.

To explore further the environmental factors underlying the maintenance of the SH tradition, (1) we tested the possible spatial

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preferences for SH at the group and individual levels, (2) we evaluated the number and relative locations of the piles of stones used, and (3) we documented the transport of stones between and around piles of stones. Finally, to assess how social constraints may either promote or inhibit the daily performance of stone-directed behaviours, and thus the long-term persistence of the SH tradition, we investigated the role of age, kinship and dominance relationships in the use of SH artefacts.

METHODS

Study Group

The following observations were made on the free-ranging Arashiyama E troop of Japanese macaques at the Iwatayama Monkey Park, Arashiyama, Kyoto Prefecture, Japan. Japanese macaques have been provisioned and studied at Arashiyama since 1954 (Huffman 1991). At the time of our observations, the study group was provisioned with wheat grains four times a day by the park staff. This type of food was eaten by the monkeys without any processing whatsoever other than chewing. Visitors were also allowed to give a small amount of extra food to the monkeys (see Leca et al. 2008b for details on provisioning conditions). Water was available ad libitum around the provisioning site. All group members were individually identified, and their ages and kin relations through maternal lineages were known. The study group contained 145 individuals of 15 separate matrilines. All age/sex classes were present, including 56 old adults, aged 16 or more years (52 females and four males), 25 middle-aged adults, between 11 and 15 years old (21 females and four males), 15 young adults, between 7 and 10 years old (14 females and one male), 22 subadults, between 4 and 6 years old (14 females and eight males), 13 juveniles, between 2 and 3 years old (six females and seven males) and 14 yearlings and infants (six females and eight males; see Leca et al. 2007b for details on age classification).

Data Collection

We defined an experimental area as a 24 m^2 surface (2 × 12 m) located on the ground and within 60 m around the feeding ground, where SH activity most visibly occurs (Huffman 1984; Leca et al. 2008b). We used only natural and already present landmarks (bushes, trees, rocks) to form the boundary of the area. To investigate local enhancement, we established four experimental areas located in different directions from the feeding ground and in places rarely disturbed by visitors and staff (Fig. 1a). There was no significant difference in stone availability within the four areas (Leca et al. 2008a). We randomly determined the area where each session took place, provided that the distribution of sessions in the four areas was homogeneous.

To investigate stimulus/local enhancement, we discreetly set out stones according to two specific spatial arrangements (called SH spots) within the chosen area, and before each experimental session. We defined an SH spot as a particular place with several stones placed on the ground, and where SH activity may occur. We distinguished two categories of SH spots: SH stations and SH zones. We defined an SH station as a set of 12 stones that we gathered into a small pile (Fig. 1b). We defined an SH zone as another set of 12 stones that we randomly scattered over a 1 × 1 m surface around a centralized SH station, and previously cleared of other stones. The stones used for the experiments were collected around the feeding ground and were typically used by the monkeys for performing SH. The number and spatial arrangement of stones used in a SH station were based on the average number and layout of stones found in a sample of 54 pictures of SH stations spontaneously set out by the group members (J.-B. Leca, unpublished data).

Within an experimental area, there were seven SH stations and seven SH zones, each numbered from 1 to 7. In an attempt to discriminate between stimulus and local enhancement, and when two consecutive sessions took place in the same area, we moved, during the second session, each SH station 2 m away from its

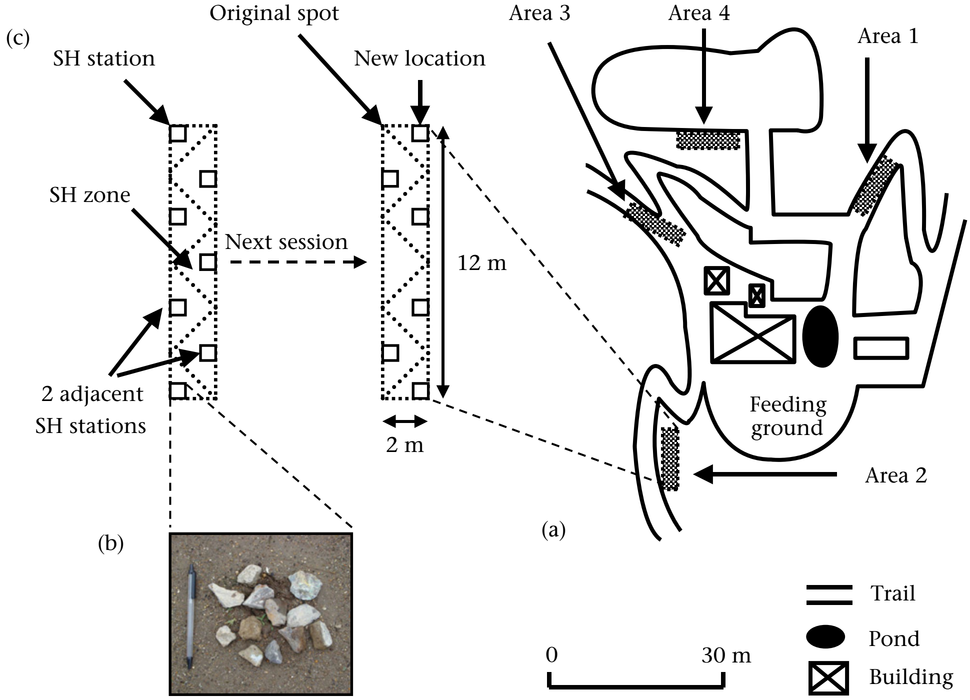

Figure 1. (a) Study site (map after Nishie 2002), (b) photo of a stone-handling (SH) station, and (c) spatial arrangement of SH stations within an experimental area during two consecutive sessions.

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original spot during the first session (Fig. 1c). We conducted each experimental session during the 20 min period immediately following food provisioning because it was the time when most SH activity occurs at the group level (Leca et al. 2008b). To ensure independence between sessions, we conducted only one session per postprovisioning period.

Each experimental session was continuously videorecorded by either J.-B.L ($N = 33$ sessions) or N.G. ($N = 15$ sessions) with a DCR-HC48 Sony digital camera from a position overhanging the experimental area. They used the focal-place sampling method (Leca et al. 2007c; Vogel & Janson 2007), focused on the experimental area, and videorecorded all individuals entering and staying within the area. The typical duration of an experimental session was 20 min. If an individual performed SH within the experimental zone during the final 2 min, the observation was extended until 2 min after this individual had stopped performing SH (Leca et al. 2007a).

Visibility during the experiments was excellent. The observers could sample the subjects within 5–10 m. We conducted a total of 48 experimental sessions between 0800 and 1500 hours, during two different periods: 26 sessions in autumn 2008 (10 September–3 October) and 22 sessions in spring 2009 (4–10 May). We conducted 15 sessions in area 1, and 11 sessions in each of the three other areas (see detailed analyses below). To establish the dominance hierarchy within the group, we recorded ad libitum data (Altmann 1974) on the direction of dyadic agonistic interactions.

Data Analysis

For each videorecorded session, N.G. continuously transcribed to the second (1) the number, identity and activity (locomoting, feeding, foraging, grooming, resting and SH) of all individuals entering and present within the experimental area, (2) whether individuals were engaged in SH activity on SH stations or SH zones, and their respective numbers, (3) all occurrences of individual changes in SH spots, and possible transport of stones between SH spots, and (4) all occurrences of supplanting interactions over SH stations or SH zones. Although we could not identify all individuals passing through the experimental areas, we could identify all individuals engaged in SH activity within these areas. We defined an SH phase as the individual performance of SH activity on a given SH spot. Each change of SH activity between SH spots marked the start of a new SH phase.

For most analyses, we report percentages of events or durations and mean values ± SD. Since our raw and transformed data violated the parametric assumptions, we conducted nonparametric tests (Siegel & Castellan 1988). To demonstrate stimulus/local enhancement, we used a Wilcoxon signed-ranks test to compare, for each individual involved in SH activity within the experimental areas, the frequency and duration of SH phases performed on SH stations versus on SH zones. Since the direction of the difference was predicted, the region of rejection was one tailed. A given individual was categorized as more attracted to SH stations, more attracted to SH zones or equally attracted to both SH spots, if the cumulated frequency or duration of its SH phases was higher on SH stations than on SH zones, higher on SH zones than on SH stations or equal for both SH spots, respectively. We also used Wilcoxon signed-ranks tests (one tailed) to compare (1) the SH frequency on the new versus the previous locations of SH stations during two consecutive sessions, and (2) the frequency of supplanting interactions over SH stations versus over SH zones.

To examine further the magnitude of stimulus/local enhancement and provide more information than the conventional statistical significance (P value), upon which we make a dichotomous decision (reject or fail to reject), we used the effect size statistic. To assess the effect size and calculate its confidence interval (95% CI), we used, respectively, the Cohen's d statistic and its related standard error (SE_d) for two dependent groups (Nakagawa & Cuthill 2007). We considered d values of 0.2, 0.5 and 0.8 as benchmarks for 'small', 'medium' and 'large' effects, respectively, and we qualified the effect size as statistically significant (at an α level of 0.05) if its CI did not include zero (Cohen 1988).

To compare the frequency of presence and SH frequency of group members in the four experimental areas, we used a Friedman test followed by multiple paired comparisons based on mean ranks. Compared with the 11 sessions conducted in areas 2, 3 and 4, the four additional sessions in area 1, an area frequented by many group members, were only used in the analyses of stimulus/local enhancement (comparing the types of SH spots used within an experimental area), not in the analyses of spatial preferences (comparing the frequency of presence and SH between experimental areas). When comparing the number of stone handlers recorded in the four areas, we drew lots for 11 sessions in area 1 to obtain data directly comparable with the three other areas.

We used chi-square goodness-of-fit tests to compare (1) the number of individuals recorded performing SH in one, two, three and four areas, (2) the number of SH stations used by stone handlers during the same session, and (3) the frequency of transport of stones between two SH stations, from an SH station to an SH zone, and from an SH zone to an SH station. For post hoc examination of chi-square tests, we calculated the adjusted standardized residuals, and considered statistically significant those values of Z scores that were $\geq |1.96|$.

We recorded 592 avoidances and dyadic unidirectional acts of aggression (see Leca et al., in press b). We used the Matman program edited by Noldus Information Technology (1998) to verify the linearity of the dominance hierarchy for 91 group members, that is, 87 adult females and the four top-ranking adult males ($h' = 0.27$, directional consistency index $= 0.97$, $P < 0.001$; de Vries et al. 1993; de Vries 1995). We distinguished three classes of individuals according to their dominance rank: high-ranking, middle-ranking and low-ranking individuals ($N = 30$, 31 and 30, respectively).

Interobserver reliability kappa coefficients were $k = 0.89$ for individual identities and 0.94 for all activities and behaviours including SH. To measure the extent to which a single observer obtained consistent results when transcribing the same videorecorded behaviours on different occasions, N.G. transcribed two times a sample of five experimental sessions, involving a total of 670 sample points. A good intracoder reliability kappa coefficient was also obtained: $k = 0.85$ (Martin & Bateson 1993). Statistical analyses were performed using the SPSS 13.0 analytical program (SPSS Inc., Chicago, IL, U.S.A.). Significance levels were set at $\alpha = 0.05$.

RESULTS

Number and Activity of Group Members Involved in Sessions

The number of identified group members entering the areas at least once during the experimental sessions was 116 (i.e. 80.0% of group members), among which 82 were engaged in SH activity (i.e. 56.6% of group members). Of 48 sessions, we recorded a total of 448 entrances, among which 247 (55.1%) were followed by SH activity, whereas 201 (44.9%) were not. The average number of entrances per session was 9.3, among which 5.1 ± 3.9 were followed by SH activity. The average duration of presence of an individual within an experimental area per session was 4.9 min, among which 0.8 ± 1.9 min were devoted to SH (Table 1). The activity budget of the individuals present in the experimental areas shows that the

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Table 1
Frequency and duration of presence of individuals within the experimental areas, according to the type of activity performed (stone handling, SH, versus other activity)

Presence within the experimental areas	Activity		Total
	SH	Other	
Per session			
Mean frequency	5.1	4.2	9.3
SD	3.9	4.6	7.4
Minimum	0	0	0
Maximum	15	19	30
Mean duration (min)	0.8	4.0	4.9
SD	1.9	5.5	6.6
Minimum	0.0	0.0	0.0
Maximum	18.9	37.3	39.1
All sessions			
Total frequency	247	201	448
(%)	55.1	44.9	100.0
Total duration (hours)	6.3	30.2	36.6
(%)	17.3	82.7	100.0

two most represented activities were locomoting and SH on SH stations (Fig. 2). In sum, most individuals entering an experimental area either walked across it, or stopped to perform SH on SH stations. A slight majority of group members were engaged in the latter activity.

