The Arashiyama group of Japanese macaques holds a distinguished place in primatology as one of the longest continuously studied non-human primate populations in the world. The resulting long-term data provide a unique resource for researchers, allowing them to move beyond cross-sectional studies to tackle larger issues involving individual, matrilineal and group histories.

This book presents an overview of the scope and magnitude of research topics and management efforts that have been conducted on this population for several decades, covering not only the original troop living around Kyoto, Japan, but also the two subgroups that were translocated to Texas, USA and to Montreal, Canada. The chapters encompass topics including life history, sexual, social and cultural behaviour and ecology, giving an insight into the range of current primatological research. The contributors underscore the historic value of the Arashiyama macaques and showcase new and significant research findings that highlight their continuing importance to primatology.

Cover illustration: heterosexual consortship between Momo-61-72-80-95 (male) and Blanche-59-64-75-82 (female) at Arashiyama, October 2009. Photo by Noëlle Gunst.

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JEAN-BAPTISTE LECA is a post-doctoral research fellow and Lecturer in the Department of Psychology, University of Lethbridge, Canada. His research explores the determinants of behavioural innovations and traditions, and the evolution of non-conceptive sexuality, including the motivational mechanisms underlying female-to-male mounting in Arashiyama Japanese macaques.

MICHAEL A. HUFFMAN is an Associate Professor in the Department of Social Behaviour and Ecology at the Primate Research Institute, Kyoto University, Japan. His research on free-ranging and captive Japanese macaques encompasses sexual behaviour, reproductive physiology and energetics, enrichment, social learning, cultural behaviour, self-medication and parasite ecology.

PAUL L. VASEY is a Professor in the Department of Psychology at the University of Lethbridge, Canada. His research focuses on the development and evolution of non-conceptive sexuality from a cross-species and cross-cultural perspective. He has conducted research on sexual behaviour in free-ranging Japanese macaques at Arashiyama and on the captive subgroup in Montreal.

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The Monkeys of Stormy Mountain

60 Years of Primatological Research on the Japanese Macaques of Arashiyama

Edited by
Jean-Baptiste Leca,
Michael A. Huffman and Paul L. Vasey

13 *Thirty years of stone handling tradition in Arashiyama-Kyoto macaques: implications for cumulative culture and tool use in non-human primates*

JEAN-BAPTISTE LECA, NOËLLE GUNST AND MICHAEL A. HUFFMAN

Glance-71–81, the oldest male (29 years) in the Arashiyama-Kyoto troop in October 2010, who still exhibits stone handling behaviour (photo by N. Gunst).

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13.1 Animal cumulative culture: a debated topic

If culture (also termed 'tradition' by ethologists) is defined as a population-specific behavioural practice, persistent in several group members across generations or at least over a number of years, and dependent on social means for its transmission and maintenance (Perry and Manson, 2003), then culture is not limited to humans. There is increasing evidence for cultural variations in a wide range of behavioural patterns (e.g. interspecific interactions, communicatory, courtship, display, grooming, object play and social play behaviours, feeding habits, food processing techniques, medicinal plant use and tool use) and across various animal taxa (including fish, birds, rodents, cetaceans and non-human primates) (for reviews, see Lefebvre and Palameta, 1988; Avital and Jablonka, 2000; Fragaszy and Perry, 2003).

However, some authors argue that 'animal traditions' and 'human culture' should be distinguished and considered analogues rather than homologues on the basis of several major differences: (1) the content of what is transmitted (simple versus elaborate behavioural patterns); (2) the social learning mechanisms that support them (local enhancement and social facilitation versus imitation and teaching); (3) the stability and durability of the phenomenon (ephemeral animal tradition drifts or fads lasting from only a portion of an individual's life span up to a few generations versus stable human cultural traits enduring across centuries); and (4) the cumulativity of the process (no obvious improvement of behavioural patterns showing little if any change over generations versus progressive accumulation of cultural modifications over time leading to increasingly complex behaviours) (Galef, 1992; Tomasello *et al*., 1993; Enquist and Ghirlanda, 2007; Caldwell and Millen, 2009; Hill, 2009).

Cumulative cultural evolution refers to situations in which 'the achievements of one pattern of behaviour form the basis for the selection of a modified and better-adapted descendant pattern' (Avital and Jablonka, 2000, p. 94). This process involves a 'ratchet-like effect' where a beneficial modification is retained until it can be improved upon, and results in behaviours or artefacts with cultural histories, i.e. that no individual could invent on their own (Tomasello, 1990; Tomasello *et al*., 1993). On the one hand, human societies typically exhibit elaborate cumulative cultural evolution, with new patterns and methods building upon their predecessors', often leading to increasing diversity, complexity and efficiency of cultural or technological products (Tomasello, 1990; Boyd and Richerson, 1996; Caldwell and Millen, 2008a, 2008b, 2010). These accumulated adaptive knowledge and artefacts have allowed our species to occupy and exploit a far wider range of habitats than any other animal (Boyd and Richerson, 1996).

On the other hand, current evidence for cumulative culture and ratcheting in non-human species remains rare and controversial (Galef, 1992; Boesch and Tomasello, 1998; Tomasello, 1999; Laland and Hoppitt, 2003; Tennie *et al*., 2009). There are only a few well-documented cases in which cultural changes seem to accumulate over generations, leading to the evolution of behavioural patterns that no single individual could invent. In New Caledonian crows, tool manufacture skills may partly be acquired through cumulative cultural evolution (Hunt and Gray, 2003). In killer whales, the foraging techniques consisting of briefly beaching in order to prey on sea-lion pups appear more diverse and complex across generations (Guinet and Bouvier, 1995). Some forms of ant-fishing and nut-cracking behaviours currently performed by particular chimpanzee communities indicate a step-by-step elaboration on earlier and simpler variants that may reflect accumulated modifications of socially transmitted behavioural patterns (Whiten *et al*., 2003).

Finally, since Japanese researchers started providing food for the Japanese macaques living on Koshima island, this troop has gradually acquired a whole new lifestyle (Avital and Jablonka, 2000). Feeding the monkeys first with sweet potatoes, then with wheat grains, on the sandy seashore of Odomari beach, directly led to the appearance of two successive food-washing traditions: (1) potato-washing, with an original form described as dipping the potatoes into the fresh water of a nearby stream, thus washing off sand and dirt before eating them, and a subsequent elaboration of this behaviour consisting of biting the potatoes before dipping them into the shallow salty seawater, not only to wash them, but also presumably to season them before they were consumed; and (2) wheat-washing, defined as picking up a handful of mixed sand and wheat and throwing it into the seawater, which resulted in separating the heavier sand that sank from the lighter wheat that floated on the surface, allowing the monkeys to collect it easily (Kawai, 1965; Itani and Nishimura, 1973; Kawai *et al*., 1992; Watanabe, 1994).

