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SPECIAL FEATURE: REVIEW ARTICLE

French-Japanese collaborations in primatology

A multidisciplinary view on cultural primatology: behavioral innovations and traditions in Japanese macaques

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Abstract Cultural primatology (i.e., the study of behavioral traditions in nonhuman primates as a window into the evolution of human cultural capacities) was founded in Japan by Kinji Imanishi in the early 1950s. This relatively new research area straddles different disciplines and now benefits from collaborations between Japanese and Western primatologists. In this paper, we return to the cradle of cultural primatology by revisiting our original articles on behavioral innovations and traditions in Japanese macaques. For the past 35 years, our international team of biologists, psychologists and anthropologists from Japan, France, Sri Lanka, the USA and Canada, has been taking an integrative approach to addressing the influence of environmental, sociodemographic, developmental, cognitive and behavioral constraints on the appearance, diffusion, and maintenance of behavioral traditions in *Macaca fuscata* across various domains; namely, feeding innovation, tool use, object play, and non-conceptive sex.

Keywords Cultural primatology · Innovation · Behavioral tradition · Japanese macaque

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Implications of cultural primatology: the Japanese foundations

Traditional behavioral research (including classical ethology) has focused on species-typical behavioral patterns (e.g., courtship and agonistic displays), whereas behavioral variation between groups of the same species has long been considered to be "noise" of little intrinsic interest. However, there is growing evidence for substantial geographic variation among conspecific groups of various animal taxa and in a wide range of behavioral domains. Such intergroup differences in behavior are generally explained in terms of ecological, genetic, or cultural factors, or, most likely, a combination of these causes (Foster and Endler 1999). Interestingly, group comparisons can sometimes provide clearer insights into the causes of behavioral differentiation than species comparisons, because groups (or populations) have often been separated for less time than species. Therefore, they tend to differ in fewer characteristics than species, which may allow researchers to reduce the effects of confounding variables, when tracing back possible behavioral precursors and discussing evolutionary scenarios about step-by-step changes in behavior. In sum, research on intergroup variation in behavior has key implications for our understanding of behavioral evolution and general evolutionary patterns and processes (Foster and Endler 1999).

In this regard, non-human primates are excellent study subjects, for at least two obvious reasons: (1) many primate taxa (prosimians, monkeys, and apes) exhibit high levels of intergroup behavioral diversity, and (2) their phylogenetic relatedness to humans makes them prime models for human behavioral evolution. Over the past 15 years, the systematic study of intergroup behavioral variation in non-human primates has produced valuable empirical data that

are used to test predictions and fit models generated from theories about the role of cultural processes in human evolution (van Schaik and Burkart 2011). Echoing the established discipline of cultural anthropology, this relatively new and promising field, often referred to as "cultural primatology," aims to explore the ecological, genetic, and sociodemographic influences on behavioral variation among groups or populations of a given non-human primate species, as a way to better understand the origins and evolution of human cultural capacities (Perry 2006).

However, it is noteworthy that this research area emerged in Japan in the early 1950s under the pioneering view of Kinji Imanishi. By emphasizing the social rather than genetic transmission of behavior, he was the first to predict that culture should be present in all socially living animals, and thus coined a new term, "kaluchua" (Imanishi 1952). Shortly after, field observations provided the first evidence of animal culture in the form of group-specific, socially learned feeding innovations and food processing techniques across multiple groups of Japanese macaques (Kawamura 1959), including the often-cited sweet potato and wheat washing behaviors performed by a group of Japanese macaques living on Koshima island, southern Japan (Kawai 1965).

In the subsequent decades, long-term collaborative field studies, including collaborations between Japanese and Western primatologists (e.g., Quiatt and Itani 1994; Whiten et al. 1999; Matsuzawa et al. 2001; Nakamura et al. 2000; Biro et al. 2003; Huffman and Hirata 2003; Leca et al. 2007a; Humle et al. 2009), have focused on various types of behaviors or variants of the same behavior, including feeding habits, foraging techniques, medicinal plant use, tool use, communication, courtship, grooming, and interspecific interactions, as well as object play and social play behaviors, and documented socially transmitted group-specific behavioral patterns and substantial intra-specific geographic variation in behavior in a large array of non-human primate species (reviewed Leca et al. 2007b). There is also increasing evidence for cultural abilities in non-primate taxa, including fish, birds, rodents, and cetaceans (Fragaszy and Perry 2003; Laland and Galef 2009). As predicted by Imanishi (1952), these findings further our understanding of the developmental processes, social learning mechanisms, functional significance, and cognitive evolution underlying cultural phenomena in animals and humans.