Stimulus/Local Enhancement

Before pooling the data obtained from all the experimental sessions, we verified that the attraction to SH stations was significantly higher than the attraction to the SH zones during each of the two study periods and in each of the four areas (Table 2). Therefore, in the following analyses, we pooled the data obtained from all the experimental sessions. When considering all sessions, we found that stone handlers were significantly more frequently attracted to SH stations than to SH zones, and spent significantly more time handling stones from SH stations than from SH zones (Table 2).

Regarding the effect sizes, we found that $d = 0.86$ with 95% CI = 0.6 to 1.1 for the frequency of SH on SH stations versus on SH zones, and $d = 0.65$ with 95% CI = 0.3 to 1.0 for the duration of SH on SH stations versus on SH zones. These results show that the effect sizes can be considered 'large' in terms of frequency, and between 'medium' and 'large' in terms of duration, and are both statistically significant (at an α level of 0.05) because the CIs do not include zero.

Whether we considered each session or all sessions, and each stone handler or all stone handlers, the mean, total frequency and duration of SH phases were systematically higher on SH stations than in SH zones (Table 3). We compared SH frequency on both types of SH spots only for the individual first entering the experimental area in each session, the strongest test of prediction 1 because the stone handler could not be affected by the behaviour or even the mere presence of a conspecific, and thus any possible direct social influence was removed. We also found that the frequency of SH behaviour was significantly higher when directed to SH stations than when directed to SH zones (17 individuals more attracted to SH stations, one more attracted to SH zones, and two equally attracted to both SH spots; Wilcoxon signed-ranks test: $Z = -3.581$, $N = 20$, $P < 0.001$). In sum, we have shown that the frequency and duration of SH behaviour were significantly higher when directed to piles of stones (SH stations) than when directed to randomly scattered stones (SH zones), for all individuals entering the experimental areas, including the first one to do so, thereby verifying prediction 1.

During two consecutive sessions, the same individuals entering the same experimental area where the SH stations had been moved 2 m away from their previous spots were significantly more attracted to the new locations of the SH stations than the previous spots to perform SH (Wilcoxon signed-ranks test: $Z = -3.473$, $N = 17$, $P = 0.001$). Thus, we verified prediction 2.

Spatial Preferences for SH at Group and Individual Levels

We found significant differences in the frequency of presence and SH frequency of group members in the four experimental areas (Friedman tests: presence: $\chi^2_3 = 88.88$, $N = 116$, $P < 0.001$; SH: $\chi^2_3 = 50.28$, $N = 82$, $P < 0.001$). Multiple paired comparisons showed that the frequency of presence was significantly higher in areas 1 and 3 than in areas 2 and 4 ($P < 0.05$) and SH frequency was significantly higher in area 1 than in area 4 and in area 3 than in areas 2 and 4 ($P < 0.05$). The other differences did not reach statistical significance ($P > 0.05$). These results were consistent with the number of group members recorded present and engaged in SH activity at least once in the four experimental areas (Table 4).

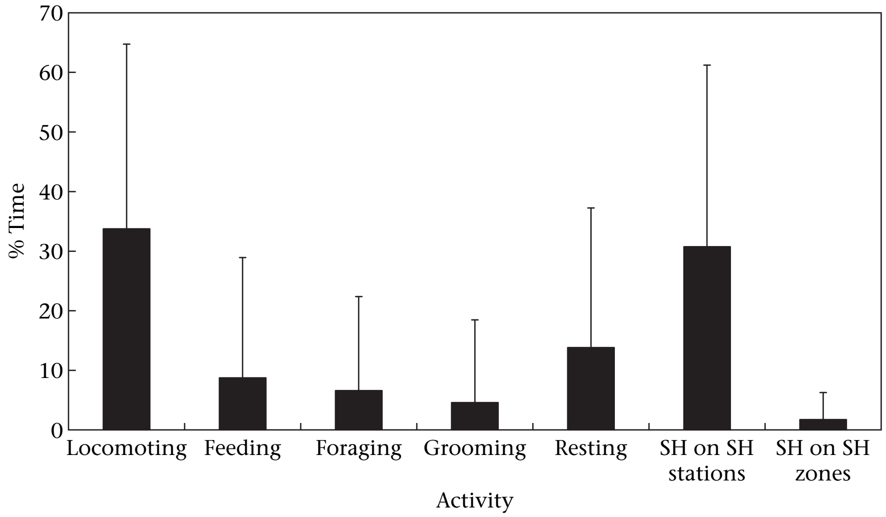

Figure 2. Mean percentage ± SD of time devoted to different activities by individuals present in the experimental areas.

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Table 2
Comparison of the number of individuals more attracted to stone-handling (SH) stations, more attracted to SH zones, and equally attracted to both SH spots, based on the frequency and duration of SH phases on SH stations versus on SH zones

Period	Variable	No. of individuals			N	Z*	P (one tailed)
		More attracted to SH stations	More attracted to SH zones	Equally attracted to both SH spots			
Autumn 2008	Frequency	42	2	2	46	−5.616	<0.001
	Duration	43	3	0	46	−5.370	<0.001
Spring 2009	Frequency	57	6	5	68	−6.347	<0.001
	Duration	61	7	0	68	−6.159	<0.001
Area							
1	Frequency	43	1	2	46	−5.722	<0.001
	Duration	44	2	0	46	−5.709	<0.001
2	Frequency	22	5	4	31	−2.761	0.006
	Duration	25	6	0	31	−3.175	0.002
3	Frequency	48	4	2	54	−5.953	<0.001
	Duration	50	4	0	54	−5.928	<0.001
4	Frequency	15	3	0	18	−2.658	0.008
	Duration	15	3	0	18	−2.592	0.010
All sessions							
	Frequency	73	3	6	82	−7.455	<0.001
	Duration	76	6	0	82	−7.307	<0.001

* Wilcoxon signed-ranks test.

Therefore, at the group level, some areas were more attractive than others in terms of presence and SH activity.

Of 82 group members engaged in SH activity during the experimental sessions, there was a significant difference in the number of individuals recorded performing SH in only one area ($N = 40$, i.e. 48.8%), in two areas ($N = 21$, i.e. 25.6%), in three areas ($N = 16$, i.e. 19.5%) and in the four areas ($N = 5$, i.e. 6.1%; chi-square test: $\chi^2_3 = 31.27$, $P < 0.001$). Post hoc examination of residuals showed that there were significantly more individuals recorded performing SH in only one area than in two, three and four areas. Thus we found, at the individual level, differential spatial preferences to engage in SH activity.

Number and Relative Location of SH Stations Used

We found a significant difference in the number of SH stations used by a given stone handler during the same session, namely only one SH station ($N = 130$, i.e. 56.6% of sessions), two SH stations ($N = 58$, i.e. 25.2%), three SH stations ($N = 24$, i.e. 10.4%) and from four to seven SH stations ($N = 18$, i.e. 7.8%; chi-square test: $\chi^2_3 = 138.07$, $P < 0.001$). Post hoc examination of residuals showed that the use of one SH station was significantly more frequent than the use of two, three and four to seven SH stations. When a given stone handler used more than one SH station per session ($N = 100$), it used adjacent SH stations in a majority of cases (59.7 ± 44.1%).

Table 3
Mean ± SD frequency and duration (in min) of stone-handling (SH) phases performed on SH stations and SH zones

	SH stations	SH zones	Total
Per session and per stone handler			
Mean frequency	2.0±1.8	0.4±0.8	2.4±2.0
Mean duration	1.5±2.4	0.1±0.4	1.6±2.4
Per session and for all stone handlers			
Mean frequency	12.8±7.5	2.3±3.1	15.1±7.9
Mean duration	9.6±8.1	0.7±1.3	10.3±8.1
For all sessions and per stone handler			
Mean frequency	5.8±6.7	1.0±1.9	6.8±7.5
Mean duration	4.4±8.5	0.8±1.0	4.6±8.5
For all sessions and for all stone handlers			
Total frequency	473	86	559
(%)	(84.6)	(15.4)	(100.0)
Total duration	5.9	0.4	6.3
(%)	(93.1)	(6.9)	(100.0)

Transport of Stones between SH Spots

We found that 68 of 559 SH phases (i.e. 12.2%) started with a transport of stones between SH spots. We did not record any transport of stones between two SH zones. There was a significant difference in the frequency of the three other categories of transport, namely between two SH stations ($N = 14$), from an SH station to an SH zone ($N = 21$), and from an SH zone to an SH station ($N = 33$; chi-square test: $\chi^2_2 = 8.15$, $P = 0.017$). Post hoc examination of residuals showed that the transport of stones from an SH zone to an SH station was significantly more frequent than the transport of stones between two SH stations.

Use of SH Artefacts across Age Classes

Across all age classes, stone handlers were significantly more frequently attracted to SH stations than to SH zones (Wilcoxon signed-ranks tests: infants and yearlings: $Z = -2.944$, $N = 11$, $P = 0.003$; juveniles: $Z = -2.536$, $N = 10$, $P = 0.011$; subadults: $Z = -3.426$, $N = 16$, $P = 0.001$; young adults: $Z = -1.992$, $N = 9$, $P = 0.046$; middle-aged adults: $Z = -2.887$, $N = 13$, $P = 0.004$; old adults: $Z = -4.018$, $N = 23$, $P < 0.001$) and spent significantly more time handling stones from SH stations than from SH zones (infants and yearlings: $Z = -2.934$, $P = 0.003$; juveniles: $Z = -2.599$, $P = 0.009$; subadults: $Z = -3.516$, $P < 0.001$; young adults:

Table 4
Number and percentage of identified group members recorded present and performing stone handling (SH) at least once in the four experimental areas

Area	Number (%) of identified group members recorded at least once	
	Present	SH
1	81 (55.9)	46 (31.7)
2	33 (22.8)	32 (22.1)
3	79 (54.5)	54 (37.2)
4	35 (24.1)	18 (12.4)

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$Z = -1.982$, $P = 0.048$; middle-aged adults: $Z = -2.760$, $P = 0.006$; old adults: $Z = -4.106$, $P < 0.001$).

Role of Kinship in the Use of SH Artefacts

Twelve group members aged 1 year and less entered the areas at least once during the experimental sessions (i.e. 85.7% of infants and yearlings), among which 11 were engaged in SH activity (i.e. 78.6% of infants and yearlings). We recorded a total of 29 entrances of infants and yearlings, among which 27 (93.1%) occurred in the presence of the mother. We recorded a total of 12 coactions of two individuals performing SH simultaneously on the same SH spot, all of which occurred on SH stations (not on SH zones), and all of which involved close kin (six involved three mother–infant dyads, three involved one mother–yearling dyad, one involved a mother and her 2-year-old daughter, one involved a mother and her 8-year-old daughter, and one involved an infant and her 2-year-old sister). In the 13 other cases when two close kin performed SH simultaneously in the same area, they did it on two adjacent SH stations in 10 cases (i.e. 76.9%).

Role of Dominance Relationships in the Use of SH Artefacts

Low- and middle-ranking stone handlers were significantly more frequently attracted to SH stations than to SH zones (Wilcoxon signed-ranks tests: low-ranking: $Z = -4.296$, $N = 25$, $P < 0.001$; middle-ranking: $Z = -3.054$, $N = 14$, $P = 0.002$), and spent significantly more time handling stones from SH stations than from SH zones (low-ranking: $Z = 4.211$, $P < 0.001$; middle-ranking: $Z = -3.233$, $P = 0.001$). We did not find such significant differences in high-ranking stone handlers ($N = 5$, frequency: $Z = -0.707$, $P = 0.480$; duration: $Z = -0.674$, $P = 0.500$). The latter result may be explained by the small sample size: only five high-ranking group members were engaged in SH activity during the experimental sessions. Supplanting interactions were significantly more frequent over SH stations than over SH zones (59 interactions (i.e. 96.7%) versus 2 (i.e. 3.3%), respectively; Wilcoxon signed-ranks test: $Z = 4.873$, $N = 33$ individuals, $P < 0.001$).