Moreover, the habit of spending more and more time on the beach, an unnatural habitat for Japanese macaques, also had ulterior indirect effects on the diffusion of additional behavioural innovations, through the influence of food provisioning on the troop's activity budget and sedentary lifestyle (cf. Huffman and Hirata, 2003; Leca *et al*., 2008a). As young monkeys brought to the beach by their mothers (who had learned washing their food) became accustomed to the salty water, they started playing in it. Thus, sea-related subsistence traditions triggered the social traditions of using the sea for swimming, jumping and diving, as well as cooling in summer, newly acquired behaviours that became characteristic of the whole troop, including the adults, and had not been reported before in this troop or in other troops of Japanese macaques (Kawai, 1965; Kawai *et al*., 1992; Watanabe, 1994). Another consequence of

these beach activities occurred later: the monkeys started to eat raw fish, a feeding habit that is still present in the troop today (Watanabe, 1989; Leca *et al*., 2007a). In sum, Koshima macaques have accumulated and elaborated over decades their food-related and social traditions in a ratcheted way by developing a new lifestyle associate with a new habitat, the sandy beach and the sea (Kawai *et al*., 1992, Watanabe, 1994; Avital and Jablonka, 2000).

However, these few cases of cumulative cultural evolution in animals are still considered speculative and contentious. Some authors argue that cognitive constraints and contrasting social learning abilities make the evolutionary improvement of behaviours by the gradual accumulation of cultural adaptations much more likely in humans than in other animals (Galef, 1992; Heyes, 1993; Tomasello, 1999). As pointed out by Boyd and Richerson (1996), while social learning and culture are common in nature, cumulative cultural evolution is strikingly rare. Therefore, the pervasive human ability to accumulate socially learned behaviours over many generations poses an evolutionary puzzle: if cumulative culture is such an effective means of adaptation, why do non-human cultures not ratchet to any substantial degree? Lack of evidence for such a process does not mean its absence in nature (Danchin and Wagner, 2008). In order to tackle this issue, more 'provocative and intriguing instances of animal cumulative culture' based on systematic and long-term research are needed (Sapolsky, 2006). This report aims to show how the longitudinal study over 30 years (1979–2009) of one of the most thoroughly documented behavioural traditions in non-human primates, namely stone handling by the Japanese macaques living at Arashiyama, Japan, can contribute to the understanding of cumulative culture in animals, through the gradual transformation of stone-directed behavioural patterns that could be regarded as tool-use precursors.

13.2 Stone handling as a behaviour: structural and functional aspects

Stone handling (SH, hereafter) activity is typically defined as the spontaneous, solitary, non-instrumental and seemingly playful manipulation of stones, through the performance of multiple behavioural variants, also called SH patterns, with one or both hands, and occasionally in combination with the feet and mouth (Huffman, 1984; Leca *et al*., 2010a, 2011). SH is typically categorised as a form of solitary object play, and differs both structurally and functionally from object exploration (Huffman and Quiatt, 1986; see also Candland *et al*., 1978; Fagen, 1981; Hall, 1998). An individual engaged in SH activity can perform, for several minutes, a series of different SH patterns, often repeated and varied in sequence, while showing a relaxed facial expression and focusing

most of its attention on the stones being manipulated (Huffman, 1984; Leca *et al*., 2007b).

Like in other types of object play (cf. Fagen, 1981), some SH patterns are similar in form to those used during foraging activity, but the behaviours are performed out of context and modified in structure (Leca *et al*., 2007c, 2008a, 2011). SH occurrence and frequency is largely dependent upon the time available for non-subsistence activities (Huffman and Hirata, 2003; Leca *et al*., 2008a). 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 (Huffman and Hirata, 2003; Leca *et al*., 2007b). Age appears to affect the diversity and type of SH patterns displayed. As they grow older, individuals tend to perform less varied and more simple patterns, such as gather, scatter or pick up stones (Huffman and Quiatt, 1986; Leca *et al*., 2007b; Nahallage and Huffman, 2007a).

Although SH is primarily a solitary activity, the social aspects involved in the occurrence of this behaviour should not be overlooked. First, there is no doubt that it is socially transmitted (Huffman, 1984; Nahallage and Huffman, 2007b; Leca *et al*., 2010b). Second, an inter-group comparative study showed that troop size was correlated with the proportion of troop members exhibiting SH simultaneously. The effect of troop size on the synchronised performance of SH may reveal the contagious nature of play (Leca *et al*., 2007b). Third, SH is occasionally integrated with social interactions such as play wrestling and allogrooming (Huffman, 1984; Leca *et al*., 2008a; Figure 13.1). Fourth, once particular stones are involved in a solitary SH episode, they appear to trigger great interest from other individuals who sometimes try to snatch them away from the handler as if they were the only stones available, and such supplanting interactions over the stones suggest the existence of a rudimentary form of 'possession' in monkeys (Huffman and Quiatt, 1986; Leca *et al*., 2010b).

Regarding functional aspects, SH is largely considered a non-directly adaptive behaviour (Huffman, 1984; Huffman and Quiatt, 1986; Leca *et al*., 2011). Most of the 45 SH patterns listed in the Japanese macaque repertoire do not seem to serve any immediate function (Leca *et al*., 2007c; Nahallage and Huffman, 2007a). Despite the rare occurrence of percussive and complex SH patterns combining two stones, stones and substrates or objects, and stones and body parts (e.g. *flint*, *pound on surface* and *put/rub on fur*, cf. Table 13.1), and with the notable exception of unaimed stone-throwing, a SH pattern that may serve to augment the effect of agonistic displays in a captive troop housed at the Kyoto University Primate Research Institute (Leca *et al*., 2008b), the stones handled are never used as tools to achieve an overt goal. 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 (Leca *et al*., 2011). Therefore, there is no local survival advantage in performing a particular SH pattern rather than another.

However, two proximate explanations for the performance of SH have been suggested. First, we believe that all monkeys, regardless of age, may simply enjoy manipulating stones, and pleasurable feedback potentially gained from the activity may be an immediate reinforcement (Huffman, 1996; Leca *et al*., 2007c; Nahallage and Huffman, 2007a). Second, and at least in troops

Figure 13.1. Examples of stone handling (SH) patterns by Japanese macaques at Arashiyama. (a) cuddle, (b) rub stones together, (c) gather, (d) carry, (e) grasp with hands, (f) rub in mouth; (g) Glance-64–76 (the SH innovator) handling stones on 7 December 1979; Social influence of the mother in SH acquisition by infants, (h) Glance-64–76 and her infants in 1987, (i) Kusha-59–71–76–82 and her infant in 2008; Handling stones while involved in a social play interaction (j) and in a grooming interaction (k) (photos a, c, e, i, j, and k by J.-B. Leca; b and f by N. Gunst; d, g, and h by M. A. Huffman).

