Chapter 9: Cultured Japanese Macaques: A Multidisciplinary Approach to Stone Handling Behavior and Its Implications for the Evolution of Behavioral Tradition in Nonhuman Primates

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9.1 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 identification of all members of several Japanese macaque (*Macaca fuscata*) groups across Japan were accomplished, including those of Koshima, Takasakiyama, Arashiyama, and Minoo. The practice of long-term comparative and collaborative research was begun, one of the many early contributions by Japanese scientists to the field of primatology (Huffman 1991; Yamagiwa and Hill 1998; Takahata et al. 1999; see also Chap. 1). 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 (for reviews, see Itani and Nishimura 1973; Nishida 1987; Thierry 1994; Huffman and Hirata 2003).

Perhaps two of these most widely cited examples of evidence for culture in Japanese macaques, and arguably all animals, is the innovation and transmission of sweet potato washing and wheat washing behavior in the Japanese macaques on Koshima Islet, Miyazaki Prefecture, Kyushu (Kawai 1965). By September 1953 on Koshima, almost 2 years after provisioning began, the macaques were regularly

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eating the sweet potatoes and wheat passed out to them on the beach. At this time a young female, *Imo*, was observed to begin to carrying soiled sweet potatoes to a small stream and to wash off sand and dirt before eating (Kawai 1965). This combination of provisioned novel foods and access to water by all individuals set the stage for the transmission of food washing behavior. The first individual other than *Imo* to display this behavior was a playmate, followed by *Imo*'s mother and other playmates, eventually spreading widely to others of the group. Next, *Imo* began to wash potatoes in sea brine instead of freshwater, supposedly to season them (Kawai 1965). The next behavior innovation to be recorded on Koshima was wheat washing behavior. Again, it was *Imo* who was first observed to exhibit this habit, whereby sand grains and wheat were separated from each other by dropping handfuls of these mixed ingredients into puddles of water on the beach or directly into the ocean. The behavior spread within the group along similar lines as potato washing.

Again on Koshima, the habit of fish eating was observed from its innovation and followed as it spread throughout the group (Watanabe 1989). A clear difference in the initial route of transmission was noted between fish eating and potato or wheat washing behaviors. That is, fish eating first appeared in an adult male living in the group's social periphery. The behavior spread to an old female, and from her the habit is reported to have eventually diffused to members within the group's social center (Watanabe 1989).

More recent work in Japanese macaques has focused specifically on the innovation and diffusion of new group-specific behavioral traditions in free-ranging provisioned groups (Huffman 1984, 1996; Huffman and Quiatt 1986; Tanaka 1995; 1998; Leca et al. 2007a). For example, Tanaka (1995, 1998) studied the changes at the individual and group levels in louse egg-handling techniques (e.g., "combing" and "pinching") to facilitate their removal during grooming in a free-ranging group of Japanese macaques living at Jigokudani Monkey Park, Shiga Heights, Nagano Prefecture. On the one hand, louse egg-handling skills were not fixed for each individual, but they changed over time. The successive shifts in the adoption of different techniques by the same individual may not only reflect structural and functional aspects of the behavior, but also some form of individual learning (Tanaka 1998). On the other hand, the maternally skewed distribution of different louse egg-handling variants strongly suggests the social transmission of behavior, possibly via imitative learning (Tanaka 1995). For example, one female's new technique was later adopted by her sister, daughters, and granddaughter. Because Japanese macaques show a high degree of kin bias and/or favoritism in most behaviors and interactions, compared to other macaque species (Chapais et al. 1997), it is not surprising that many innovative behaviors were shown to first diffuse widely within kin lineages before being adopted by unrelated individuals (Watanabe 1989; Kawai et al. 1992; Tanaka 1995).

Dental flossing has been reported in a group of long-tailed macaques (*Macaca fascicularis*) in Thailand (Watanabe et al. 2007). The use of hair as dental floss to remove food remains stuck between the teeth, dental flossing is a form of tool-use (sensu Beck 1980) and may be considered a form of self-medication *(*sensu Huffman 2007). It has been discussed as a group-specific behavior in terms of culture, and social learning has been invoked by clear descriptions of mothers exaggerating their flossing actions in the presence of their offspring, supposedly to facilitate the learning of the behavior by infants (Watanabe et al. 2007; Masataka et al. 2009). Recently, Leca et al. (2010a) reported the first case of dental flossing behavior in a Japanese macaque at Arashiyama, Kyoto. Although this behavior was performed frequently by a central middle-ranking middle-aged female during her grooming interactions, and appeared several years ago, it remains idiosyncratic to its innovator, and up to now has not spread to other group members.