DISCUSSION

Through the semicontrolled conditions of field experiments, we aimed to simulate the context under which SH might be socially maintained in the wild, and infer which form(s) of social influence might support the persistence of the SH culture in Japanese macaques. Our results supported the 'stimulus/local enhancement hypothesis' that individuals preferentially direct their SH behaviour towards typical physical traces of SH activity (piles of stones) over randomly scattered stones. In other words, encountering SH artefacts enhanced the use of these particular stones to perform SH activity in that particular part of the environment. Therefore, we have provided the first experimental evidence for the role of indirect social influence in the daily performance of SH behaviour by most group members, and thus the maintenance of the SH tradition. By supporting the view that SH is a socially influenced behaviour, this study helps validate the concept of SH culture (see also Huffman 1984, 1996; Leca et al. 2007b, 2008c; Nahallage & Huffman 2007b).

Some authors have argued for a formal difference between stimulus enhancement (Spence 1937) and local enhancement (Thorpe 1963); the former would refer to an individual aiming its responses towards particular objects, whereas the latter would refer to an individual focusing its attention towards particular places in the environment. However, in practice, it is difficult to make an operational distinction between the two mechanisms. This may explain why they are often associated in the literature as a single stimulus/local enhancement process (Tomasello et al. 1993; Byrne & Russon 1998; Visalberghi & Adessi 2001; Visalberghi & Fragaszy 2002). Some of our results were more consistent with stimulus enhancement, such as (1) the preferential attraction to the new locations (where the piles of stones were) over the original locations (from when the piles of stones were removed), (2) the generalized attraction for SH artefacts, found in all experimental areas, and (3) the fact that most stone handlers mainly used one pile of stones during the same session. Other results rather supported local enhancement, such as (1) clear spatial preferences for SH at the group and individual levels, and (2) the use of adjacent piles of stones by the same stone handler. The relatively frequent transport of stones between SH spots could be interpreted as stimulus or local enhancement. The two processes are apparently not mutually exclusive, and they both influence the relative probability of encountering stones.

In our case, local and stimulus enhancement could even occur sequentially. We argue that prospective stone handlers first aim for a particular area where stones are usually available, and then they may preferentially direct their SH behaviour towards already gathered stones, if any, rather than randomly scattered stones. During our experiments, some individuals were first seen walking across the entire experimental area, visually scanning all the local piles of stones, occasionally touching some of them, and then coming back to one particular artefact to start performing SH (J.-B. Leca, personal observation).

From an evolutionary perspective, the niche construction process refers to the environmental alterations caused by organisms, and their consequences for their community members, including cultural changes (Odling-Smee 1996). As typical SH by-products, the occurrence of multiple piles of stones left in particular places by previous stone handlers are attention getting and could be considered conspicuous visual cues of SH activity even between SH events. As they become more deeply ingrained into the behavioural landscape of the monkeys, these 'play stations' (Quiatt & Huffman 1993) could ensure a baseline level of visual persistence of this form of material culture in Japanese macaques. This is particularly true for free-ranging provisioned troops, characterized by an increased sedentary lifestyle, with most group members staying around feeding grounds, that is, open areas with stones (Leca et al. 2008b). Smaller home ranges are likely to increase an individual's probability of encountering SH artefacts, which, in turn, may enhance SH activity. Moreover, we showed that piles of stones are frequently reused and constantly modified by the monkeys themselves through the transport of stones between and around SH artefacts. The frequent transport of randomly scattered stones to already gathered stones suggests cumulative environmental modifications. Therefore, through the ever-changing physical traces they leave in the environment, their subsequent stimulating effect on other group members and across generations, and their possible role in the maintenance of the SH tradition, we argue that stone handlers can be considered niche constructors.

Our study suggests that a niche construction process could underlie the cultural maintenance of SH behaviour in Japanese macaques. Niche construction, through the creation of enduring physical artefacts, occurs in other taxa as well. As extractive and destructive foragers, capuchin monkeys can be labelled as 'ecosystem engineers' (Fragaszy et al. 2004). When wild brown capuchins, *Cebus apella*, forage on invertebrates embedded in bamboo stalks, they leave in the environment specific physical traces, that is, numerous holes in bamboo segments previously ripped apart for larvae. These conspicuous foraging artefacts are attractive visual cues for young individuals (Gunst et al. 2007). Through drawing their attention to a particular foraging spot, even

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after the original forager had left the site, stimulus enhancement may contribute to naïve foragers becoming more familiar with the food items and substrates, learning the characteristics of appropriate substrates, acquiring specific detection techniques, and maintaining them at the group level (Gunst et al. 2008, in press). In capuchins, learning can also be delayed in time and separate in space from others, and in this sense, niche construction has an extended time frame and lesser dependence on copresence with others (Gunst et al. 2008).

Similar indirect social influences are likely to occur in the acquisition and maintenance of tool use behaviours in wild chimpanzees, *Pan troglodytes*, and brown capuchins, through the stimulating effect of nut-cracking by-products (nutshells, stones) left by skilled foragers around nut-cracking ateliers (Tomasello et al. 1993; Inoue-Nakamura & Matsuzawa 1997; Visalberghi et al. 2009). Situations in which artefacts of others' activity promote practice of relevant behaviours and may foster learning effectively can also be found in nonprimate taxa, as shown by experimental studies of birds learning to open the lids on milk bottles (Sherry & Galef 1984, 1990), a behaviour observed to occur spontaneously (Fisher & Hinde 1949), as well as bower birds' nests that can be considered artefactual niches (Odling-Smee et al. 2003). In general, conspecifics provide 'tools' (sensu sociocultural learning theory: Forman et al. 1993) for the individual acquisition, as well as the diffusion and maintenance, of behaviours at the group level.

From a developmental perspective, constant exposure to various artefacts could increase individual attention to some relevant environmental features, as suggested by Furlong et al. (2008) with respect to young chimpanzees reared in a human sociocultural environment. For young Japanese macaques growing up in a troop where the SH tradition is well established and has reached its transformation phase (defined as the late period of cultural transmission during which the behaviour is consolidated through integration with other daily activities: Huffman & Hirata 2003), resulting in a stimulating environment enriched in SH artefacts, a form of 'SH enculturation' process may facilitate their early acquisition of the behaviour. This argument is all the more relevant as we found a preferential use of piles of stones for SH across all age classes, including infants and yearlings.

The finding that the first individual to enter an experimental area preferred the piles of stones to scattered stones (prediction 1) provides evidence that a pile of stones per se is a sufficient stimulus to enhance the performance of SH activity in any individual, and without any direct social influence from other group members. It is beyond the scope of this study to evaluate the possible role of other social influences supporting the persistence of SH activity within Japanese macaque troops over decades. However, our results on the positive role of kinship in the use of SH artefacts, and particularly the common occurrence of mother–infant dyads around SH artefacts, sometimes coacting on the same pile of stones, are consistent with the view that the motivation for young individuals to engage in SH activity on a daily basis, and thus the maintenance of the SH tradition across generations, can also be explained by direct social influence such as social facilitation or social enhancement.

Through the controlled study conditions of a captive group of Japanese macaques, Nahallage & Huffman (2007b) showed that social facilitation, involving the observation by naïve infants of their mothers as SH demonstrators, may better explain the acquisition of SH during the first 6 months of life than merely the infant's early exposure to stones. Leca et al. (2008c) recently suggested that the early diffusion of stone-throwing behaviour, a particular SH pattern, may be socially mediated within strongly affiliated dyads. An intertroop comparative study suggested that sociodemographic constraints such as group size and composition in age classes, as well as group spatial cohesion, might impact the synchronized performance of SH at the group level, thereby confirming the contagious nature of play behaviours (Leca et al. 2007b, 2008b). Overall, the conformity-enforcing hypothesis, which proposes that culturally nonconforming individuals may be discriminated against (Lachlan et al. 2004), predicts that immature individuals should adopt the same type of stone-directed activities as most of the older group members. Our findings show that even traditional behaviours with no obvious function and no apparent adaptive value, such as SH, can be practised on a daily basis and maintained over several years within a large proportion of group members via indirect social influences. By contrast, when a behavioural practice is restricted to a particular class of group members, it is supposed to spread very slowly and its maintenance may be jeopardized (Huffman & Hirata 2003; Leca et al. 2007b, c, in press b).

Our result on supplanting interactions being more frequent over piles of stones than randomly scattered stones is consistent with previous observations showing that once particular stones, or sets of stones, are involved in an SH episode, they seem to become valuable objects for the handler who may pick them up and carry them to different places rather than leave them behind, and they appear to trigger great interest from others who try to snatch them away from the handler as if they were the only stones available (Huffman & Quiatt 1986; Leca et al. 2008b). These reports suggest the existence of a rudimentary form of 'possession' in monkeys, also reported in chimpanzees at Bossou, Guinea, where some individuals seem to have their favourite stone tool (Matsuzawa 1999). However, the present results cannot be exclusively interpreted from the viewpoint of competition for stones, social status and dominance relationships, since the attraction for SH artefacts was higher for low-ranking than high-ranking individuals.

We have provided evidence for the role of indirect social inputs on the maintenance of the SH tradition in Japanese macaques, through the stimulating effect of SH artefacts. To some extent, our findings allowed us to reconstruct some elements of the environmental and social contexts underlying the SH culture. We clearly found that where an individual was likely to handle stones was affected by the distribution of the stones manipulated by others. To claim unequivocally that piles of stones induce SH activity, further experiments should show that SH frequency is higher in areas with piles than in areas with no piles. Our study emphasizes the utility of field experiments as a way to explore further the determinants of the diffusion of novel behaviours and their long-term persistence in free-ranging animal populations (see also Heberlein & Turner 2009; Thornton & Malapert 2009a, b). Future experiments will investigate the stimulating effect of different sizes of SH artefacts, and will test auditory stimulus enhancement via the playback of sounds generated by percussive SH patterns.

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Principles and levels of laterality in unimanual and bimanual stone handling patterns by Japanese macaques

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The preferential use of one hand over the other is considered the primary behavioral expression of structural and functional asymmetry in cerebral structures, which is a decisive factor in human evolution. We present the first analysis of manual laterality in a form of object play—stone handling (SH) behavior—in a free-ranging group of Japanese macaques. Defined as a stone-directed manipulative activity, and comprised of multiple one-handed SH patterns (e.g., grabbing a stone in one hand and cradling it against its chest), as well as coordinated two-handed SH patterns with manual role differentiation (e.g., holding a stone with one hand and rubbing it with the other), SH behavior is a good candidate for the study of hand lateralization. We systematically followed the methodological framework developed by McGrew and Marchant (1997) to measure and analyze the presence, strength, and direction of manual preference in the performance of SH behavior and in various SH patterns, both at the individual and group level. Some individuals showed a significant manual lateral bias on a single SH pattern (*hand preference*), whereas others showed consistency in laterality across all or most of the SH patterns they performed (*hand specialization*). At the group level, we found that, although their collective distribution of left versus right remained random, most subjects were either significantly but incompletely lateralized, or completely lateralized within particular SH patterns (*pattern specialization*), but not across all SH patterns (no *handedness* for SH behavior as a whole). As predicted by the task-complexity model, *hand specialization* and *handedness* were stronger in the coordinated bimanual SH patterns than in the unimanual patterns. We discuss the implications of our findings for the evolution of manual preferences in noninstrumental object manipulation versus stone tool use in nonhuman primates and hominins.

Introduction

Two main reasons may account for the interest in the nature, form, distribution, and possible function of manual laterality in nonhuman primates (cf. MacNeilage et al., 1987; Ward and Hopkins, 1993; McGrew and Marchant, 1997; Papademetriou et al., 2005 for a review). First, the preferential use of one hand over the other is considered the primary behavioral expression of structural and functional asymmetry in cerebral structures, the latter being a decisive factor in human evolution (Corballis, 1983; Vallortigara and Rogers, 2005). Different hypotheses propose that the translation of complex manipulative skills into a right-hand preference, linked to a specialization of the left hemisphere of the brain to control it (cf. Corballis, 1983; Annett, 1985), are associated with the emergence of bipedalism, object-throwing behavior, and elaborate cognitive processes such as tool use and language in early hominins (Frost, 1980; Calvin, 1982; Bradshaw and Rogers, 1993; Sharer, 1993). Second, the search for a possible precursor of human manual laterality in animals has primarily focused on nonhuman primates because of their phylogenetic relatedness to humans (*Homo sapiens*).