Figure 13.1. (*cont.*)

Figure 13.1. (*cont.*)

Figure 13.1. (*cont.*)

Figure 13.1. (*cont.*)

Figure 13.1. (*cont*.)

provisioned with cereal grains several times a day, like at Arashiyama, handling stones may be an extension of foraging-like behaviours, a continuation of manipulatory actions directed at alternative objects, while chewing food that does not require further food-processing behaviours (Huffman and Hirata, 2003; Leca *et al*., 2008a).

13.3 Stone handling as a tradition: inter-group variation, social transmission and long-term maintenance

Japanese macaques are known for their cultural behaviours, among which is SH. The behaviour meets the set of criteria typically used to define a tradition. First a systematic comparative survey of SH in multiple populations of

Table 13.1. *Comprehensive list of the 35 stone handling (SH) patterns performed by Japanese macaques at Arashiyama between 1979 and 2009, and categorised according to general activity patterns*

Category	Name (code)	Definition
Investigative activities	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	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	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)
	Clack (CL)	Clack stones together (both hands moving in a clapping gesture)
Percussive or rubbing sound-producing activities	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
	Grind with teeth (GWT)	Press and rub with a crushing noise one's teeth against a stone held in hand
	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
	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
	Swipe (SW)	Swipe stones together (both hands moving in a sweeping gesture)

Table 13.1. (*cont*.)

Category	Name (code)	Definition
Other complex manipulative activities	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)
	Wash (W)	Put a stone in water or pick up a stone from water and rub it with hands

Japanese macaques revealed substantial inter-group variation in the frequency and form of the behaviour, with a minor role of genetic determinants and environmental factors in explaining such differences (Leca *et al*., 2007c, 2008c). Instead, the geographic distribution of clear troop-dependent clusters of SH variants was 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 (Leca *et al*., 2007c). Second, longitudinal and experimental studies provided sound evidence for the role of social factors in the acquisition of the behaviour 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, such as piles of stones left on the ground by previous stone handlers (Nahallage and Huffman, 2007b; Leca *et al*., 2010b). Moreover, the pathways of intra-group diffusion of SH were in accordance with affiliated networks: the behaviour spread among social partners, along matrilineages, or within same-age classes (Huffman, 1984; Leca *et al*., 2007b, 2008b). Third, transmitted over generations, SH behaviour persists over decades within several groups of Japanese macaques, where it occurs on a regular basis (Leca *et al*., 2007c, 2010b).

13.4 What makes the Arashiyama-Kyoto troop 'special' for the study of the SH tradition?

When SH behaviour is mentioned in the primate culture literature, it is often associated with one particular location in Japan: Arashiyama, Kyoto Prefecture (e.g. Thierry, 1994, p. 98; de Waal, 2001, p. 230). However, it is not the place where SH was first noticed or reported. The very first observation of SH in Japanese macaques might have occurred around 1966 at Funakoshiyama,

Table 13.2. *The different periods of survey of stone handling at Arashiyama. MAH: Michael A. Huffman, DQ: Duane Quiatt, JBL: Jean-Baptiste Leca, NG: Noëlle Gunst*

Survey period	No. observation days	Main observers	Troop name	Troop size	No. stone handlers	% of stone handlers	No. SH patterns	Reference
Aug. 1979–Sept. 1980	170	MAH	B	243	1	0.4	4	Huffman (1984)
Nov. 1983–Jun. 1984	47	MAH	B	236	115	48.7	8	Huffman (1984)
Sept. 1984–Feb. 1985	113	MAH, DQ	B	236	142	60.2	8	Huffman and Quiatt (1986)
May–Jul. 1991	41	MAH	E	139	113	81.3	17	Huffman (1996)
May–Aug. 2004	96	JBL	E	141	131	92.9	32	Leca *et al*. (2007b, 2007c)
Jun.–Oct. 2008	66	JBL, NG	E	132	123	93.2	35	Leca *et al*. (2010a, 2010b)

Hyogo Pref. (cf. I. Narahara cited in Huffman and Hirata, 2003), and the first published study on SH was conducted at Takagoyama, Chiba Pref. (Hiraiwa, 1975). Moreover, Arashiyama is only one of the ten sites across the Japanese archipelago where SH behaviour has been observed, reported to occur or studied (Huffman and Hirata, 2003; Huffman *et al*., 2010; Leca *et al*., 2007c).

There are two reasons to account for the association between SH and Arashiyama in the public and scholars' minds. First, the initial research article written in English and providing original detailed descriptions about the conditions of appearance and initial diffusion of SH behaviour within a group of Japanese macaques was drawn from observations done at Arashiyama (cf. Huffman, 1984). Second, Arashiyama is the only study site where the prevalence of SH behaviour among individually identified group members and the diversity of SH patterns have been documented at several points in time for three decades (Figure 13.2, Table 13.2). As Perry (2006) pointed out, cultural primatology is a relatively new discipline and long-term databases that could bring a historical perspective on cultural modifications within the same populations and across multiple generations are lacking (but see Kawai *et al*., 1992; Perry *et al*., 2003; Nishida *et al*., 2009; this study for notable exceptions). In sum, Arashiyama is the first field site where a combination of longitudinal,