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 (*Macaca tonkeana*; Drapier and Thierry 2002), abnormal behaviors of captive rhesus macaques (*Macaca mulatta*; Hook et al. 2002), and prey capture by killer whales (Rendell and Whitehead 2001). All these studies have investigated determinants of cultural behavior, including innovation, transmission, acquisition, developmental constraints thereof, long-term maintenance, and intergroup variation. However, none has considered the role of all these factors in 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, that is, "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 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 et al. 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 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 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 intergroup behavioral variation, the emergence and transformation of culture, and the potential importance of culture in the process of biological evolution.

9.2 Stone Handling Behavior

SH is a seemingly nonadaptive solitary object play activity (Huffman 1984, 1996; but see Nahallage and Huffman 2007a and Sect. 9.5.8). SH consists of manipulation of stones in various ways, including rubbing or clacking them together, pounding them onto other hard surfaces, picking them up and rolling them together in the hands, and cuddling, carrying, pushing, or throwing them (Fig. 9.1 and Table 9.1). Currently, 45 different behavioral patterns are documented in Japanese macaques (Leca et al. 2007a).

SH is reported to occur in four captive groups and six provisioned free-ranging groups 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 group, Kyoto, Japan, beginning from its innovation (Huffman 1984, 1996; Leca et al. 2007a). In contrast to 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 5 years of age.

9.3 Long-Term Observation of the Arashiyama Group

9.3.1 Innovation

Japanese macaques have been studied at Arashiyama since 1954, after macaques 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 behavior was the 3-year-old, middle-ranking female *Glance-6476* (Fig. 9.2). 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 12-month study lasting up to September 1980.

9.3.2 Transmission

In October 1983, when Huffman returned again to Arashiyama to resume research, SH had already diffused to many members of the group and had become a daily

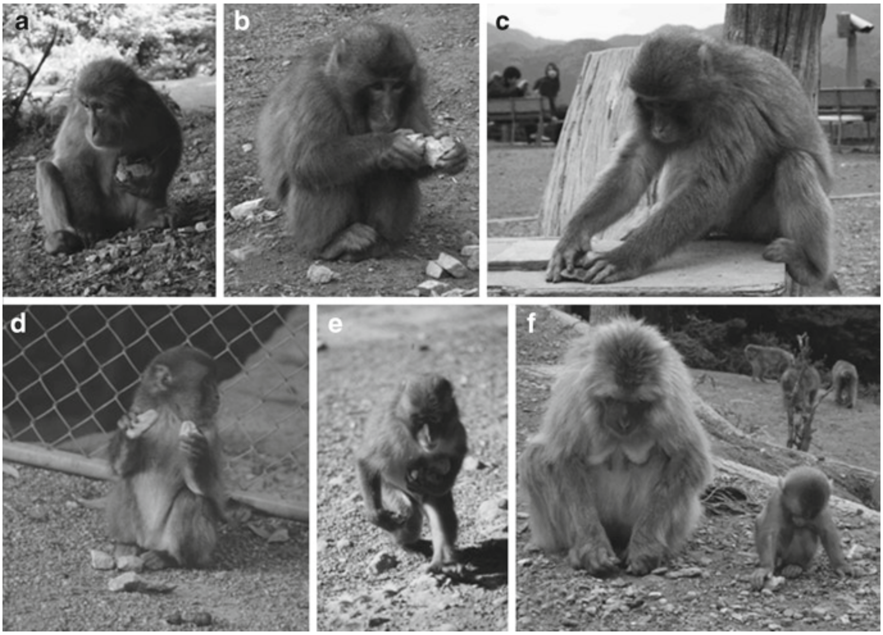

Fig. 9.1 Five stone handling (SH) patterns (**a**, cuddle; **b**, rub together; **c**, rub on surface; **d,** clack; **e**, carry;) and a mother–infant dyad performing SH simultaneously (**f**). (Photographs **a, c** and **f**, courtesy of J.-B. Leca; photographs **d** and **e**, courtesy of M.A. Huffman; photograph **b**, courtesy of N. Gunst)

occurrence. SH was classified into eight basic behavioral patterns: gathering, pick up, scatter, roll in hands, rubbing stones, clacking, carry, and cuddle (Huffman 1984). By 1985, an additional nine behavioral patterns were also recognized, with six of those patterns being variations of the original eight (pick up and drop, rub of surface, flinting, pick up small stones, rub with hands, and grasp with hands). The three 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 group daily activity.