However, the evolution of hand lateralization has been a topic of historical and contemporary debate (Warren, 1980; MacNeilage et al., 1987; Fagot and Vauclair, 1991; Marchant and McGrew, 1991; Hopkins, 1999; McGrew and Marchant, 1997; Palmer, 2002). Despite a plethora of published studies, there was never anything approaching a scientific consensus on that issue. The causes of such controversy are both theoretical and methodological.

The most comprehensive evolutionary model of manual laterality to date was proposed by MacNeilage et al. (1987) and referred to as "the postural origins theory" (MacNeilage, 1991). This model advocates a phylogenetic continuity of hand lateralization within the order Primates, originating from an adaptation to unimanual predation in our primate ancestors, and whose evolutionary history

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Table 1
Principles of laterality in the performance of SH behavior (after Marchant and McGrew, 1998)[a]

		Subject(s)	
		Within	Across
SH pattern(s)	Within	Hand preference *Yes*	Pattern specialization *Yes*
	Across	Hand specialization *Yes* *(Sim-Comp > Uni)*	Handedness *No* *(Sim-Comp > Uni)*

[a] The results of the present study are in italics. *Sim-Comp*: coordinated bimanual patterns where both hands operate simultaneously but complementarily; *Uni*: unimanual patterns.

could be traceable through the pattern of manual laterality in modern nonhuman primates. More than two decades later, and despite an extensive database on manual laterality in various primate taxa, there is scant support for the postural origins theory. Overall, measures of hand preferences in prosimians, monkeys, and apes have yielded negative, inconsistent, contradictory, or far from conclusive results (McGrew and Marchant, 1997). Many living primates showed individual-level bias toward the left or right hand in certain contexts and when performing particular behaviors. However, significance and directional consistency in manual lateralization in free-ranging or semi-free-ranging populations of nonhuman primates have not yet been found in any species and for any type of task (but see Hopkins [2006] in captive chimpanzees and for specific tasks). Since *Homo sapiens* appears to be the only species predominantly right-handed, the question arose as to whether the patterns of manual preferences in nonhuman primates are more analogous than homologous to those observed in humans (Warren, 1980; Bradshaw and Rogers, 1993; McGrew and Marchant, 1997).

Furthermore, the lack of methodological consensus among the studies of laterality undoubtedly precludes systematic comparisons and meaningful interpretations of the results obtained. Differences in the way to measure manual preferences, the terminology used, and the statistical procedures employed are also likely to explain the considerable disagreement about the evolution of hand lateralization (McGrew and Marchant, 1997; Palmer, 2002). Moreover, various environmental, experiential, social, and biological factors that seem to influence directly or indirectly the development, expression, and maintenance of manual laterality in individuals are simply ignored in many studies. Intrinsic variables include the morphological and behavioral characteristics of the species under study, life history traits such as age and sex, particular haplotypes, individual experience and practice, and situational variables such as emotional state, body posture, and positioning. Extrinsic variables include the complexity and novelty of the behavior measured, procedural conditions, and habitat (see McGrew and Marchant, 1997 for a review). Finally, most data on manual laterality come from studies of captive primates, which may be problematic since notable differences in hand use patterns were found between captive and free-ranging subjects (McGrew and Marchant, 1997).

The following example illustrates the need for both theoretical and methodological considerations when tackling the issue of manual laterality. In the context of extractive foraging, most studies showed that populations of wild chimpanzees were significantly lateralized for tool use (wadge-dipping: Boesch, 1991; nut-cracking: Boesch, 1991; Matsuzawa et al., 2001; termite-fishing: McGrew and Marchant, 1996; Lonsdorf and Hopkins, 2005; *Strychnos* fruit-pounding: McGrew et al., 1999; but see Marchant and McGrew, 2007 for ant-fishing). This contrasts markedly with other food processing activities involving object manipulation but not tool use, where no significant lateral bias was found at the group level (food-reaching/picking: Boesch, 1991; Sugiyama et al., 1993; food-plucking: Marchant and McGrew, 1996; McGrew and Marchant, 2001; eating: McGrew and Marchant, 2001; *Saba* fruit-peeling: Corp and Byrne, 2004).

The main reason that may account for this discrepancy is conceptual and is due to the fact that tool use behaviors are usually more complex than other object manipulation tasks (but see Byrne and Byrne [1991, 1993] for complex food processing by mountain gorillas). According to the "task-complexity" model, complex tasks, such as precise coordinated bimanual and sequential actions, should elicit a greater strength of manual laterality at the group level than simple tasks, such as unimanual object reaching (cf. Fagot and Vauclair, 1991 for a review). This model is supported by an extensive database from several primate taxa (*Cebus*: Westergaard and Suomi, 1993a; Anderson et al., 1996; *Cercopithecus*: Trouillard and Blois-Heulin, 2005; *Lophocebus*: Blois-Heulin et al., 2007; *Pan*: Hopkins and Rabinowitz, 1997; *Papio*: Vauclair et al., 2005). However, methodological flaws could also explain the lack of lateralization found for object manipulation. In numerous studies, two variables are often confounded: unimanual versus bimanual manipulation, and simple versus complex tasks (cf. Marchant and McGrew, 1991; McGrew and Marchant, 1997, for a review).

In the quest for uniformity in the empirical assessment of manual preference and for parsimony in the interpretations of the results, the most extensive review on manual laterality in nonhuman primates urged the systematic use of the "principles of laterality" (sic McGrew and Marchant, 1997:215) that can be summarized in a 2 × 2 matrix representing the degree of variation of hand-use within and across subject(s), and within and across task(s) (Marchant and McGrew, 1998:223). Unfortunately, the evaluation of the principles of laterality is difficult because few studies have systematically documented manual preference at the individual and group levels for one and multiple behavioral patterns (Fagot and Vauclair, 1991; Marchant and McGrew, 1991; Papademetriou et al., 2005). To provide a better overall picture of behavioral laterality of hand function in nonhuman primates, there is a need for more data obtained from various behaviors spontaneously performed by several free-ranging group members to fill all four cells of the 2 × 2 matrix generated from the principles of laterality (McGrew and Marchant, 1997; see also Table 1).

In particular, studies systematically testing the consistency of manual preference in unimanual and bimanual object manipulative patterns and across different levels of task complexity in free-ranging groups of primates are lacking. Previous research on hand use in Japanese macaques (*Macaca fuscata*) showed some cases of individual manual preferences but no significant group-level lateralization for simple food reaching, foraging, or grooming behaviors (Tokuda, 1969; Watanabe and Kawai, 1993; Takeda, 1994). However, some form of group-level lateralization appeared as the task increased in complexity, such as when carrying handfuls of wheat grains or when catching sweet potatoes in midair (Kawai, 1967; Watanabe and Kawai, 1993). Recently, Leca et al. (2008a) found marked individual hand preferences for spontaneous stone throwing in a group of captive Japanese macaques but no consistent lateral bias across all throwers.

In this study, we present the first analysis of manual laterality in a form of object play—stone handling (SH) behavior—in a free-ranging group of Japanese macaques. SH is the longest studied and best-documented cultural behavior in monkeys to date (Huffman, 1984, 1996; Huffman and Hirata, 2003; Leca et al., 2007a,b, 2008b,c; Nahallage and Huffman, 2007a,b). SH is a form of object play consisting of various non-instrumental stone-directed behavioral patterns (Huffman, 1984), as illustrated in the following examples. Some of the SH patterns are simple and unimanual, such as grabbing a stone in one hand and cradling it against the chest, or

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clutching with one hand a small pile of stones gathered and placing the pile in front of oneself. Others are more complex in terms of sequential-movement skills needed to finely control hand muscles and may require asymmetric but coordinated bimanual hand use with manual role differentiation, such as picking up a set of stones with one hand and placing it into the other hand, or holding a stone with one hand and rubbing it with the other (Leca et al., 2007a,b). Therefore, SH behavior, defined as an object manipulative behavior comprised of multiple behavioral variants also called SH patterns, is a good candidate for the study of manual laterality.

Our main objective was to evaluate the principles of laterality in the performance of SH behavior by documenting the presence, strength, and direction of manual preference in SH behavior and in various SH patterns, both at the individual level and group level. We adapted the terminology used by McGrew and Marchant (1997) to the particular case of SH. Thus, we defined: 1) *hand preference* as when an individual showed a significant lateral bias on a single SH pattern; 2) *hand specialization* as when an individual showed a significant lateral bias across all SH patterns performed (i.e., the SH behavior as whole) or at least a range of SH patterns; 3) *pattern specialization* as when all (or at least a majority of) group members showed a collective significant lateral bias on a single SH pattern; and 4) *handedness* as when all (or at least a majority of) group members showed a collective significant lateral bias across all SH patterns performed (i.e., the SH behavior as whole) or at least a range of SH patterns (see Table 1).

On the basis of the task-complexity model, and if we consider that coordinated bimanual SH patterns are more complex than one-handed patterns, then *hand specialization, pattern specialization,* and *handedness* should be stronger in the former than in the latter (*Prediction #1a, #1b*, and *#1c*, respectively). In other words, the strength of manual laterality, defined as the absolute value of an individual's deviation from a random 50% hand usage, should be significantly higher in all coordinated bimanual patterns than in all unimanual patterns (*Prediction #1a*). We also predict that the proportion of group members showing a significant lateral bias on any coordinated bimanual pattern should be higher than that on any unimanual pattern (*Prediction #1b*). Finally, if any *handedness* (i.e., a group-level significant lateral bias) should emerge across some ranges of SH patterns, it should be higher in coordinated bimanual patterns than in unimanual patterns (*Prediction #1c*). However, since SH is not stone tool use, no significant lateral bias should emerge at the group level and across all SH patterns (i.e., no *handedness* for the SH behavior as a whole is expected [*Prediction #2*]). If these predictions are confirmed, our study will provide further support for the "task-complexity" hypothesis and will add to the arguments about the discrepancy between noninstrumental object manipulation and tool use in the evolution of manual preference.

Besides behavioral complexity, we also aimed to examine the relationship of hand preference to other major and most relevant variables, such as the age, sex, and body posture of subjects, and to test the heritability of hand preference. We considered the remaining potentially influential variables either minor (e.g., emotional state, positioning) or irrelevant to SH (novelty of the behavior, procedural conditions, habitat; Leca et al., 2007b, 2008b).

Materials and methods

Study group and data collection

We studied a free-ranging provisioned troop of Japanese macaques (Arashiyama E troop) at the Iwatayama Monkey Park, Arashiyama, Kyoto Prefecture. The group comprised 141 members, among which 132 were sampled for SH behavior. Individual identities, exact age, and matrilineal membership were known for all subjects. The study subjects could be approached and observed within 3–5 m. None of the sampled individuals sustained obvious hand injuries. From April 30 to August 28, 2004, between 08:00 and 17:00, JBL collected a total of 160.6 hours of continuous video-recorded focal-animal samples (Altmann, 1974). We selected focal individuals by using a semi-random procedure: the focal target was chosen independently of its activity, and the subject with least cumulative data was given priority. Whenever possible, they were filmed from the front, within an area of 1 m^2 (for details, see Leca et al., 2007a).

Data analysis

We distinguished between two major categories of SH patterns, namely the patterns performed unimanually, with only one hand involved in a SH action while the other hand is either idle or involved in another activity (e.g., foraging, locomotion, or postural support), and the patterns performed bimanually, with both hands involved in SH activity (Table 2). Among the patterns performed bimanually, we considered four categories (after McGrew and Marchant, 1997): 1) *Sim-Id*: both hands operate simultaneously and identically on the same (set of) stone(s), e.g., rubbing the same stone on a surface with both hands or using both hands to gather a pile of stones in front of oneself; 2) *Alt-Id*: both hands operate alternately but identically on the same (set of) stone(s), e.g., rubbing two stones together with one stone in each hand; 3) *Sim-Comp*: both hands operate simultaneously but complementarily on the same (set of) stone(s) with one hand (termed dominant hand) performing the finer, more skilful component, often a precision grip and the most precise movements of the fingers, while the other hand (termed subordinate hand) has a supportive role and is doing the more gross, less skilled component that involves less differentiation and accuracy of the fingers, often with some form of power grip; there were three *Sim-Comp* patterns: *pick up* with the dominant hand that picks the stone from the ground and places it into the subordinate hand that receives it; *flint* with the dominant hand that strikes a stone against another held stationary in the subordinate hand; and *rub with hand* with the dominant hand that rubs a stone held in the subordinate hand; and 4) *Sim-Diff*: both hands operate simultaneously but perform different patterns on different (sets of) stones, e.g., one hand performing *grasp with hand* and the other *cuddle*.