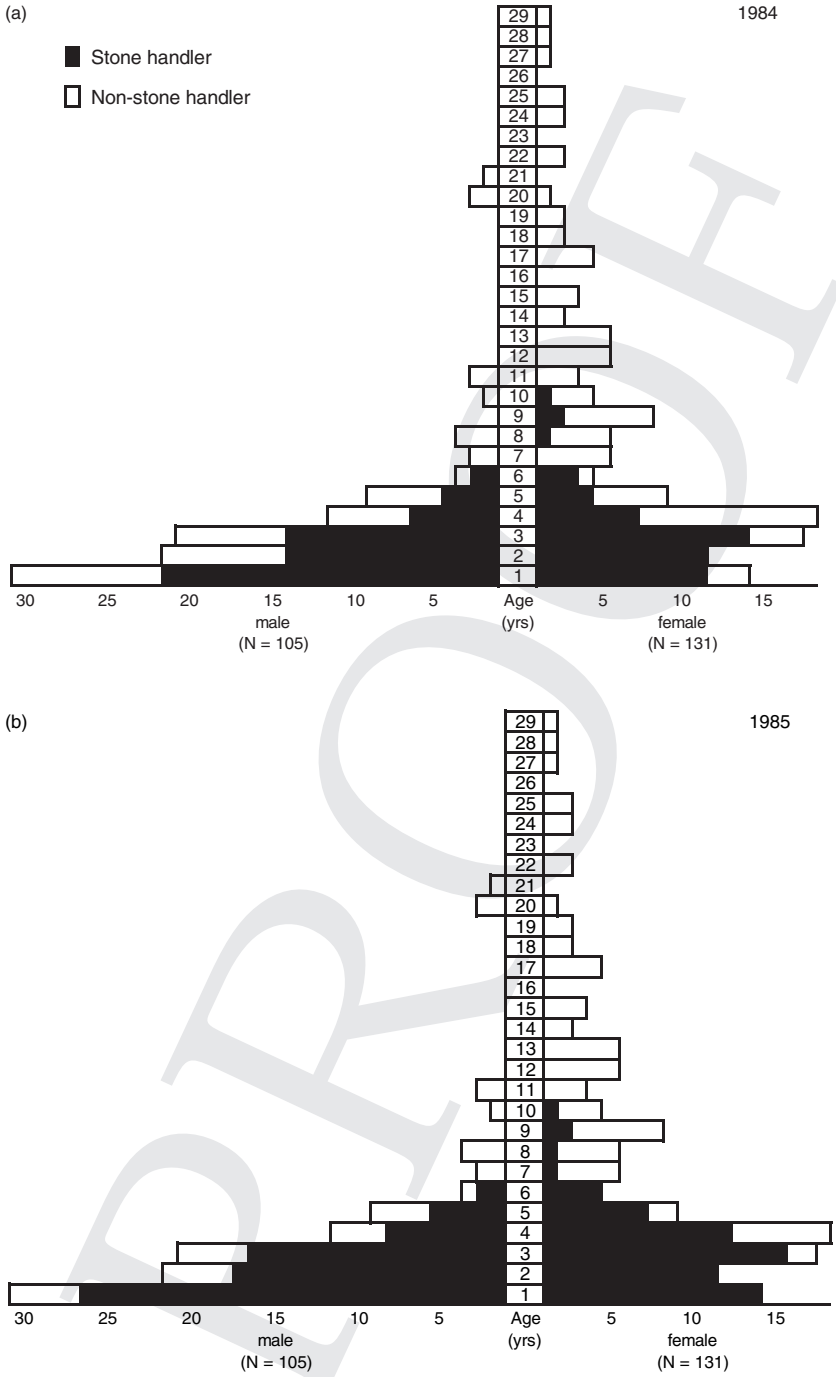

Figure 13.2. Distribution of stone handlers and non-stone handlers at Arashiyama, according to age and sex classes, and at several points in time: (a) 1984, (b) 1985, (c) 1991, (d) 2004, (e) 2008.

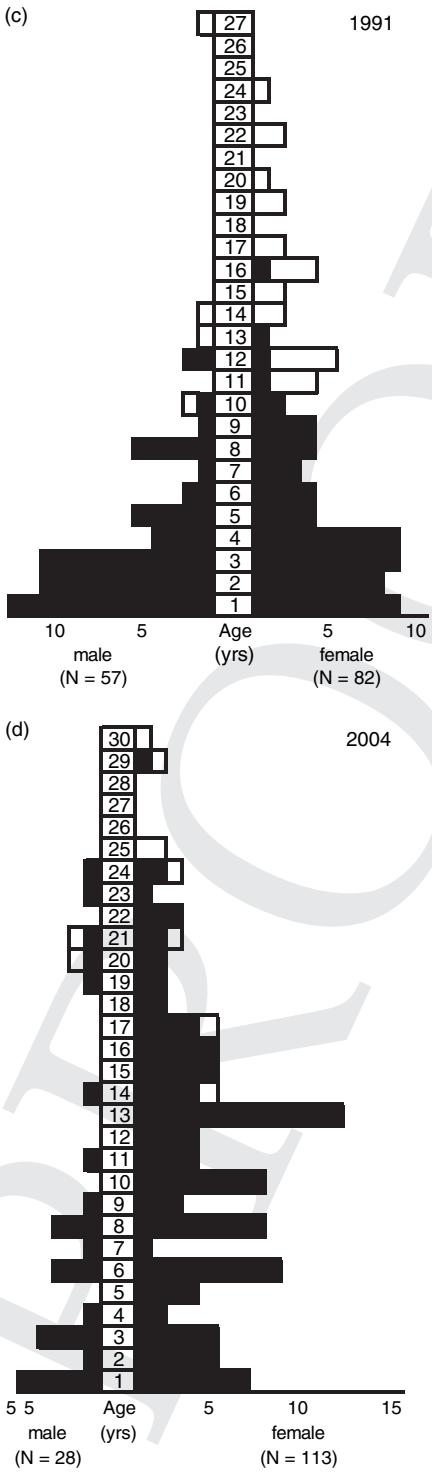

Figure 13.2. (*cont.*)

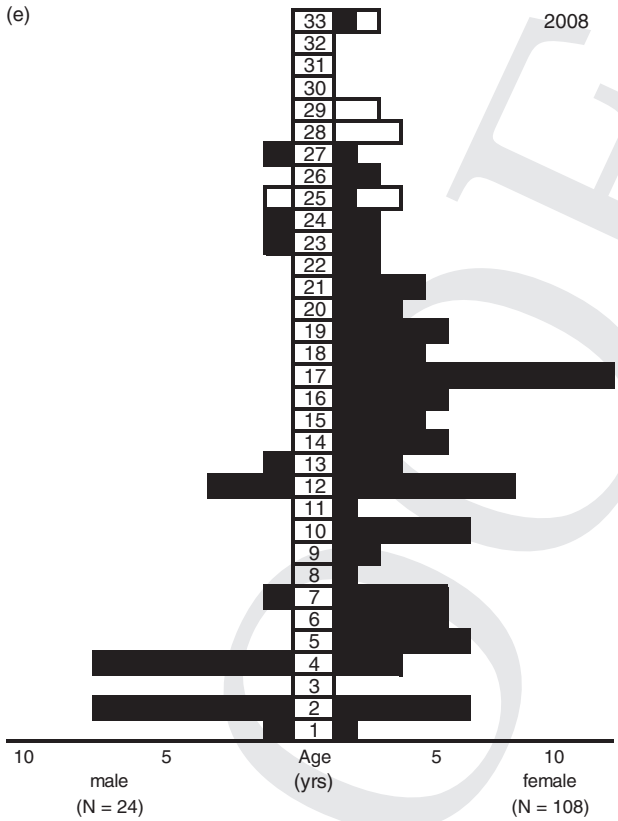

Figure 13.2. (*cont*.)

comparative and experimental approaches has provided sound evidence for the long-term maintenance, inter-troop variability and social transmission of a single cultural behaviour in Japanese macaques (reviewed in Huffman *et al*., 2010).