In June 1984, 49% (115/236) of the group exhibited SH and by June 1985, 60% (142/236) of the group members born before June 1984 were verified to be new SH users. 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+ 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 exhibit SH in 1979, the only older individuals noted to perform SH were her two female cousins, *Glance-6775* and *Glance-6774*, and a lower-ranking female, *Blanche-596475*. In contrast to 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 finding supports our

Table 9.1 Forty-five stone handling (SH) patterns performed by Japanese macaques and categorized according to general activity patterns

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 some time
	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)

Source: After Leca et al. (2007a)

Fig. 9.2 *Glance-6476* (3-year-old, middle-ranking female): first individual recognized to perform SH on December 7, 1979

observation that SH was not likely innovated earlier than 1978 or 1979, as 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, in contrast to 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 individuals 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).

9.4 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. On 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 sites, 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 and 2005, during which 14 infants were born.

9.4.1 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, which states that the total time spent in areas with high stone availability and, therefore, exposure to more stones increases the likelihood that an infant will acquire SH behavior. We found no significant correlations between the age of SH acquisition and the rate of stones encountered from birth to acquisition of the behavior.

9.4.2 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 interindividual 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 3 months of life, infants spent 75% of the time within 1 m 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 exhibit the behavior earlier than infants of less frequent SH mothers. Two infants who were 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 mothers 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 a mother's SH frequency could affect their infant's exposure to SH, opportunities to handle stones, and practice SH.

9.4.3 Constraints of Neuromotor Development on the Expression of SH Behaviors

Few longitudinal studies have been conducted on the ontogeny of specific cultural behaviors; rather, most tend 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 showed that although 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 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 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 6 to 12 months of age. According to neuromotor studies on macaques, the earliest sign of relative independent finger movement (RIFM) occurred at 2 to 3 months, with mature patterns occurring at 7 to 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 finding agrees with our study showing infants starting the behavior between 2 and 3 months and performing activities that require firm grasp of the stones around 6 months. Even though the neuromotor 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 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 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 because of their level of neuromotor 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 group. Her son first started throwing stones when he was 1.5 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 group (Nahallage and Huffman 2007b; Leca et al. 2008c).

9.5 Exploring and Explaining Intergroup Behavioral Differences

9.5.1 The Method of Elimination

Recently, primatologists have found evidence of intergroup behavioral variation in several nonhuman 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 multistep 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. Similar to some ethnographic research in human social sciences or 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 (Whiten et al. 1999).

Second, intergroup 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 intergroup 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 attributable 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).

9.5.2 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 intergroup 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 intergroup 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, *M. fuscata fuscata*, widely distributed in the Japanese archipelago, and *M. fuscata yakui*, endemic to Yakushima Island, 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 intergroup differences in SH; (5) to consider the influence of various sociodemographic constraints on the appearance, diffusion, and maintenance of SH; (6) to test the association between geographical proximity and behavioral similarity as a way to infer a phenomenon of cultural zone; and (7) to explore the transformation over time in the form of SH from the perspective of stone-tool use in nonhuman primates.

We conducted a systematic comparison of SH in ten groups of Japanese macaques. Nine groups belonged to the *M. fuscata fuscata* subspecies and one group was *M. fuscata yakui* (see Chap. 2). Four captive groups were housed in large outdoor enclosures at the Kyoto University Primate Research Institute (PRI), and Japan Monkey Centre, Inuyama, and six free-ranging provisioned groups lived at four geographically isolated sites in Japan, namely, Arashiyama, Takasakiyama, Koshima Islet, and Shodoshima Island (Fig. 9.3). The comparison represented a total of 2,328 individuals and included two long-term studied groups at Arashiyama and Takasakiyama. We used the same observation procedure in all groups 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 h 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).