Core methodological issues in cultural primatology: the Japanese contribution

Accordingly, we will adopt a definition of culture that allows for the inter-species comparison of the cultural capabilities. If culture (also termed "behavioral tradition" by ethologists) is defined as (1) a population-specific behavioral practice, (2) persistent over time in several group members, (3) dependent on social means for its transmission and maintenance, and (4) possibly locally adaptive, then culture is certainly not limited to humans (Fragaszy and Perry 2003). Each component of this definition corresponds to a particular methodological approach to studying culture, to which Japanese primatologists have largely contributed.

For the first component, "population-specific," the intergroup comparative approach emphasizes the product, by focusing on what the animals do and don't do in the wild and the diversity within and between groups in the form of naturally expressed behaviors. In other words, cultural primatologists look for patterns of geographic variation in behavior and seek to rule out obvious genetic and ecological explanations for such differences (e.g., Whiten et al. 1999; Nakamura et al. 2000). The other three approaches emphasize the mechanism; that is, the type of processes involved in producing these differences. For the second component, "persistent over time," the developmental or longitudinal approach aims to assess whether social or individual learning is more likely to be involved in the gradual spread of a novel behavior within a group. For example, Japanese primatologists combined long-term field observations and decades of genealogical records of the Japanese macaques living on Koshima island to provide detailed information on the timing and context of acquisition of the sweet potato washing behavior by young individuals, its rate and pathways of intra-group diffusion as a function of social proximity, and its possible transformation across generations (Hirata et al. 2001). For the third component, "dependent on social means," the experimental approach aims to determine which learning processes underlie the cultural behaviors observed in the wild via the direct manipulation of physical or social environmental contexts under the controlled conditions of captive settings or during field experiments (e.g., Biro et al. 2003). For the fourth component, "locally adaptive," the functional approach aims to assess the fitness consequences of behavioral traditions by conducting cost/benefit analyses, generating models to investigate the social learning strategies of individuals, and exploring arbitrary and seemingly functionless primate cultural practice (e.g., Nakagawa et al. 2015).

Arguably, while research on behavioral innovations and traditions in non-human primates straddle different major disciplines (e.g., biology, psychology, and anthropology), it truly expands our understanding of evolutionary processes and the variety of behavioral patterns they produce. In the search for homologous traits, the striking similarities in cultural variation, mechanisms and contents between chimpanzees and humans allowed Whiten et al. (2003) to

make inferences about the cultural profiles of our common ancestor, and to coin the term "cultural panthropology." However, because the comparison of analogous traits resulting from convergent evolution is equally informative, cultural primatologists often turn to the study of behavioral traditions in primates that are more distant from us, like monkeys.

Cultured Japanese macaques and our international multidisciplinary team of cultural primatologists

In this paper, we return to the cradle of cultural primatology by revisiting our original articles on behavioral innovations and traditions in Japanese macaques. For the past 35 years, our international team of biologists, psychologists and anthropologists from Japan, France, Sri Lanka, USA and Canada, with each member bringing his/her own cultural and scholarly background and perspective, has been taking an integrative approach to addressing the influence of environmental, sociodemographic, developmental, cognitive and behavioral constraints on the appearance, diffusion, and maintenance of behavioral traditions in *Macaca fuscata*. The bulk of our previous research has addressed the mechanisms that underpin adaptive, questionably adaptive, and non-adaptive cultural behaviors in this primate species. To do so, we combined intergroup comparative approaches, intra-group cross-sectional and longitudinal studies, and field experiments.

First, we investigated how socio-ecological features may constrain the long-term maintenance of a particular feeding innovation—fish-eating behavior—in a free-ranging group of Japanese macaques living on Koshima island, southern Japan (Leca et al. 2007a). We documented a seldom-observed event of fish-eating, involving a new fish food species for these monkeys. Following the discovery of a large beached sea bass by a peripheral male (Fig. 1a), we observed a total of 16 individuals feeding on the fish in turns, and interacting around it. The rank order of access to the fish was mainly explained by the spatial position of group members, whereas dominance determined how long the fish was monopolized. Although limited, the tolerated presence of close bystanders while feeding was affected by kinship and affiliation. We examined the complex ecological and social conditions under which a feeding innovation and its subsequent propagation may occur in natural populations of Japanese macaques. We also assessed the long-term diffusion and maintenance of the fish-eating habit in Koshima monkeys by updating an existing genealogy of lineages of fish eaters recorded on the island. Genealogical data suggested that fish-eating behavior was well maintained in terms of maternal lineages. This study contributed to a better understanding of the various factors facilitating and those limiting the appearance and maintenance of feeding innovations in wild primate groups (Leca et al. 2007a).