For the present report, we conducted long-term analyses (1979–2009) on the free-ranging provisioned troop of Japanese macaques living at the Iwatayama Monkey Park, Arashiyama, Kyoto Prefecture. In 1986, a troop fission occurred at Arashiyama, splitting the original B troop into two sister troops named E and F; from then, only E troop stayed around the provisioning area and could be surveyed (cf. Huffman, 1991). According to the survey period, the group comprised between 132 and 243 members, of all age and sex classes, and the vast majority of them were sampled for SH behaviour (Table 13.2). Individual identities, exact age and kin relations through maternal lineages were known. The study subjects could be approached and observed within

3–5 metres. Throughout the entire study, data on SH were collected by using continuous video-recorded focal-animal sampling, occasionally supplemented with instantaneous group activity scan sampling, as well as video-recorded and pen-and-paper *ad libitum* sampling (Altmann, 1974).

13.5 Early history of the SH tradition at Arashiyama: innovation and diffusion

13.5.1 Describing and explaining the origins of SH at Arashiyama

Although the Arashiyama-Kyoto troop had been studied since 1954, and despite long-term and intensive research conducted at the site by many scientists successively (cf. Huffman, 1991), SH had never been observed until 7 December 1979, when a 3-year-old middle-ranking female, called Glance-64–76, started to exhibit the behaviour (Figure 13.1; cf. Huffman, 1984). After bringing several flat stones from the forest to the open area of the provisioning site, she repeatedly gathered them into a small pile in front of herself and then scattered them about on the ground with the palms of her hands. When another monkey approached, she picked up a few stones, carried them to a nearby place, and resumed SH (Huffman, 1996). This was the only SH episode observed by MAH during the 14-month survey lasting from August 1979 to September 1980.

Like in most innovations, defined as the discovery of novel information, the emergence of new behavioural patterns, or the performance of existing behaviours in a novel context (reviewed in Kummer and Goodall, 1985; Reader and Laland, 2003), we can only speculate about the factors that may have favoured the appearance of SH at Arashiyama, including the environmental context, the structural and functional aspects of the behaviour, and the individual characteristics of the innovator. First, food provisioning has undoubtedly affected the animals' activity budget, relaxed selective pressures on foraging, and created favourable environmental conditions under which various behavioural innovations by Japanese macaques may occur (Huffman and Hirata, 2003; Leca *et al*. 2007c, 2008a, 2010c). More specifically, attracting monkeys to the open space of feeding areas, where many stones occur, increases considerably their opportunities to encounter these objects. Feeding monkeys also gives them 'free time' since they can devote less time to foraging compared with their wild counterparts.

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, non-provisioned troops of Japanese macaques at other sites (e.g. Kinkazan: Shimooka, personal communication; Yakushima: Hanya, personal

communication). In non-provisioned troops, foraging interspersed with travelling between food patches accounts for a large proportion of the daily activity budget (Hanya, 2004), and there may simply be less time available for non-subsistence activities such as SH (Huffman and Hirata, 2003; Leca *et al*., 2008a). Therefore, food provisioning is likely to enhance the chances for SH to emerge. Although at Arashiyama (and other field sites too), there is now a strong temporal relationship between SH and feeding activities, with most SH episodes occurring within 20 minutes after food was distributed, it should be noted that the SH tradition emerged several decades after the onset of provisioning in these troops (Huffman and Hirata, 2003; Leca *et al*., 2008a). 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).

Second, the general behavioural predispositions of a species make behavioural innovation relatively predictable (Huffman and Hirata, 2003). Considering the natural propensity for Japanese macaques to manipulate stones (cf. Leca *et al*., 2007c), and provided equivalent stone availability (cf. Leca *et al*., 2008c), 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 and Huffman, 2007b). Because chance may account for a good number of behavioural innovations (Reader and Laland, 2003), and SH is essentially a playful activity, we suggest that the SH innovation is an accidental by-product of object playing. Finally, individual characteristics of the SH innovator may partly account for the appearance of the novel behaviour. The fact that the first individual observed to perform SH at Arashiyama was a juvenile emphasises the playful nature of this behaviour (Huffman, 1984). Glance-64–76 might have temperamental traits that made her prone to behavioural innovation. This is consistent with previous research showing that most Japanese macaque innovators are juvenile females (Kawai, 1965; Itani and Nishimura, 1973; Kawai *et al*., 1992; Leca *et al*., 2010c).

13.5.2 Analysing the diffusion of SH at Arashiyama

During the time elapsed between the first two surveys (October 1980–October 1983), SH behaviour has spread to almost half of the Arashiyama-Kyoto troop and has become a daily occurrence (Table 13.2). Despite this 3-year gap in observation, a detailed analysis of the 1984 distribution of identified stone handlers according to age/sex classes and matrilineal membership allowed MAH to reconstruct, at least partially and a posteriori, the initial pathway of diffusion of SH within the troop (Figure 13.2; Huffman, 1984). In order to facilitate

the comparison with other behavioural traditions, Huffman and Quiatt (1986) proposed that the diffusion of innovative behaviours could be chronologically divided into two distinct stages, namely the 'transmission phase' and the 'tradition phase' (after Itani, 1958; Kawamura, 1959; Kawai, 1965).

Transmission phase

This early period of behavioural diffusion is typically similar across groups and presumably species. The first individual(s) to display a novel behaviour may do so repeatedly and persistently, which facilitates its initial transmission to a network of close spatial-interactional associates of the innovator (Huffman and Quiatt, 1986; Nishida *et al*., 2009; Leca *et al*., 2010c). According to Coussi-Korbel and Fragaszy (1995), the spatial proximity and behavioural coordination exhibited by tolerant partners are expected to enhance opportunities for social learning, and therefore, the rate and speed of behavioural diffusion should be high within these subgroups.

Previous studies of subsistence traditions involving the diffusion of food-related innovations in Japanese macaques showed that most of these behaviours initially spread among young individuals, immediately followed by the upwardly vertical transmission to older kin members and to other adults regardless of kinship (Kawai, 1965; Itani and Nishimura, 1973; Kawai *et al*., 1992; but see the special case of fish eating in Watanabe, 1989 and Leca *et al*., 2007a). In contrast, it appeared that the transmission phase of SH behaviour occurred exclusively horizontally and among a particular cohort of young individuals, mainly peer playmates, starting with the innovator's cousins (Huffman, 1984). After a few years, as the first stone handlers grew older and their social networks extended, new and younger siblings and peers became stone handlers. Unlike food-washing behaviours, as no individuals over 5 years old were seen to perform SH behaviour during the transmission phase, there would be a critical period after which SH cannot be acquired (Huffman, 1984).