9.5.3 Intergroup 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

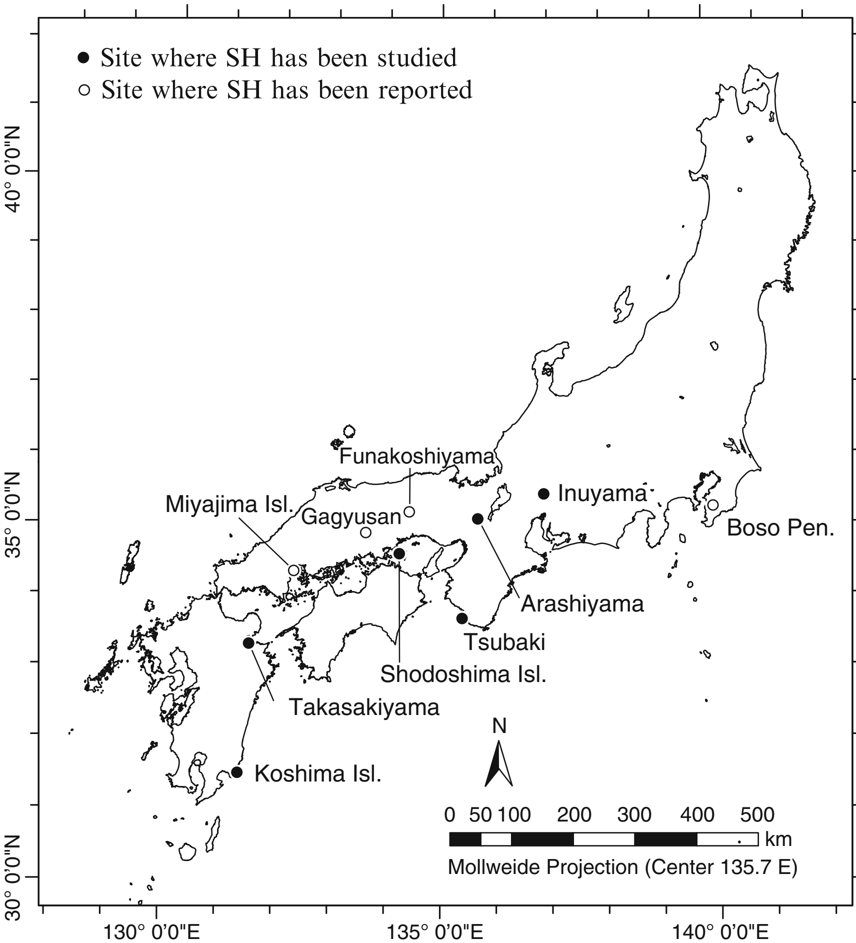

Fig. 9.3 Map of the sites in Japan where SH has been studied or reported. [*Sources:* Arashiyama, Funakoshiyama, Gagyusan, Boso Peninsula, Takasakiyama, Yakushima (Huffman and Hirata 2003); Arashiyama, Inuyama (Primate Research Institute and "Monkey Valley" at Japan Monkey Centre); Koshima, Shodoshima, Takasakiyama (Leca et al. 2007a); Tsubaki (Leca, unpublished data); Miyajima (Watanabe, personal communication). The base map is originated from "Boundary data of cities, towns and villages of Japan ver. 6.2," by ESRI Japan Corporation, with permission]

group-contrast approach to chart intergroup diversity in SH, Leca et al. (2007a) showed substantial variability in the frequency of occurrence and form of SH among the ten study groups. We found major intergroup differences in the frequency of occurrence and the prevalence of most of the 45 SH patterns, with local variants being customary in some groups, and rare or even absent in others although they were ecologically possible, and performed by a majority of individuals in some groups or only idiosyncratically in others (Leca et al. 2007a,b; see Table 9.2 for definitions).

Table 9.2 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 Centre = JMC) and six free-ranging troops (Koshima = Kosh., Arashiyama E = Ara.E, Shodoshima = Sho.A and Sho.B, Takasakiyama = Tak.B and Tak.C)

	Captive troops				Free-ranging provisioned 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. of pattern occurrence	5	20	32	19	4	20	11	10	15	19

No asterisks, *Macaca fuscata fuscata* troops; asterisk, *M. f. yakui* troop; neighboring troops living at the same site (respectively, two troops at Shodoshima and two troops at Takasakiyama)

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 h of total observation time); (–), unknown: not observed but absence uncertain because of insufficient observation time (less than 90 h of total observation time); no. of pattern occurrence, number of SH patterns scoring at least the present status

The frequency of occurrence of SH patterns was highly variable according to the pattern and group in question. Very few patterns were unique to any group, as most were shared between two or more groups. Even though most simple SH patterns (corresponding to investigative, locomotion, and collection activities) could be observed in most study groups, 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 groups, but again highly variable depending on the pattern. Finally, a few complex SH patterns were specific to one group, such as *tap in mouth*, *spin*, and *wrap in leaf* in the Takahama group, and *stone-groom* in the Shodoshima A group.