Second, we discussed the determinants of a particular tool-use innovation—dental flossing behavior—and the constraints on its social transmission in the free-ranging group of Japanese macaques living at Arashiyama, central Japan (Leca et al. 2010a; Leca 2012). This behavior, consisting of using hair as dental floss, had never been reported in Japanese macaques before. So far, it is idiosyncratic, i.e., performed by only one individual at Arashiyama: an adult female named Chonpe-69-85-94. Among the three different techniques she used to floss her teeth, the "plucking" technique consisted of pulling out her own hair with one hand, holding the hair horizontally by grasping and pulling the tips of the hair between the thumb and forefinger of both hands, taking the hair to the mouth, and inserting the hair between the front teeth by performing repeated teeth-chattering (Fig. 1b). Because chance may account for a good number of behavioral innovations, and dental flossing was always associated with grooming activity, we suggested that the dental flossing innovation was an accidental by-product of grooming. We also argued that dominance relationships may restrict the expression of this innovation and a limited kinship network around the innovator may limit the opportunities to learn this behavior by observation. Finally, we suggested that dental flossing was less likely to spread within the group than other tool use innovations, because (1) it was not conspicuous enough to be reliably noticed and learnt by naive group members, and (2) like most other "comfort innovations," the window of applicability of this behavior was narrow and its adaptive value was questionable (Leca et al. 2010a; Leca 2012).

Third, we drew an overall picture of rich cultural diversity in a particular type of playful activity in Japanese macaques—stone handling (SH) behavior—by considering both the product and the mechanisms of this intriguing behavioral tradition. SH is a form of solitary object play consisting of the non-instrumental manipulation of stones by performing various behavioral patterns, such as gathering stones into a pile, rubbing stones together (Fig. 1c), or repeatedly pounding a stone on a substrate. The systematic analysis of a total of 4530 observation hours, including 2460 h of video-recorded data collected from 12 groups of Japanese macaques in which SH occurred—three captive groups held at the Kyoto University Primate Research Institute, Inuyama, and nine free-ranging groups from six field sites, namely Tsubaki, Arashiyama, Funakoshiyama, Shodoshima, Takasakiyama, and Koshima—allowed us (1) to establish the comprehensive repertoire of 45 SH patterns in this species, (2) to reveal substantial intergroup variation in the frequency, form, and context of