For *Sim-Id* and *Alt-Id* patterns, no manual laterality is possible. The *Sim-Diff* patterns were discarded from the analyses. Only unimanual and *Sim-Comp* patterns were considered in the analysis of manual laterality. The unimanual patterns were coded according to the hand used—namely left or right—to handle the stone(s). The *Sim-Comp* patterns were coded according to the dominant hand. From all the video-recorded samples, NG scored a total of 13.7 hours of SH video-records onto an Excel spreadsheet, coding to the second: 1) the SH pattern performed by the focal individual, 2) the (predominant) hand used, and the posture adopted by the stone handler (sitting, quadrupedal, bipedal, or lying). We assessed intra-coder reliability for NG by measuring consistency in transcribing the same samples of SH video-records on two separate occasions and on a total of 146 data points ($k = 0.96$; Martin and Bateson, 1993).

For the analyses on the SH patterns performed unimanually, 83 individuals were taken into account. For the analyses on *Sim-Comp* patterns, 31 individuals were considered. We categorized individuals according to seven age classes: Yrg = yearling (1 yr), Juv = juvenile (2–3 yrs), SuAd = subadult (4–6 yrs), YgAd = young adult (7–10 yrs), MdAd = middle-aged adult (11–15 yrs), OlAd = old adult (16–20 yrs), Sen = senescent (21 yrs and more; cf. Leca et al., 2007b).

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Table 2
List and definition of the 28 SH patterns sampled in the study group, with their categories, depending on whether they were performed unimanually (Uni) or bimanually

Name (code)	Definition	Category[a]
Bite (B)	Bite a stone	Uni or *Sim-Diff*
Carry (CA)	Carry a stone cuddled in hand from one place to another	Uni or *Sim-Diff*
Combine with object (COO)	Combine (mainly grasp or gather) a stone with an object different from a stone (mainly food item)	Uni or *Sim-Diff*
Cuddle (CD)	Take hold of, grab or cradle a stone against the chest	Uni or *Sim-Diff*
Flint (FL)	Strike a stone against another held stationary	*Sim-Comp*
Flip (FP)	Turn a stone over with both hands	*Alt-Id*
Gather (GA)	Gather stones into a pile in front of oneself	Uni, *Sim-Id*, or *Sim-Diff*
Grasp walk (GW)	Walk with one or more stones in the palm of one or both hands	Uni, *Alt-Id*, or *Sim-Diff*
Grasp with hands (GH)	Clutch a stone or a pile of stones gathered and placed in front of oneself	Uni or *Sim-Diff*
Hold (H)	Pick up a stone in one's hand and hold on to it, away from the body	Uni or *Sim-Diff*
Lick (L)	Lick a stone held in one's hand	Uni or *Sim-Diff*
Move and push/pull (MP)	Push/pull a stone with one or both hands while walking forward/backward	Uni or *Sim-Id*
Move inside mouth (MIM)	Make a stone move inside one's mouth with hands	Uni, *Sim-Id*, or *Sim-Diff*
Pick (P)	Pick up a stone	Uni or *Sim-Diff*
Pick up (PU)	Pick up a stone and place it into one's hand	*Sim-Comp*
Pick up small stones (PUS)	Pick up small stones and hold them between fingertips (like the picking up of wheat grains)	Uni or *Sim-Diff*
Pound on surface (POS)	Pound a stone on a substrate	Uni or *Sim-Diff*
Put in mouth (PIM)	Put a stone in one's mouth and keep it some time	Uni or *Sim-Diff*
Roll in hands (RIH)	Roll a stone in one's hands	*Alt-Id*
Roll on surface (ROS)	Roll a stone on a substrate	Uni, *Sim-Id*, or *Sim-Diff*
Rub on surface (RUS)	Rub a stone on a substrate	Uni, *Sim-Id*, or *Sim-Diff*
Rub stones together (RT)	Rub stones together	*Alt-Id*
Rub with hands (RWH)	Hold a stone in one hand and rub it with the other (like potato-washing)	*Sim-Comp*
Scatter (SC)	Scatter stones about, on a substrate, in front of oneself	Uni or *Sim-Diff*
Sniff (SN)	Sniff a stone held in one's hand	Uni or *Sim-Diff*
Swipe (SW)	Swipe stones together (both hands moving in a sweeping gesture)	*Alt-Id*
Toss walk (TW)	Toss a stone ahead (repeatedly) and pick it up while walking	Uni or *Sim-Diff*
Wash (W)	Put a stone in water or pick up a stone from water and rub it with hands	*Sim-Id*

[a] *Sim-Id*: both hands operate simultaneously and identically on the same (set of) stone(s); *Alt-Id*: both hands operate alternately but identically on the same (set of) stone(s); *Sim-Comp*: both hands operate simultaneously but complementarily on the same (set of) stone(s) with manual role differentiation; *Sim-Diff*: both hands operate simultaneously but perform different patterns on different (sets of) stones.

We conformed to the methodological list of criteria by McGrew and Marchant (1997): 1) we specified the age and species of the subjects, 2) we sampled at least six subjects to allow binomial testing of distribution of individuals in the group, 3) we recorded at least six data points per subject to allow each subject to be categorized as *lateralized* by binomial test (two-tailed, $p < .05$), 4) we presented raw data on manual preference to allow each subject to be classified as AL (*Always Left*-preferent: uses left hand in 100% of cases), SL (*Significantly Left*-preferent: uses left hand significantly more often than right hand), A (*Ambi-preferent:* ratio of left to right hand usages does not differ from 50:50 or random), SR (*Significantly Right*-preferent: uses right hand significantly more than left hand), or AR (*Always Right*-preferent: uses right hand in 100% of cases), and 5) we provided specifically-defined behavioral categories (i.e., discrete SH patterns; cf. Table 2). Finally, we established the independence of behavioral data points (referred to as SH events, and defined as the occurrence of an individual hand use event must not bias the chances of the occurrence of another equivalent event, if each is to be counted as a separate data point) when a different SH pattern performed by the same hand intervened between two instances of the same pattern (cf. McGrew and Marchant, 1997).

To express an individual's direction of manual laterality, we used the percentage of right-hand use, defined as $(R \times 100)/(R + L)$ (e.g., Fagot and Vauclair, 1991). To calculate the strength of manual laterality, regardless of the direction, we took the absolute value of an individual's deviation from a random 50% hand usage, i.e., |direction-50| (e.g., Corp and Byrne, 2004).

To investigate hand preference at the group level, we used McGrew and Marchant's (1997:216) classification of "levels of laterality." According to this classification, a population of individuals can be categorized as one of five levels: Level 1 is defined as "when the majority of individuals are ambi-preferent and the minority of individuals are lateralized to either side to varying degrees"; Level 2 is defined as "when most of the subjects are significantly but incompletely (not 100%) lateralized, but their collective distribution to left versus right does not depart from randomness"; Level 3 is defined as "when most subjects use only one hand for a task, but their distribution to left vs. right remains random"; Level 4 is defined as "when the majority of individuals are significantly but incompletely lateralized, and when their distribution is significantly skewed to the left, or the right"; Level 5 is defined as "when the majority of individuals are completely lateralized, and when their distribution is significantly skewed to the left or the right."

In most analyses, we reported mean values ± the standard deviation (SD). To test the effect of posture on manual laterality, we used Wilcoxon tests to compare the direction and strength of hand preference when performing SH in a sitting versus a quadrupedal posture. For this analysis, we considered only the SH patterns performed unimanually and we discarded the individuals that did not provide the required minimum number of six data points in each posture. There were too few data to test a possible effect of the bipedal and lying postures on manual laterality. Regarding correlation tests, we used Spearman rank-order coefficients when $n < 30$ and Pearson product-moment coefficients when n was equal to or more than 30 (Siegel and Castellan, 1988). Statistical analyses were performed using the SPSS 12.0 analytical program. Significance levels were set at $\alpha = 0.05$.

Results

Lateral bias within subject and pattern: hand preference

Table 3 shows the hand preferences (labelled as AL, SL, A, SR, and AR) of 70 individuals and for the 15 most frequent SH patterns. To appear in the table, an individual should have a minimum of 6 data points for at least one SH pattern, and a SH pattern should have been performed at least 6 times by one individual or more. Of the 1050 generated cells, 873 had fewer

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Table 3
Hand preferences of 70 individuals (females and males ranked by descending age) for the 15 most frequent SH patterns[a]

Subject	Age class	Sex	SH pattern														
			CA	CD	COO	FL	GA	GH	GW	H	PU	PUS	ROS	RUS	RWH	SC	W
Bl1	Sen	F	–	–	–	–	–	SR	–	–	–	–	–	–	–	SR	–
Bl2	Sen	M	–	–	–	–	–	SL	–	–	–	–	–	–	–	–	–
Me1	Sen	F	–	–	–	–	SR	SR	–	–	–	–	–	–	–	–	–
Co2	Sen	F	–	–	–	–	–	A	–	–	–	–	–	–	SR	A	–
Gl1	Sen	M	–	–	–	–	–	AL	–	–	–	–	–	–	–	AL	–
Bl3	Sen	F	–	–	–	–	–	AL	–	–	–	AL	–	–	–	–	–
Ku1	Sen	F	–	A	–	–	–	A	–	A	A	–	–	–	AR	–	–
Mi1	Sen	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Ai1	Sen	F	–	–	–	–	A	SR	–	–	SR	A	–	–	–	–	–
Op1	Sen	M	–	–	–	–	A	A	–	–	–	–	–	–	–	AL	–
Bl4	OlAd	M	–	–	–	–	A	AL	–	–	–	–	–	–	–	A	AL
Cho1	OlAd	F	–	–	–	–	–	AL	–	–	–	–	–	–	–	–	–
Ko1	OlAd	F	–	–	–	–	A	SL	–	–	–	–	–	–	–	A	–
Cho2	OlAd	F	–	–	–	–	–	A	–	–	AR	–	–	–	–	–	–
Ko2	OlAd	F	–	–	–	–	–	A	–	–	A	–	–	–	–	–	–
Op2	OlAd	M	AR	–	–	–	–	A	–	AR	AL	–	–	–	A	AL	–
Co3	OlAd	F	–	–	–	–	–	A	A	–	–	–	–	–	–	–	–
Me2	OlAd	F	–	–	–	–	A	A	–	–	–	–	–	–	–	–	–
Gl2	OlAd	F	–	–	–	–	–	A	A	–	–	–	–	–	AR	AR	–
Mi2	OlAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Yun1	OlAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Bl5	OlAd	F	–	–	–	–	–	–	A	–	–	–	–	–	–	–	–
Cho3	OlAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Ku2	OlAd	F	–	–	–	–	–	A	–	–	SL	–	–	–	AL	–	–
Co4	MdAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Ku3	MdAd	F	–	–	–	–	A	A	–	–	–	–	–	–	–	–	–
Co5	MdAd	F	–	–	–	–	A	A	–	–	–	–	–	–	–	A	–
Gl3	MdAd	F	–	–	A	–	SR	SR	A	–	–	–	–	–	–	A	–
Ra1	MdAd	F	–	–	–	–	–	A	A	–	AL	–	–	–	–	–	–
Ai2	MdAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Ko4	MdAd	F	–	–	–	–	A	–	–	–	–	–	–	–	–	–	SR
Mi3	MdAd	F	–	–	–	–	–	A	–	–	A	–	–	–	–	–	–
Yun2	MdAd	F	–	–	–	–	–	A	–	–	SR	–	–	–	–	–	–
Cho4	MdAd	F	–	–	–	–	–	A	–	–	AR	–	–	–	–	–	–
Ra2	MdAd	F	–	–	–	–	–	A	–	–	A	–	–	–	–	–	–
Cho5	YgAd	F	–	–	–	–	A	A	–	–	–	–	–	–	–	A	SL
Cho6	YgAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Me3	YgAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Ai3	YgAd	F	–	–	–	–	SL	A	–	–	–	–	–	–	–	–	–
Bl7	YgAd	M	–	SR	–	–	–	–	–	–	–	–	–	–	–	–	–
Gl4	YgAd	M	–	–	–	–	–	A	–	–	AR	–	–	–	–	–	–
Ku4	YgAd	F	–	–	–	–	–	–	–	–	AR	–	–	–	–	–	–
Me4	YgAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Shi1	YgAd	F	–	–	–	–	SR	SR	–	–	–	–	–	–	–	AR	–
Yun3	YgAd	F	–	–	–	–	A	A	SR	–	–	–	–	–	–	A	–
Yun4	YgAd	F	AR	AR	–	–	–	A	–	–	AL	–	–	–	–	–	–
Op3	YgAd	M	–	–	–	–	–	–	–	–	–	–	–	–	–	AL	–
Yun5	YgAd	F	–	–	–	–	–	A	–	–	AR	–	–	–	–	–	–
Ku5	SuAd	F	–	–	–	–	–	SR	SR	A	–	–	AR	A	–	–	–
Mi6	SuAd	F	–	–	–	–	AR	AR	–	–	–	–	–	–	–	–	–
Mo1	SuAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Ai4	SuAd	M	–	–	–	–	A	SR	–	–	–	–	–	–	–	–	–
Gl5	SuAd	F	–	–	–	–	–	A	–	–	–	–	–	–	–	–	–
Cho8	Juv	F	–	–	–	–	–	–	–	–	AR	–	–	–	–	–	–
Ku6	Juv	F	–	–	–	–	–	–	A	–	–	–	–	–	–	–	–
Me5	Juv	M	–	–	–	–	A	A	A	–	SR	–	–	–	–	A	–
Ra3	Juv	M	AR	SR	–	–	–	A	SR	–	AL	–	–	–	–	–	–
Shy1	Juv	F	–	–	–	–	–	–	A	–	–	–	–	–	–	–	–
Ai5	Juv	F	–	–	–	–	–	A	A	–	A	–	–	–	–	–	–
Co7	Juv	F	–	–	–	–	–	A	A	–	–	–	–	A	–	–	A
Co8	Juv	F	A	–	–	–	–	–	A	–	–	–	–	–	–	–	–
Yun6	Juv	F	–	–	–	AR	–	A	–	–	A	–	–	–	–	–	–
Cho9	Yrg	F	A	A	–	–	–	–	A	–	–	–	–	–	–	–	–
Cho10	Yrg	M	–	–	–	–	–	–	A	–	–	–	–	–	–	–	–
Co9	Yrg	M	SL	A	–	–	–	A	–	–	–	–	–	–	A	–	–
Co10	Yrg	M	–	–	–	–	–	A	A	–	–	–	–	–	–	–	–
Co11	Yrg	M	–	A	–	–	–	A	A	A	–	–	–	–	–	–	–
Mi7	Yrg	F	A	–	–	–	–	A	A	–	–	–	–	–	–	–	–
Shi2	Yrg	F	A	A	–	–	–	A	A	–	A	–	–	–	–	–	–
Yun7	Yrg	M	SL	SL	–	–	A	A	A	–	SR	–	–	A	SR	A	–