Following Whiten (2005), we defined a "tradition" as a local behavioral variant, showing different frequencies of occurrence across the study sites, that is, 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, that is, 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 group-dependent clusters of SH traditions (Leca et al. 2007a).

In summary, our results revealed a significant intergroup variability in the form of SH, consistent with the extensive and multiple intersite behavioral differences recorded in chimpanzees, and interpreted as cultural variation (cf. Whiten et al. 1999).

9.5.4 No Major Evidence for Genetic Determinants in SH Variation

First, our comparative study revealed that *M. fuscata yakui* did not notably differ from *M. fuscata fuscata* in the SH repertoire, as well as in the occurrence, form, and context of SH. We found that SH patterns varied as much among seven groups of the same subspecies (*M. fuscata fuscata* in Wak.A, Takh., Ara.E, Sho.A, Sho.B, Tak.B, and Tak.C) as between subspecies themselves (*M. fuscata fuscata* versus *M. fuscata 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; that is, 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 geographical distribution of extant populations of Japanese macaques, including continuities and discontinuities, migration, and genetic variability. There was evidence for geographical 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 stones rather than rub the 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 intergroup variability in the form of SH in macaques (Leca et al. 2007a; Nahallage and Huffman 2008a).

9.5.5 Role of Ecological Factors in SH Variation Between Groups

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 intergroup variation (Leca et al. 2008b). Among the most obvious ecological differences that could affect SH, we addressed site-specific availability in stone number and size, the degree of terrestriality of individuals, and food provisioning constraints.

9.5.5.1 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 intergroup 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 finding 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 group. 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).

9.5.5.2 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 macaques gives them "free" time because they can devote less time to foraging. Moreover, attracting macaques to the open space of feeding sites, 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 group's food-related activities and feeding style, which in turn could affect several aspects of SH. In groups provisioned several times a day, SH was more frequent, lasted longer, and was more prevalent during provisioning than nonprovisioning periods. These effects of provisioning were not significant in groups provisioned less frequently. Moreover, SH was more frequently integrated with food-related activities in groups supplied with food several times a day than in the other groups. Thus, we argued that the context of occurrence, frequency, and form of SH in a given group 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, as 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).

9.5.6 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, and the age structure of the group, may account for the substantial intergroup variations in SH reported in Japanese macaques.

The ten study groups varied greatly both in size and in proportion of individuals belonging to the different age classes (Leca et al. 2007b).

9.5.6.1 Group Size

We found that group size was positively correlated with the percentage of group 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 group 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 group members and eventually result in a form of "hysterical contagion." This finding may help to explain the increase in number of SH individuals (synchronized occurrence) around feeding time in free-ranging provisioned groups, as this is the only time when most group members are all together in the same location.

9.5.6.2 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 a 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 group, 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 group 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 group members may not be sufficient to maintain the behavior in this group in the long term.

These findings are consistent with long-term field observations conducted at Arashiyama and described earlier, 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 of age); 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, 2010b).

In sum, the present findings supported the hypothesis that patterns of variation in SH across groups reflected variability in group size and composition in age classes.

9.5.7 Social Influences and Observational Learning in SH

9.5.7.1 Cultural Zones

We found a positive correlation between geographical proximity and cultural similarity in SH between groups. In other words, there were significantly greater similarities in SH patterns in the groups living at the same site, compared to other groups. The numbers of patterns showing the same occurrence in the two groups living at Shodoshima (Sho.A and Sho.B) and in the two groups living at Takasakiyama (Tak.B and Tak.C) were 25 and 24, of 33, respectively (see Table 9.2). These neighboring groups 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 geographical distribution of clear group-dependent clusters of SH variants and the similarities in the SH repertoires between the free-ranging groups living at the same site were suggestive of the phenomenon of cultural zones, because any alternative explanation is hard to imagine. Although food provisioning schedules were different, neighboring groups 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) intergroup observation when macaques come into occasional contact around the feeding sites where most SH activity occurs and (2) males transferring SH patterns when migrating from one group to another. When such intergroup social influences do not exist (e.g., groups separated by substantial geographical distance in natural situations or by artificial barriers such as concrete walls in captive conditions), the groups showed more differences in their SH repertoires: their mean number of behaviors showing the same frequency of occurrence was only 12.1 ± 7.3. Intergroup 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 group members around feeding sites. Attracting macaques to the open space of feeding sites, 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).