Most feeding and food-washing innovations found in Japanese macaques showed a wide and rapid intra-group diffusion – it took less than 4 years for most of these novel behaviours to be transmitted to at least a second group member – probably because information about food is critical to every individual (Itani, 1958; Kawai, 1965; Azuma, 1968; Itani and Nishimura, 1973; Watanabe, 1989; Kawai *et al*., 1992; Nakamichi *et al*., 1998). Likewise, the playful nature of SH behaviour could account for its fast transmission within the Arashiyama-Kyoto troop (Huffman, 1996; Leca *et al*., 2007b). Seeing group members playing is a reliable cue for more individuals that the current environmental conditions are safe enough to engage in play (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 may increase an individual's probability to start handling stones (Leca *et al*., 2007b). 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 (synchronised occurrence) around feeding time at Arashiyama, as this is the only time when most troop members are all together in the same location (Leca *et al*., 2008a). The rapid transmission of SH at this site may also have been enhanced by local construction projects when a large number of stones were left at the edge of the feeding area (Huffman and Hirata, 2003).

Tradition phase

In this later period of diffusion, the behaviour is passed down along multigenerational lines. At Arashiyama, when the first female stone handlers reached reproductive maturity, SH was mainly acquired vertically from mothers to offspring via observational learning (Huffman, 1984, 1996; see also Nahallage and Huffman, 2007b). During the tradition phase, the rate of SH diffusion was approximately equal to the birth rate: an infant primarily learnt SH from its mother, and complementarily from an infant playmate whose mother handles stones, or from an older sibling who had learned SH from a playmate (Huffman, 1996). However, it should be noted that the mother is the primary source of an infant's early exposure to SH (Huffman, 1984, 1996; see also Nahallage and Huffman, 2007b). From 1985, all infant macaques living at Arashiyama acquired SH behaviour within their first 6 months of life and thus, the increase in the number of new stone handlers was purely a function of new births (Huffman and Quiatt, 1986).

Since 1979, SH has spread gradually within the Arashiyama-Kyoto troop and across multiple generations of all matrilineages. Cross-sectional and longitudinal analyses on a 30-year time scale allowed us to assess the rate, speed and pathways of diffusion of this behaviour (Figure 13.2; Table 13.2; see also Huffman, 1996; Huffman and Hirata, 2003). In June 1984, 48.7% of the troop exhibited SH, and by February 1985, an additional 27 individuals (i.e. 60.2% of the troop) born before June 1984 were added to the list. In 1991, 12 years after the appearance of SH at Arashiyama, the diffusion rate increased to 81.3%, and every member of F troop under the age of 10 was verified to have acquired SH (Huffman, 1996; Figure 13.2). Finally, during more recent surveys in 2004 and 2008, the percentages of stone handlers in the troop were 92.9% and 93.2%, respectively. In 2008, only nine individuals (eight females and one male) out of 132 troop members were qualified as verified non-stone handlers, i.e. they were sufficiently sampled but were not observed performing SH. They were all 25

years and older. Among them, the five youngest individuals (25–28 years old) were recorded as stone handlers in the 1991 or 2004 survey but had stopped engaging in this behaviour since then, whereas the four oldest individuals (28 years and older) had never acquired SH. At Arashiyama, as well as several other study sites, SH frequency was significantly lower in old adults than in younger troop members (Leca *et al*., 2007b; Nahallage and Huffman, 2007a).

During the tradition phase, as long as mothers continue to practice SH, and provided the initial environmental conditions (in terms of food provisioning and stone availability) prevail, this behaviour will persist in young individuals and will thus become established in the troop across generations (Huffman and Hirata, 2003). However, the case of Takagoyama – where 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) – suggests that the persistence of the cultural practice of SH may be contingent on diet and foraging circumstances (Leca *et al*., 2008a).

13.6 Cumulative transformation of the SH tradition

With a 30-year history, the SH tradition at Arashiyama has now reached its 'transformation phase', defined as the late period in which long-enduring practice with the behaviour and acquired familiarity with the properties of the stones are gained through the integration of SH with other daily activities by many age and sex classes (cf. Huffman and Quiatt, 1986; Huffman and Hirata, 2003). In 2004, we conducted a comparative survey of SH among multiple troops of Japanese macaques. We found that the Arashiyama-Kyoto troop presented a unique profile in terms of frequencies of SH patterns, i.e. its own SH tradition (Leca *et al*., 2007c). However, a longitudinal study of SH in this troop showed that the emergence of this tradition was not an overnight process. By using similar methods of data collection for three decades of continued observation at Arashiyama, we found that the monkeys have gradually increased the size and the complexity of their SH repertoire and largely diversified the contexts in which SH activity was practiced compared to earlier generations of stone handlers (Leca *et al*., 2007c, 2008a).

13.6.1 Gradual increase in the size and complexity of the SH repertoire

The first aspect of the transformation of the SH tradition is an increase in the size and complexity of the SH repertoire over a number of years, that is an accumulation across generations of stone-related behavioural diversity

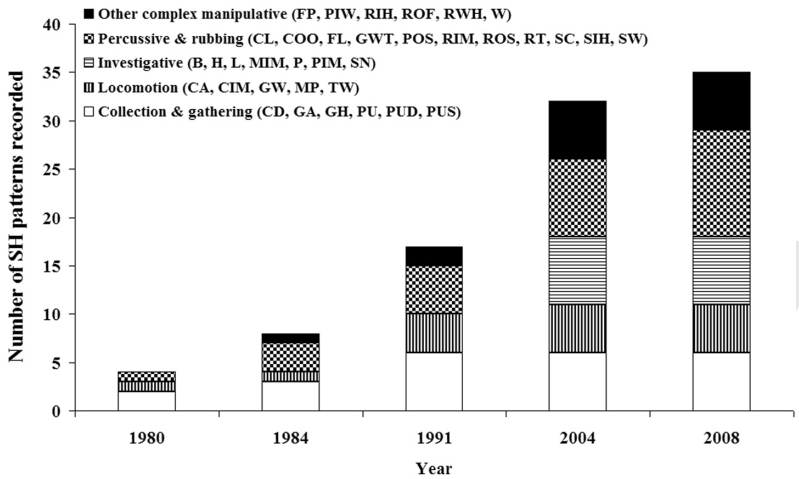

Figure 13.3. Accumulation over time and generations of stone handling (SH) patterns diversity and complexity (for categories, names and definitions of SH patterns, please see Table 13.1).