[a] Each cell was assigned one of six outcomes: –, fewer than six data points (ignored since no valid statistical testing can be done); A, ambi-preference; SL, significant left preference; SR, significant right preference; AL, systematic left preference; and AR, systematic right preference.

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Table 4
Distribution of statistically significantly ($p < 0.05$, two-tailed) lateralized individuals for the 15 most frequent SH patterns ($n = 70$ subjects)[a]

SH pattern	Manual laterality					Total	No. lat	% lat
	AL	SL	A	SR	AR			
CA	0	2	4	0	3	9	5	55.6
CD	0	1	5	2	1	9	4	44.4
COO	0	0	1	0	0	1	0	0.0
FL	0	0	0	0	1	1	1	100.0
GA	0	1	13	3	1	18	5	27.8
GH	4	2	45	7	1	59	14	23.7
GW	0	0	18	3	0	21	3	14.3
H	0	0	3	0	1	4	1	25.0
PU	4	1	7	4	6	22	15	68.2
PUS	1	0	1	0	0	2	1	50.0
ROS	0	0	0	0	1	1	1	100.0
RUS	0	0	3	0	0	3	0	0.0
RWH	1	0	2	2	2	7	5	71.4
SC	4	0	9	1	2	16	7	43.8
W	1	1	1	1	0	4	3	75.0
Total	15	8	112	23	19	177	65	36.7

[a] No. lat = number of significantly lateralized individuals (AL + SL + SR + AR); % lat = percentage of significantly lateralized individuals.

than 6 data points and so were ignored, since no valid statistical testing could be done, and 177 cells could be statistically tested for hand preference. Among them, 112 cells indicated ambi-preference, 8 cells showed significant left preference, 23 cells showed significant right preference, 15 cells showed systematic left preference, and 19 cells showed systematic right preference (Table 4). Therefore, we found a total of 65 cases (36.7%) of *hand preference* for particular SH patterns.

Lateral bias within subject and across patterns: hand specialization

SH behavior as a whole We analyzed the manual laterality of 84 individuals for all SH patterns (unimanual and *Sim-Comp* patterns pooled together: $n = 3{,}740$ SH events, mean $= 44.5 \pm 50.2$ SH events per individual, ranging from 6 to 312). We found that 18 individuals (45.0%) were significantly biased toward the left hand (including 4 systematic left-preferent individuals), and 22 (55.0%) toward the right hand (including 4 systematic right-preferent individuals). Therefore, we recorded a total of 40 cases (47.6%) of *hand specialization* for the SH behavior as a whole.

However, Table 3 shows that among the 14 individuals for which statistical testing could be done in at least 4 patterns and with at least one significantly lateralized pattern (Ku1, Ai1, Bl4, Op2, Gl2, Gl3, Cho5, Yun3, Yun4, Ku5, Me5, Ra3, Co9, and Yun7), none exhibited a lateral bias in all these patterns. The 3 individuals showing the highest number of lateralized outcomes (4 statistical departures from 50 L:50 R) had mixed results, that is for none of them the lateral bias was toward the same side (Op2 was AL for 2 patterns and AR for 2 patterns, Yun7 was SL for 2 patterns and SR for 2 patterns, and Ra3 was AL for one pattern, SR for 2 patterns, and AR for one pattern). Therefore, the type of SH pattern appeared to affect the strength and direction of manual laterality in individuals.

Unimanual versus bimanual complementary SH patterns In the 30 testable individuals (subject Bl4 had too few data points for any single *Sim-Comp* pattern), we compared the strength of manual laterality in all unimanual patterns and in all *Sim-Comp* patterns. We found that the latter was significantly higher than the former (Wilcoxon signed rank test, $n = 30$, $z = -3.363$, $p = 0.001$). This result showed that *hand specialization* was stronger in coordinated bimanual SH patterns than in unimanual patterns, thus verifying Prediction #1a.

To determine whether each subject was consistent in its lateral bias across unimanual SH patterns, we used Spearman rank-order correlation tests between two SH patterns, using the indexes of direction and strength of manual laterality. We restricted the analyses to the individuals with statistically significant lateral bias for at least one pattern and to pairs of unimanual SH patterns showing structural similarities in their sequences of actions.

We found no consistency in manual laterality, neither in direction nor in strength 1) between two SH patterns involved in locomotion activities (*carry* and *grasp walk*, $n = 6$; for direction, $r_s = .794$, $p = 0.059$, two-tailed; for strength, $r_s = 0.000$, $p = 1.000$, two-tailed), 2) between two SH patterns involved in collection activities (*cuddle* and *grasp with hand*, $n = 7$; for direction, $r_s = 0.649$, $p = 0.115$, two-tailed; for strength, $r_s = -0.216$, $p = 0.641$, two-tailed), and 3) between two SH patterns consisting of moving several stones on the ground simultaneously (*gather* and *scatter*, $n = 10$; for direction, $r_s = 0.579$, $p = 0.091$, two-tailed; for strength, $r_s = -0.531$, $p = 0.114$, two-tailed). For example, Ra3 switched from always right-hand preferent for *carry* to significant left-hand preferent for *grasp walk*; Yun4 switched from always right-hand preferent for *cuddle* to ambi-preferent for *grasp with hand*; Op1 switched from always left-hand preferent for *scatter* to ambi-preferent for *gather*.

Lateral bias across subjects and within pattern: pattern specialization

With the exception of *combine with object* (only one individual with sufficient data points), each of the 15 most frequent SH patterns showed at least one significantly lateralized subject (Table 4). When the sample size was more than two individuals classified as AL, SL, A, SR, or AR, the group could be categorized as Level 1 for seven SH patterns (namely CD-*cuddle*, GA-*gather*, GH-*grasp with hand*, GW-*grasp walk*, H-*hold*, RUS-*rub on surface*, and SC-*scatter*, all performed unimanually), Level 2 for two SH patterns (CA-*carry* and W-*wash*, both performed unimanually), and Level 3 for two patterns (PU-*pick up* and RWH-*rub with hand*, both bimanual complementary patterns). We found no evidence for a majority of individuals being significantly lateralized with their distribution significantly skewed to one side (Level 4), nor being completely lateralized with their distribution significantly skewed to one side (Level 5).

When considering the nine unimanual patterns, we found that only seven out of the 49 individuals with at least 10 data points (i.e., 12.2%) were systematically lateralized. For *grasp with hand*, three individuals were always left-preferent (Bl3 with 14L:0R, Gl1 with 11L:0R, and Cho1 with 10L:0R) and one individual was always right-preferent (with Mi6 0L:13R). For *gather*, one individual was always right-preferent (Mi6 with 0L: 13R). For *scatter*, one individual was always left-preferent (Op3 with 11L:0R). For *carry*, one individual was always right-preferent (Ra3 with 0L:14R).

By contrast, when considering the three *Sim-Comp* patterns, we found that 11 out of the 23 individuals with at least 10 data points (i.e., 47.8%) were systematically lateralized. For *pick-up*, four individuals were always left-preferent (Op2 with 70L:0R, Ra3 with 23L:0R, Yun4 with 16L:0R, and Ra1 with 10L:0R) and four individuals were always right-preferent (Cho4 with 0L:38R, Cho8 with 0L:17R, Cho2 with 0L:14R, and Yun5 with 0L:10R). For *rub with hand*, one individual was AL (Ku2 with 30L:0R) and one individual was AR (Ku1 with 0L:95R). For *flint*, one individual was AR (Yun6 with 0L:22R).

In sum, most group members showed a collective significant lateral bias on a single SH pattern and especially for *Sim-Comp* patterns. We found evidence for *pattern specialization*, and this

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Table 5
Manual lateralization of 83 individuals (females and males ranked by descending age) for SH patterns performed unimanually.[a]