9.5.7.2 Social Tolerance and Spatial Cohesion

To test the hypothesis that SH will be more prevalent in more cohesive groups, we calculated, for the ten study groups, 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 groups showing higher levels of positive social interactions (such as grooming and playing) were not necessarily the groups 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 groups characterized by closer physical proximity among individuals feeding on provisioned food also showed higher percentages of group members exhibiting SH simultaneously (Leca et al. 2007b).

Therefore, intergroup differences in SH prevalence and cultural similarity in SH between neighboring groups were better explained by intergroup transfers, as well as opportunities for observational learning and behavioral coordination both within and between groups rather than intragroup social tolerance alone.

9.5.7.3 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 macaques have almost doubled the size of their SH repertoire and largely diversified the contexts in which SH activity was practiced (Leca et al. 2007a).

We expect such an increase over time in the number and diversity of SH patterns to be found in other groups where the SH tradition is well established. Based on data from Arashiyama and Takasakiyama, we also expect to find in other groups a cumulative increase in the complexity of the SH repertoire, from simple SH patterns observed in the first year following the appearance of the behavior within the group, to more complex SH patterns performed after several years of daily practice of the behavior at the group level.

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 groups 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 point of view, almost all the 45 SH patterns currently observed in Japanese macaques are regarded as a noninstrumental 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 noninstrumental 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 macaques 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. In contrast to all other SH patterns performed by Japanese macaques, unaimed stone-throwing was exclusively observed in the captive Takahama group 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 group was the only one to show a complexity level-3 SH culture. This group also exhibited the most diverse SH repertoire (44 patterns of a total of 45) and showed the highest frequencies of occurrence in SH patterns (28 habitual or customary patterns) among all groups. These findings suggest that, although SH was observed in the ten studied groups, the transformation of SH into an adaptive behavior is more likely in groups 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 nonfunctional 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).

9.5.8 Possible Functions of Stone Handling Behavior

Although 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 groups 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 (Pellis 1991; Hall 1998; Pellis et al. 1988). However, SH as described here is not consistent with the misdirected foraging behavior hypothesis (pseudo-feeding behavior) proposed by Pellis (1991). Even in provisioned groups, 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).

Although 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 groups, and age-class differences within the same group 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 expectation 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 macaques suppress SH for days following periods of externally induced intense stress, such as capturing the entire group for annual checkups, or 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 distinction is of particular interest to us, given that the behavior is only acquired by individuals when young. This difference leads us to speculate that in contrast to 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, as any other form of object play, is most likely to be that it is intrinsically an enjoyable activity (Hall 1998). The young 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 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 (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 neuromotor developmental activity. These findings are consistent with Fairbanks’ (2000) model describing the heightened frequency of object manipulation in correlation with synaptic development in juvenile savanna monkeys (*Cercopithecus aethiops*) and rhesus macaques (Rakic et al. 1986). We believe 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 the young. With age, adults exhibit fewer bouts of longer duration, involving relatively more complex behavioral patterns than in the young (Nahallage and Huffman 2007a). Adults focus on these more demanding manipulative activities, with seemingly intense concentration. They carry stones to their individually preferred locations to handle them in an unhurried, seemingly “leisurely,” manner. Sometimes older individuals sit nearby their preferred location, waiting for others to leave, before going there to handle the stones, 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. As 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 the 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 (see 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 neuromotor development when 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.

9.6 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 intergroup variation in the frequency, form, and context of occurrence of SH, were better explained by neuromotor developmental constraints, sociodemographic factors (namely, group size, age structure, intergroup 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 intergroup variability of a single type of behavior in macaques 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. Among the rare nonadaptive proposed traditional behaviors [see also "leaf-pile pulling" in chimpanzees (*Pan troglodytes*); 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 the 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 geographical 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 primates (Huffman et al. 2008).

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