and sophistication (Figure 13.3). In 1980, the SH innovator, Glance-64–76, displayed only four SH patterns, namely *gather*, *pick up*, *scatter* and *carry*. In 1984, eight basic SH patterns were reported in the Arashiyama-Kyoto troop, including the original ones: *gather*, *pick up*, *scatter*, *carry*, *cuddle*, *roll in hands*, *rub stones together* and *clack* (Huffman, 1984). In 1991, an additional nine SH patterns were recognised – making a total of 17 patterns in the SH repertoire of the troop – with six of those patterns being obvious variations of the previous eight (*pick up and drop*, *pick up small stones*, *rub on surface*, *rub with hands*, *flint* and *grasp with hands*). The three new variants were *toss walk*, *move and push* and *grasp walk*, behavioural patterns considered to reflect an increasing familiarity with stones in general and their integration with locomotion activity, as the practice of SH spread and became a substantial part of the individual and the troop's daily activities (Huffman, 1996).

Between 1991 and 2004, the size of the SH repertoire almost doubled. During the 2004 survey, a total of 32 SH patterns were observed in the Arashiyama-Kyoto troop (Leca *et al*., 2007c). The late emergence of SH patterns not recorded before involved percussive and complex manipulative actions, such as *pound on surface*, *combine with object*, *rub/put on fur* and *wash*, revealed an increased diversity in the combination of stones with other objects or substrates (Leca *et al*., 2008a). Finally, in 2008, two new SH patterns were recorded – i.e. 34 patterns in the group SH repertoire – *grind with teeth* and *rub in mouth*, that

could be considered variations of patterns already observed in 2004, such as *bite*, *put in mouth* and *move inside mouth* (Figure 13.2; Table 13.2).

As the duration of the Arashiyama-Kyoto troop'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 troop's behavioural repertoire which gradually diffuses within the group (Huffman *et al*., 2008). Another explanation for this increase in SH diversity and complexity could be that the young individuals growing up with SH about two decades ago are now at an advanced age, and they carry on with more elaborate patterns than they showed when they were young, compared with the earliest generation of stone handlers. This is reminiscent of the accumulation of several behavioural variants of food washing (e.g. seasoning, rinsing, rubbing between hands, brushing, throwing, etc.) across generations in the troop of Japanese macaques living at Koshima (Watanabe, 1994). Changes in the frequency of cultural behavioural patterns over time and at the group level may be referred to as a 'faddish shift in the practice of certain behavioural sub-types' (Huffman and Quiatt, 1986, p. 413). In the case of SH, numerous behavioural patterns are accumulated modifications of earlier forms. For example, the recently appeared *flint* and *swipe* patterns can be considered slight variations of the original form *clack* (Leca *et al*., 2007c). Despite such accumulation, it should be noted that all the original variants were also maintained in the Arashiyama-Kyoto troop over 30 years of continued observation at this site.

13.6.2 Diversification of the contexts of SH practice

The second aspect of the transformation of the SH tradition is the expansion of the contexts in which SH is practiced, also referred to as 'mixed-activity SH'. Recently, SH was found to be integrated with social play or grooming interactions (Figure 13.1: j–k) and during inter-mount intervals taking place within the context of heterosexual and homosexual consortships (Leca, pers. obs.). In free-ranging troops where food provisioning plays a central role in the activity budget (e.g. at Arashiyama), our long-term study also revealed the integration of SH with food-related activities and the gradual emergence of food-directed SH patterns (e.g. rubbing stones and peanuts together on the ground). From 1985 to 1991, a few instances of expansion of SH practice to feeding context were reported at Arashiyama. For example, during the winter of 1985, there were two incidents of monkeys rubbing a stone on food items such as an acorn and a sweet potato (Huffman and Quiatt, 1986). However, these observations were too anecdotal to refer to them as a new SH pattern (Huffman, 1996).

By contrast, in the 2004 survey, various behavioural patterns combining provisioned and natural food items with stones (e.g. scattering stones mixed with chestnut shells on the ground, rolling a stone and pieces of peanut shell in one's hands, and the SH pattern called *combine with object*) were more frequently observed (mean = 1.3 bouts/hour of SH activity; cf. Leca *et al*., 2008a). Moreover, the recent appearance of SH variants combining the use of hands and mouth (*put in mouth*, *carry in mouth*, *move inside mouth*, *bite*, *lick*, *flint in mouth* and *rub in mouth*) suggested that SH had become more integrated with foraging and feeding activities.

The intergroup comparative study showed that 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 (Leca *et al*., 2008a). In troops frequently provisioned, the daily performance of SH was highly contingent on food provisioning: SH mainly occurred immediately after feeding on provisioned food (Huffman, 1984, 1996; Leca *et al*., 2008a). Because they are provisioned with food several times a day, Arashiyama-Kyoto troop members have 'free time on their hands', and this opportunity could lead them to further explore various objects (including stones) and incorporate them into feeding activities (Huffman and Quiatt, 1986; Leca *et al*., 2008a). Thus, food provisioning may be a key factor in the transformation phase of the SH tradition in Japanese macaques. Considering a troop's ranging conditions and its history in relation to feeding habits may be crucial in predicting the transformation phase of the SH tradition. This does not mean that a particular type of food provisioning is a necessary and sufficient condition for SH to appear and diffuse among group members. However, the way SH is practiced by most group members on a daily basis, and its integration with other activities may differ from one troop to another, depending on the type of food provisioning (Leca *et al*., 2008a).

13.6.3 Role of SH artefacts in the maintenance of the SH tradition

Recent field experiments conducted at Arashiyama 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 (Leca *et al*., 2010b). Our main goal was to investigate experimentally how the physical traces typically left in the environment by previous stone handlers (such as piles of stones left on the ground) 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. Our results supported the 'stimulus/local enhancement hypothesis' that individuals preferentially direct their SH behaviour toward typical physical traces of SH activity (piles of stones) over randomly scattered stones (Leca *et al*., 2010b). In other words, encountering SH artefacts enhanced the subsequent use of these particular stones to perform SH activity in that particular part of the environment. Therefore, we 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, through the stimulating effect of SH by-products. To some extent, our findings allowed us to reconstruct some elements of the environmental and social contexts underlying the SH culture. By supporting the view that SH is a socially influenced behaviour, this study contributes to validate the concept of SH culture (see also Huffman, 1984, 1996; Leca *et al*. 2007b, 2007c, 2008a, 2008c; Nahallage and Huffman, 2007b).