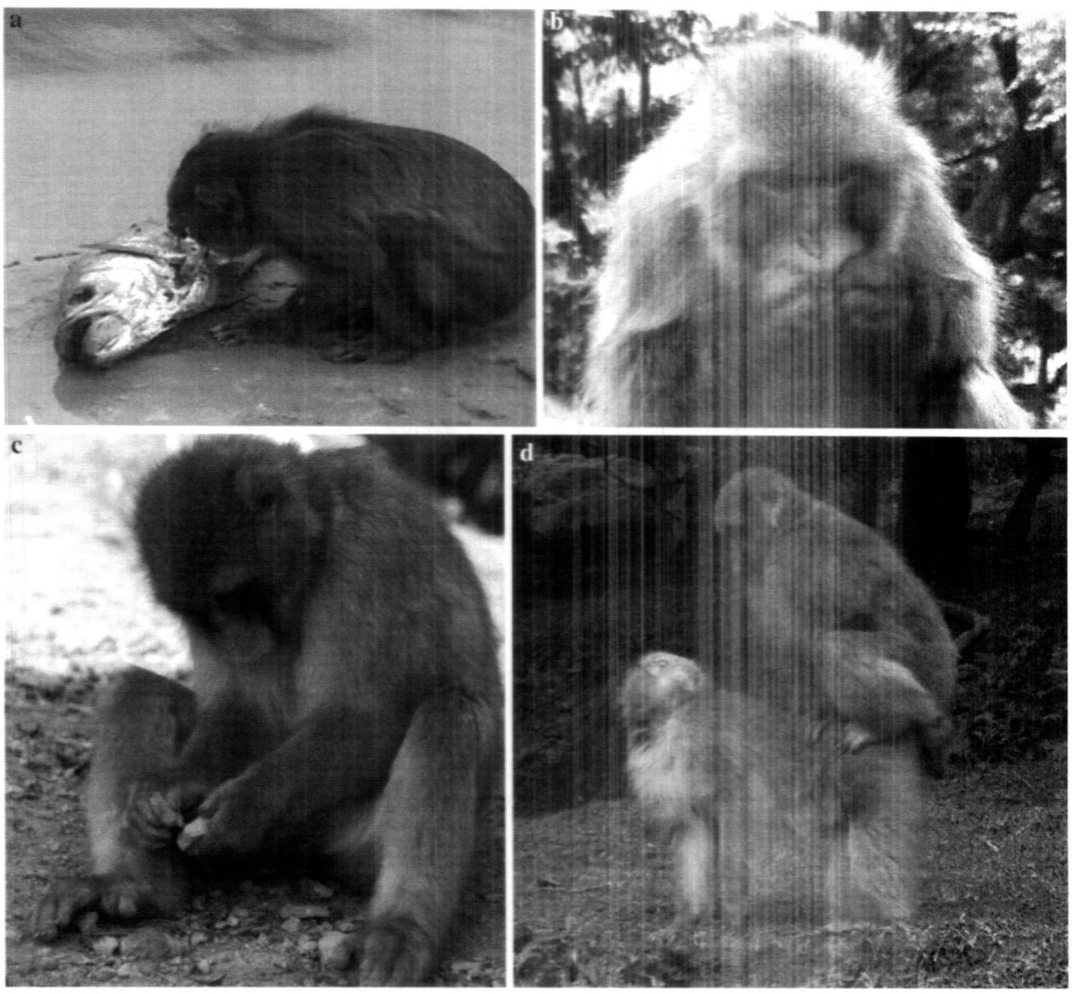

Fig. 1 Four examples of behavioral innovations and traditions in Japanese macaques: **a** fish-eating (Koshima), **b** dental flossing (Arashiyama), **c** stone handling (Funakoshiyama), and **d** female–female mounting (Arashiyama). Photos by Jean-Baptiste Leca

SH behavior, (3) to rule out simple alternative explanations for such behavioral variability, such as genetic determinants or obvious environmental differences like stone availability, (4) to show similarities in SH profiles among neighboring groups, referred to as cultural zones, possibly resulting from intergroup observation or males transferring SH patterns when migrating from one group to another, (5) to indicate that group size and composition in age classes, as well as group spatial cohesion may impact the prevalence of SH, (6) to demonstrate that direct and indirect social influences (via observational learning and behavioral artefacts, respectively) enhanced the acquisition of SH behavior and the maintenance of the tradition, (7) to document the transformation of the SH tradition across generations, with an increase in SH diversity and complexity, and an expansion of the contexts in which SH is practiced, also arguably referred to as "cumulative culture," (8) to hypothesize that a lifetime of sustained SH practice could contribute to slowing down the impairment of sensorimotor skills associated with advanced age, and (9) to suggest that under relaxed selective pressures on foraging, SH may simply serve the function of maintaining in some populations a set of behaviors that could evolve into tool-use (Huffman 1984; Huffman and Quiatt 1986; Leca et al. 2007b, c, 2008a, b, c, 2010b, 2011, 2012; Nahallage and Huffman 2007a, b). SH is arguably the longest studied and best-documented cultural behavior in monkeys to date.

Fourth, our intergroup comparative study of non-conceptive sexual behavior in female Japanese macaques suggested that some intergroup differences in the frequency and form of female-male and female–female mounting (Fig. 1d) could be associated with cultural practices that arise in groups when certain sociodemographic conditions are met. Indeed, we found that female-male and female–female mounting were more frequent and more diverse in groups with few resident males, most of them being old, sexually under-motivated, and less aggressive/controlling than the typical male Japanese

macaques. Although genetic explanations could not be ruled out, we suggested that arbitrary behavioral patterns such as intergroup differences in female mounting postures could be purely cultural, as any alternative explanation is difficult to imagine (Leca et al. 2014).

Taken together, our findings are consistent with the view that culture is more than a group-specific acquisition of new behavioral techniques. It is also about identification and bonding. As nicely phrased by Imanishi (1952, cited in Nakamura and Nishida 2006): "A group does not split into individuals because of *kaluchua*."

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