Subject	Age class	Sex	L	R	Direction	Strength	p	Lat.
Bl1	Sen	F	20	77	79.4	29.4	<0.001	SR
Bl2	Sen	M	13	1	7.1	42.9	0.002	SL
Co1	Sen	F	0	6	100.0	50.0	0.031	AR
Me1	Sen	F	6	33	84.6	34.6	<0.001	SR
Co2	Sen	F	18	5	21.7	28.3	0.011	SL
Gl1	Sen	M	23	0	0.0	50.0	<0.001	AL
Bl3	Sen	F	28	2	6.7	43.3	<0.001	SL
Ku1	Sen	F	26	30	53.6	3.6	0.689	A
Mi1	Sen	F	9	0	0.0	50.0	0.004	AL
Ai1	Sen	F	20	49	71.0	21.0	0.001	SR
Op1	Sen	M	21	8	27.6	22.4	0.024	SL
Bl4	OlAd	M	46	23	33.3	16.7	0.008	SL
Cho1	OlAd	F	14	0	0.0	50.0	<0.001	AL
Ko1	OlAd	F	4	3	42.9	7.1	1.000	A
Cho2	OlAd	F	13	7	35.0	15.0	0.263	A
Ko2	OlAd	F	7	0	0.0	50.0	0.016	AL
Op2	OlAd	M	39	82	67.8	17.8	<0.001	SR
Co3	OlAd	F	11	5	31.3	18.8	0.210	A
Me2	OlAd	F	43	23	34.8	15.2	0.019	SL
Gl2	OlAd	F	15	32	68.1	18.1	0.019	SR
Mi2	OlAd	F	6	12	66.7	16.7	0.238	A
Yun1	OlAd	F	9	6	40.0	10.0	0.607	A
Bl5	OlAd	F	12	5	29.4	20.6	0.143	A
Cho3	OlAd	F	5	2	28.6	21.4	0.453	A
Ku2	OlAd	F	8	10	55.6	5.6	0.815	A
Co4	MdAd	F	3	12	80.0	30.0	0.035	SR
Ku3*	MdAd	F	13	13	50.0	0.0	1.000	A
Co5	MdAd	F	23	6	20.7	29.3	0.002	SL
Gl3	MdAd	F	19	59	75.6	25.6	<0.001	SR
Ra1	MdAd	F	17	31	64.6	14.6	0.059	A
Ai2	MdAd	F	5	17	77.3	27.3	0.017	SR
Bl6	MdAd	F	4	2	33.3	16.7	0.688	A
Ko3	MdAd	F	3	6	66.7	16.7	0.508	A
Ko4	MdAd	F	26	8	23.5	26.5	0.003	SL
Ko5	MdAd	F	6	2	25.0	25.0	0.289	A
Mi3	MdAd	F	8	12	60.0	10.0	0.503	A
Yun2	MdAd	F	13	7	35.0	15.0	0.263	A
Cho4	MdAd	F	11	15	57.7	7.7	0.557	A
Ra2	MdAd	F	4	13	76.5	26.5	0.049	SR
Cho5	YgAd	F	60	43	41.7	8.3	0.114	A
Cho6	YgAd	F	28	7	20.0	30.0	0.001	SL
Me3	YgAd	F	4	7	63.6	13.6	0.549	A
Mi4	YgAd	F	2	8	80.0	30.0	0.109	A
Mi5	YgAd	F	8	2	20.0	30.0	0.109	A
Ai3	YgAd	F	39	9	18.8	31.3	<0.001	SL
Bl7	YgAd	M	3	14	82.4	32.4	0,013	SR
Gl4	YgAd	M	3	8	72.7	22.7	0,227	A
Me4	YgAd	F	11	4	26.7	23.3	0.118	A
Shi1	YgAd	F	9	43	82.7	32.7	<0.001	SR
Yun3	YgAd	F	146	166	53.2	3.2	0.282	A
Yun4	YgAd	F	11	30	73.2	23.2	0.004	SR
Op3	YgAd	M	16	7	30.4	19.6	0.093	A
Yun5	YgAd	F	14	3	17.6	32.4	0.013	SL
Co6	SuAd	M	7	1	12.5	37.5	0.070	A
Ko6	SuAd	M	4	20	83.3	33.3	0,002	SR
Ku5	SuAd	F	27	73	73.0	23.0	<0,001	SR
Mi6	SuAd	F	0	41	100.0	50.0	<0,001	AR
Cho7	SuAd	F	3	3	50,0	0,0	1,000	A
Mo1	SuAd	F	12	13	52,0	2,0	1,000	A
Ai4	SuAd	M	6	15	71,4	21,4	0,078	A
Gl5	SuAd	F	6	12	66,7	16,7	0,238	A
Ko7	SuAd	F	20	23	53,5	3,5	0,761	A
Cho8	Juv	F	7	1	12,5	37,5	0,070	A
Ku6	Juv	F	6	16	72,7	22,7	0,052	A
Me5	Juv	M	51	47	48,0	2,0	0,762	A
Ra3	Juv	M	18	84	82,4	32,4	<0,001	SR
Shy1	Juv	F	8	7	46,7	3,3	1,000	A
Ai5	Juv	F	24	26	52,0	2,0	0,888	A
Co7	Juv	F	22	27	55,1	5,1	0,568	A
Co8	Juv	F	9	15	62,5	12,5	0,307	A
Ku7	Juv	F	2	4	66,7	16,7	0,688	A
Yun6	Juv	F	10	6	37,5	12,5	0,454	A
Cho9	Yrg	F	23	12	34.3	15.7	0.090	A
Cho10	Yrg	M	8	12	60.0	10.0	0.503	A
Cho11	Yrg	F	1	5	83.3	33.3	0.219	A
Co9	Yrg	M	28	11	28.2	21.8	0.009	SL
Co10	Yrg	M	16	9	36.0	14.0	0.230	A
Co11	Yrg	M	23	42	64.6	14.6	0.025	SR
Mi7	Yrg	F	23	10	30.3	19.7	0.035	SL
Shi2	Yrg	F	26	35	57.4	7.4	0.306	A
Yun7	Yrg	M	86	46	34.8	15.2	0.001	SL
Yun8	Yrg	F	6	4	40.0	10.0	0.754	A
Yun9	Yrg	F	0	7	100.0	50.0	0.016	AR

[a] L = number of SH events performed with the left hand, R = number of SH events performed with the right hand, Direction = direction of hand preference, Strength = strength of hand preference, p = probability obtained from binomial test (two-tailed), Lat. = manual laterality (A: ambi-preferent, SL: significant left-preferent, SR: significant right-preferent, AL: systematic left-preferent, and AR: systematic right-preferent). * denotes subject with cleft hands (cf. text for detail).

principle of laterality was stronger in coordinated bimanual SH patterns than in unimanual patterns, thereby confirming Prediction #1b.

Lateral bias across subjects and patterns: handedness

First, we considered unimanual and *Sim-Comp* patterns separately. Table 5 shows the manual lateralization of 83 individuals for the SH patterns performed unimanually. Since there were still more ambi-preferent individuals ($n = 46$, i.e., 56.4%) than significantly lateralized individuals ($n = 37$, i.e., 44.6%), the study group was also categorized as Level 1 for unimanual SH patterns. The average direction of manual laterality was 49.2 ± 25.7 (ranging from 0.0 to 100.0) and the average strength of manual laterality was 21.8 ± 13.4 (ranging from 0.0 to 50.0). Among individuals showing a statistically significant preference for one hand, 18 (48.6%) were biased toward the left hand and 19 (51.4%) toward the right hand. Manual laterality was normally distributed, with a maximum number of ambi-preferent individuals and a minimum number of systematically biased individuals: 4.8% of individuals were AL, 16.9% were SL, 55.4% were A, 19.3% were SR, and 3.6% were AR (Fig. 1). It should be noted that three out of the 69 individuals with at least 10 data points (i.e., 4.3%) were systematically lateralized: Mi6 with 0L:41R, Gl1 with 23L:0R, and Cho1 with 14L:0R.

However, a subanalysis on bimanual complementary SH patterns revealed a slightly different picture of the manual laterality at the group level. Table 6 shows the manual lateralization of 31 individuals for *Sim-Comp* patterns. Contrary to the results on all SH patterns and unimanual SH patterns, there were more

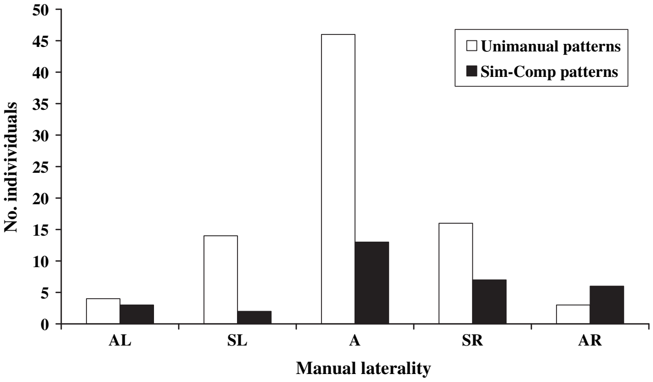

Fig. 1. Distribution of manual laterality across individuals and in two types of SH patterns: unimanual patterns and coordinated bimanual patterns (Sim-Comp).

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Table 6
Manual lateralization of 31 individuals (females and males ranked by descending age) for *Sim-Comp* SH patterns.[a]

Subject	Age class	Sex	L	R	Direction	Strength	p	Lat.
Co2	Sen	F	1	27	96.4	46.4	<0.001	SR
Ku1	Sen	F	5	102	95.3	45.3	<0.001	SR
Ai1	Sen	F	2	36	94.7	44.7	<0.001	SR
Bl4	OlAd	M	4	3	42.9	7.1	1.000	A
Cho2	OlAd	F	0	14	100.0	50.0	<0.001	AR
Ko2	OlAd	F	7	1	12.5	37.5	0.070	A
Op2	OlAd	M	77	2	2.5	47.5	<0.001	SL
Gl2	OlAd	F	0	8	100.0	50.0	0.008	AR
Ku2	OlAd	F	49	4	7.5	42.5	<0.001	SL
Co4	MdAd	F	5	1	16.7	33.3	0.219	A
Ra1	MdAd	F	10	0	0.0	50.0	0.002	AL
Mi3	MdAd	F	6	1	14.3	35.7	0.125	A
Yun2	MdAd	F	2	26	92.9	42.9	<0.001	SR
Cho4	MdAd	F	1	42	97.7	47.7	<0.001	SR
Ra2	MdAd	F	9	12	57.1	7.1	0.664	A
Cho6	YgAd	F	3	3	50.0	0.0	1.000	A
Gl4	YgAd	M	0	6	100.0	50.0	0.031	AR
Ku4	YgAd	F	0	6	100.0	50.0	0.031	AR
Yun4	YgAd	F	16	0	0.0	50.0	<0.001	AL
Yun5	YgAd	F	0	10	100.0	50.0	0.002	AR
Ku5	SuAd	F	4	2	33.3	16.7	0.688	A
Cho8	Juv	F	0	18	100.0	50.0	<0.001	AR
Me5	Juv	M	4	16	80.0	30.0	0.012	SR
Ra3	Juv	M	24	0	0.0	50.0	<0.001	AL
Ai5	Juv	F	5	2	28.6	21.4	0.453	A
Yun6	Juv	F	3	31	91.2	41.2	<0.001	SR
Cho9	Yrg	F	2	5	71.4	21.4	0.453	A
Co9	Yrg	M	7	5	41.7	8.3	0.774	A
Co10	Yrg	M	3	6	66.7	16.7	0.508	A
Shi2	Yrg	F	12	6	33.3	16.7	0.238	A
Yun7	Yrg	M	23	52	69.3	19.3	0.001	A

[a] See Table 5 for legends.

significantly lateralized individuals ($n = 18$, i.e., 58.1%) than ambi-preferent individuals ($n = 13$, i.e., 41.9%). The average direction and strength of manual laterality were stronger than for the SH patterns performed unimanually: 57.9 ± 38.1 (ranging from 0.0 to 100.0) and 34.8 ± 16.3 (ranging from 0.0 to 50.0), respectively. Among individuals showing a statistically significant preference for one hand, five (27.8%) were biased toward the left hand and 13 (72.2%) toward the right hand. Manual lateralization was still normally distributed, but with a higher proportion of lateralized individuals than for the SH patterns performed unimanually, and slightly skewed to the right: 9.7% of individuals were AL, 6.4% were SL, 41.9% were A, 22.6% were SR, and 19.4% were AR (Fig. 1). In sum, we found that *handedness* was stronger in coordinated bimanual SH patterns than in unimanual patterns, thus verifying Prediction #1c.

When considering all SH patterns (unimanual and *Sim-Comp* patterns pooled together), the study group showed a majority of ambi-preferent individuals (44 out of 84, i.e., 52.4%). It was categorized as Level 1 (i.e., unlateralized) for the SH behavior, according to McGrew and Marchant's (1997) classification of "levels of laterality." The average direction of manual laterality was 51.9 ± 25.5 (ranging from 0.0 to 100.0), and the average strength of manual laterality was 21.1 ± 14.3 (ranging from 0.0 to 50.0). We found no *handedness* for SH behavior as a whole, thus verifying Prediction #2.

Finally, when pooling only the significantly lateralized individuals across the 15 SH patterns, we found a significant bias toward the right hand (Binomial test, $n = 62$, 20 L:42 R, $p = 0.007$, two-tailed). However, this overall effect could not be found on a SH pattern basis.

Age, sex, and diversity in SH patterns

When pooling unimanual and *Sim-Comp* patterns, we found a significant positive correlation between age and the strength of manual laterality (Pearson correlation test, $n = 84$, $r = 0.316$, $p = 0.003$). The analysis based on age classes confirmed the overall effect of age on the strength of lateralization (Kruskal-Wallis test, $df = 6$, $\chi^2 = 16.1$, $p = 0.013$), and post-hoc paired comparisons between age classes showed that senescent individuals were significantly more lateralized than yearlings and juveniles ($p < 0.05$; Fig. 2). Other paired comparisons between age classes were not significant ($p > 0.05$).