As they become more deeply ingrained into the behavioural landscape of the monkeys, these 'play stations' (sic Quiatt and 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, characterised by an increased sedentary lifestyle, with most group members staying around feeding grounds, i.e. open areas with stones (cf. Leca *et al*. 2008a, 2008c). Smaller home ranges are likely to increase individual probability to encounter 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 suggest 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 on 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.

Similar indirect social influences are likely to occur in the acquisition and maintenance of tool-use behaviours in wild chimpanzees 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; Visalberghi *et al*., 2009). 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 socio-cultural environment. For young Japanese macaques growing up in a troop where the SH tradition is well-established and has reached its transformation phase, 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 (Leca *et al*., 2010b).

13.6.4 Towards a stone-related cumulative culture in Japanese macaques?

Our results clearly show an accumulation over time and generations of SH diversity and complexity. However, in the light of the main definition of cumulative culture, which is based on the accumulation of *beneficial* modifications, this phenomenon will not be referred to as 'cumulative SH culture' because we could not demonstrate any direct benefits in the practice of SH (but see Leca *et al*., 2008b). However, the transformation phase of the SH tradition is all the more likely and flexible since SH is currently acknowledged to be a non-adaptive behaviour with no obvious survival value (Huffman, 1984, 1996; Leca *et al*., 2007c), as opposed to stone tool-use traditions for which an efficient behavioural pattern should be maintained unchanged (e.g. Sumita *et al*., 1985; Boesch, 1991). The long-term cultural transformation of the SH tradition, associated with a generational increase in the diversity and complexity of SH patterns could ultimately result in future stone-tool use, as stone-related behaviours become more deeply ingrained into the behavioural landscape of Arashiyama-Kyoto macaques at the group level (Huffman and Quiatt, 1986; Leca *et al*., 2008a).

13.7 Functional considerations: SH as a behavioural precursor to stone tool-use

13.7.1 Maintenance of a selectively neutral tradition

It has been argued that 'whether or not a particular pattern of behaviour persists obviously depends on its effects on the survival and reproductive success of its bearers' (Avital and Jablonka, 2000, p. 99). However, our findings show that even traditional behaviours with no obvious function and no apparent adaptive value, such as SH at Arashiyama, can not only be practiced on a daily basis and maintained over several decades within a large proportion of group

members, but can also be modified on the basis of a transgenerational accumulation (Huffman, 1996; Leca *et al*., 2010b; see also 'games' as social conventions in white-faced capuchins: Perry *et al*., 2003). How can we account for such a puzzling phenomenon?

Several reasons may partly explain the maintenance of the SH tradition at Arashiyama (and presumably at other sites). First, the original motivations underlying SH may be different from what they are today, both at the individual and group levels. Most Arashiyama-Kyoto monkeys observed handling stones in 2008 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 non-conforming 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 (Leca *et al*., 2008a). Individually, the immediate motivation to perform SH could be mere serendipity, as this behaviour appears to be self-rewarding (Huffman, 1984). As Avital and Jablonka (2000, p. 85) pointed out, animals may engage in 'apparently non-functional activities that seem like the luxurious by-products of extensive behavioural plasticity'. SH behaviour may also be maintained because of some internal (physiological and/or psychological) consequences that we cannot measure yet (Huffman and Hirata, 2003).

Second, although SH is not a subsistence activity, it should be noted that no SH pattern is deleterious and the SH tradition is not locally maladaptive but selectively neutral, at least under the favourable environmental conditions of food provisioning (Huffman and Hirata, 2003; Leca *et al*., 2008a). Third, 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 behavioural 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*., 2008b). By relaxing selective pressure on foraging, food provisioning has created favourable environmental conditions under which SH may simply serve the function of maintaining in some troops (such as Arashiyama-Kyoto) a set of behaviours, involving a high level of behavioural complexity and familiarity with stones, that could evolve into tool-use provided particular environmental circumstances.

13.7.2 SH as an exaptive tradition?

Can the daily performance of SH with feeding activity by Arashiyama-Kyoto macaques lead by transformation to stone-tool use in a foraging context? If

tool-use is defined as moving a detached object for the purpose of changing the condition and/or position of another object or organism (Beck, 1980), then SH behaviour as a whole and most SH patterns cannot be considered stone-tool use. However, there is a series of arguments suggesting that when practiced 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 and Quiatt, 1986; Huffman, 1996; Leca *et al*., 2008b).

First, the non-instrumental manipulation of objects, such as SH, has long been recognised as a behavioural precursor to tool-use, in terms of individual development and cross-species comparison (Beck, 1980; Huffman and Quiatt, 1986; Hayashi *et al*., 2005). Second, at several sites such as Arashiyama, the SH tradition is undergoing a phase of transformation, including an increase in the diversity and complexity of the behavioural patterns and the integration of SH with foraging activities (Leca *et al*., 2008a). Third, the occurrence of SH spots or 'play stations' revisited daily by Arashiyama-Kyoto macaques is likely to lead to an increased familiarity with SH artefacts that may result in the use of stones as tools (Huffman and Quiatt, 1986; Leca *et al*., 2010b). Fourth, although macaques are not frequent tool-users (Beck, 1980; but see Weinberg and Candland, 1981; Sinha, 1997; Leca *et al*. 2008b, 2010c), long-tailed macaques have recently been reported to display oyster-cracking behaviour with stones (Malaivijitnond *et al*., 2007). Finally, we recently witnessed a first case of tool-use probably derived from prolonged SH practice: spontaneous stone-throwing as an agonistic display (Leca *et al*., 2008b).

Therefore, although most SH patterns do not currently meet the criteria used to define tool use, we hypothesised that the long-enduring practice of stone-related combinatorial behaviours by Arashiyama-Kyoto macaques could be considered a behavioural precursor to the use of stones as tools. This scenario is 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 *et al*., 2010). As an unselected but eventually beneficial trait, the SH tradition would be an exaptation (cf. Gould and Vrba, 1982).

13.8 Conclusion and future directions

Arashiyama-Kyoto macaques largely contributed to make SH the best-known non-adaptive traditional behaviour in non-human primates. Three decades of continued observation at Arashiyama showed that the monkeys have largely

extended and diversified their SH repertoire. Our findings have important implications for understanding cumulative cultural evolution, particularly the reasons for its rarity in non-humans. Research on SH as a tool-use precursor also provides new insights into the emergence of hominid material culture through stone-tool technology. We drew an overall picture of rich cultural diversity in a particular type of object-play behaviour in macaques, and suggest that multiple factors should be jointly considered to identify the mechanisms of emergence, diffusion and maintenance of a behavioural tradition in animals.

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