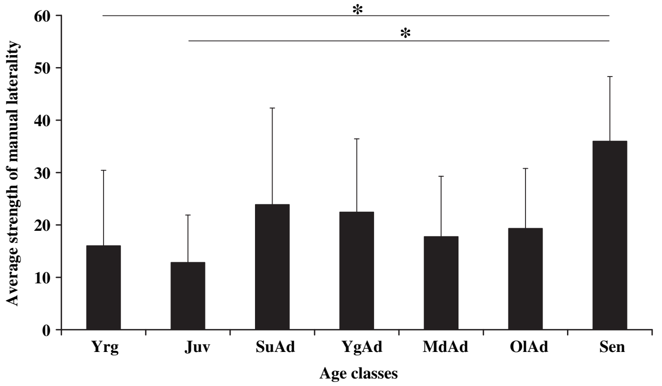

Fig. 2. Effect of age on the strength of manual laterality. Yrg = yearling (1 yr, $n = 11$), Juv = juvenile (2–3 yrs, $n = 10$), SuAd = subadult (4–6 yrs, $n = 9$), YgAd = young adult (7–10 yrs, $n = 15$), MdAd = middle-aged adult (11–15 yrs, $n = 14$), OlAd = old adult (16–20 yrs, $n = 14$), Sen = senescent (21 yrs and more, $n = 11$). The lines at the top indicate the two sets of paired comparisons (between age classes) that were significant * $p < 0.05$; see text.

Interestingly, we found: 1) a significant negative correlation between age and SH pattern diversity, defined as the total number of SH patterns observed in each individual (Pearson correlation test, $n = 84$, $r = -0.229$, $p = 0.036$) and a significant negative correlation between SH pattern diversity and the strength of manual laterality (Pearson correlation test, $n = 84$, $r = -0.304$, $p = 0.004$). Therefore, extrapolating from the cross-sectional data, it appeared that as individuals became older, they tended to perform a smaller range of SH patterns and to become more lateralized for object manipulation.

We found no significant effect of age on the direction of manual laterality (Pearson correlation test, $n = 84$, $r = -0.188$, $p = 0.087$; Kruskal-Wallis test, $df = 6$, $\chi^2 = 7.5$, $p = 0.277$) and no significant sex differences in the direction and strength of manual laterality (Mann-Whitney U tests, $n_{\text{female}} = 66$, $n_{\text{male}} = 18$, direction: $U = 443.5$, $p = 0.101$, strength: $U = 564.0$, $p = 0.743$).

Heritability of manual preference

To test the heritability of manual preference, we compared the 12 mother/offspring pairs that showed a statistically significant preference for one hand in all unimanual and *Sim-Comp* patterns. In four pairs the manual preference was the same, and in eight pairs it was opposite. Thus, there was no significant concordance in laterality between mother and offspring (Binomial test, $n = 12$, $p = 0.388$, two-tailed). We found the same negative result when comparing the 6 mother/offspring pairs that showed a statistically significant preference for one hand in at least one SH pattern. In two pairs the manual preference was the same (Cho4/Cho8 with 0L:38R/0L:17R for *pick up*, and Yun2/Yun5 with 2L:22R/0L:10R for *pick up*), and in four pairs it was opposite (Binomial test, $n = 6$, $p = 0.688$, two-tailed). In the Ku1/Ku2 pair, the mother was always right-preferent for *rub with hand* (0L:95R) where her daughter was always left-preferent for the same pattern (30L:0R).

Body posture and a case of manual disability

We found no significant effect of the posture of the stone handler (sitting versus quadrupedal) neither in the direction nor in

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the strength of manual laterality (Wilcoxon test, $n = 32$, direction: $z = -1.481$, $p = 0.139$; strength: $z = -0.584$, $p = 0.559$). Table 5 shows that among the 69 individuals with at least 10 data points in the SH patterns performed unimanually, Ku3 was the only one exhibiting exactly the same number of left-hand and right-hand usages (13L:13R). It should be noted that Ku3 was the only group member with a congenital hand malformation characterized by an anomaly in the digit morphology: she had cleft hands with only two fingers on each hand (cf. Homma, 1980 for further description).

Discussion

We evaluated the principles of laterality in the performance of SH behavior in a troop of free-ranging Japanese macaques. For individual subjects, we found evidence for manual lateral bias within particular SH patterns (*hand preference*) and consistency in laterality across SH patterns (*hand specialization*). At the group level, we found evidence for manual lateral bias at Level 2 and Level 3 within particular SH patterns (*pattern specialization*) but not across all SH patterns (no *handedness* for the SH behavior as a whole). As predicted by the task-complexity model, the type of SH pattern significantly affected the strength and direction of manual laterality in individuals, since *hand specialization* and *handedness* were stronger in the coordinated bimanual SH patterns than in the unimanual patterns. Our data allowed us to fill the four cells of the 2 × 2 matrix generated from the principles of laterality within and across free-ranging Japanese macaque subjects, and within and across various SH patterns (Table 1).

Complementary analyses on the factors that may influence hand lateralization in the performance of SH showed that as individuals became older, they tended to perform a smaller range of SH patterns and to become more lateralized in their stone-directed manipulative actions. We found no effect of age on the direction of manual laterality. Manual laterality was not significantly affected by sex and body posture (sitting versus standing quadrupedally). Finally, we found no evidence for heritability of hand preference in the performance of SH.

Our results on the principles of laterality are consistent with most studies in nonhuman primates that often showed hand preference and task specialization (referred to as "pattern specialization" in the case of SH), sometimes hand specialization, and only very occasionally handedness (cf. McGrew and Marchant, 1997 for a review). Within-individual consistency in laterality across several behavioral measures, including simple and complex tasks, has been found in chimpanzees (Sugiyama et al., 1993; Colell et al., 1995). However, individuals do not always show consistent lateral biases across multiple complex tasks (Anderson et al., 1996; Spinozzi and Truppa, 1999; Lilak and Phillips, 2008).

Likewise, our results on the levels of laterality are consistent with the general pattern found in prosimians, monkeys, and apes. At the group level, most nonhuman primate species were either unlateralized (Level 1) or showed Level 2 laterality. The results showing Level 3 and Level 4 laterality were often associated with postural readjustments or complex motor tasks, whereas no clear cases of true handedness (Level 5) were reported (McGrew and Marchant, 1997; but see Byrne and Byrne, 1991).

We found that some SH patterns elicited more lateralization than others. More particularly, coordinated bimanual SH patterns performed by the Arashiyama E troop members gave rise to significant manual preferences at the group level. This result further supports the "task-complexity" hypothesis proposing that lateralization increases with the complexity of the task (Fagot and Vauclair, 1991). When considering coordinated bimanual SH patterns, we found that the distribution of manual lateralization across all group members was slightly skewed to the right hand. This finding is in agreement with the postural origins theory that postulates, for nonhuman primates, a group-level right-hand preference for more complex tasks that require bimanual actions (MacNeilage et al., 1987). In the genus *Macaca*, strong evidence for a right-hand bias for complex tasks at the group level was found in stump-tailed macaques, *M. arctoides* (Beck and Barton, 1972) and in pig-tailed macaques, *M. nemestrina* (Rigamonti et al., 1998). Such findings suggest that manual laterality is labile and may emerge only when the task demand is sufficiently high to involve motor and cognitive abilities that are specific to one hemisphere (Anderson et al., 1996).

The lack of significant lateral bias at the group level and for SH behavior as a whole is consistent with the view that population-level manual preference is less likely to emerge for non-instrumental object manipulation than for tool use (cf. Marchant and McGrew, 2007; see also Westergaard and Suomi, 1996; Westergaard et al., 1998a). SH is typically defined as a form of object play and, with the notable exception of stone-throwing, the 45 SH patterns listed in the repertoire of Japanese macaques do not seem to serve any immediate function (Huffman, 1984; Leca et al., 2007a, 2008a; but see Nahallage and Huffman [2007a] for a possible ultimate function of SH). Even the stone-throwing pattern, that may serve to augment the effect of agonistic displays and can be regarded as spontaneous tool use, did not show a group-level lateral bias (Leca et al., 2008a).

Instead of cognitive and functional reasons, Corp and Byrne (2004) proposed that the temporal and spatial coordination of both hands, with role-differentiated actions, may account for the strong manual preference reported in tool use. If so, this argument would also explain the increased lateralization observed in coordinated bimanual SH patterns. Ethological analyses in humans also showed that lateralization increases with the level of skill required for manipulating objects, suggesting a marked distinction between non-instrumental object manipulation and tool use in the evolution of manual preference. Marchant et al. (1995) found that in three traditional societies, the most common non-tool use activities, including non-instrumental object manipulation, were unlateralized (Level 1 laterality), whereas gross tool use with power grip and skilled tool use with precision grip were at Level 4 and 5, respectively.

Given the gradual maturation of motor control during ontogeny, age is one of the most significant factors to be considered in relation to manual laterality in nonhuman primates (cf. McGrew and Marchant, 1997 for a review; see Nahallage and Huffman [2007b] for ontogeny of SH motor development). The fact that older individuals became more lateralized for SH activity is consistent with previous findings on Japanese macaques. In this species, adults have greater strength of manual laterality than young individuals (Itani et al., 1963; Kubota, 1990; but see Takeda, 1994). Older infant macaques even showed stronger hand preferences than younger infants (Lehman, 1980). Most studies on the ontogeny of behavioral laterality in humans and nonhuman primates show increased lateralization with age (e.g., McManus et al., 1988; Bard et al., 1990; Westergaard and Suomi, 1993b; Hopkins, 1995; Schaafsma et al., 2009; but see Boesch, 1991; McGrew and Marchant, 1992).

The lack of a sex effect on manual laterality is consistent with most studies on nonhuman primates, including Japanese macaques (Itani et al., 1963; Tokuda, 1969; Kubota, 1990; Byrne and Byrne, 1993; Harigel, 1994; Colell et al., 1995). Likewise, no clear evidence for the heritability of manual preference was found in most primate species (Kubota, 1990; Boesch, 1991; Westergaard and Suomi, 1997; but see Hopkins et al., 1993a). One reason for the lack of postural effect on manual preference could be that we only compared sitting versus quadrupedal postures, whereas the majority of studies in monkeys and apes showed that the direction and strength of

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laterality was greater in bipedal or vertical clinging postures than in a quadrupedal posture (Olson et al., 1990; King and Landau, 1993; Hopkins et al., 1993b; Westergaard et al., 1998b; Blois-Heulin et al., 2007).

In this study, our main goal was to provide an explicit and heuristic picture of the intrinsic and extrinsic variables that may affect directly or indirectly the expression of manual laterality in a nonhuman primate species, for one or several manipulative tasks, and at the individual and group levels. We systematically followed the methodological framework developed by McGrew and Marchant (1997) to measure, label, and analyze manual preference in a group of Japanese macaques. Overall, our results contribute to the growing database of manual laterality in nonhuman primates and provide additional evidence that Japanese macaques, like other primate species, display some form of group-level bias in manual preference when performing asymmetric but coordinated bimanual action involving role differentiation between hands.

Further study will focus on the inter-group comparison of hand lateralization in SH by Japanese macaques, a cultural behavior with considerable geographical variation (Leca et al., 2007a). We encourage similar detailed studies of manual laterality in primates to shed further light upon the origins of functional laterality in the order Primates and its implications for the evolution of tool use in early hominins.

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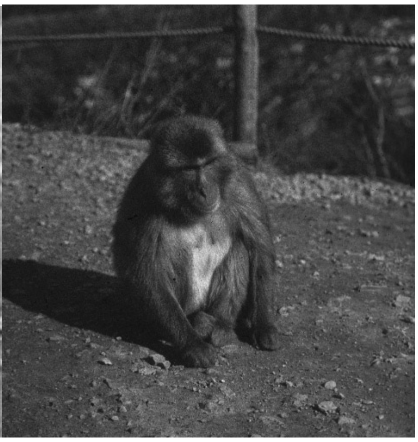
Glance-6476 and her infant (Arashiyama)



Glance-6476 in January 1987

Momo-5978 and her infant in 1989 (Arashiyama)

Stone handling juveniles at Takasakiyama (Nov. 1989)

Stones left on flat stone surface by free-ranging stone handlers) at Takasakiyama

Photos by M.A. Huffman

Cuddling (young)[1] Cuddling (adult)[1] Grasp with hand[1] Gathering[1]

Scattering[2] Move and push[2] Rub with hand[2] Rub together[2]

Examples of stone handling patterns by Japanese macaques
([1]: photos by J.-B. Leca, [2]: photos by N. Gunst)

Social influence of the mother in stone handling acquisition by infants[1]

Handling stones while involved in a social play interaction…[1]

… or in a grooming interaction[1]

Stone handling in long-tailed macaques[1]

Fish eating by Japanese macaques at Koshima[1]

Dental flossing (Arashiyama)[1]