15 Box *Dental flossing behaviour as a grooming-related innovation by a Japanese macaque*

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15 Box.1 Evolutionary significance of animal innovation

Innovation is typically defined as the discovery of novel information, the emergence of new behavioural patterns or the performance of established behaviours in a novel context (Reader and Laland, 2003). Various animal taxa – including fish, birds, rodents and non-human primates – are known to innovate in a wide range of behavioural domains such as travel routes, song acoustic patterns, food selection, food-processing techniques, agonistic display and tool use (see Reader and Laland, 2003 for a review).

In many ways, innovation is related to cultural diversity and evolution. First, when a novel behavioural practice, initially invented by an individual – the innovator – spreads to other group members, and is dependent on social means for its diffusion and maintenance, it becomes a tradition (Fragaszy and Perry, 2003). Second, similar factors may affect the likelihood of innovation and subsequent propagation within a group, including individual attributes, social relationships, group size and structural, contextual and functional aspects of the new behaviour (Huffman and Hirata, 2003). Third, several comparative research programmes linked innovation rate, cultural transmission and the relative size of brain associative areas in birds and primates (Lefebvre *et al*., 2004). Therefore, investigating the determinants of the spontaneous appearance of new behavioural patterns in non-human animals, and particularly tool-use innovations, is of special interest to understanding the evolution of material culture in hominids (cf. McGrew, 1992).

However, little is known about the initial process by which novel behavioural patterns emerge spontaneously (but see Kummer and Goodall, 1985; Huffman and Hirata, 2003 for a few notable exceptions). It is not clear whether innovators are exceptionally creative individuals, subjects with a particular motivational state, or individuals that simply adjust their behavioural responses to novel,

appropriate or stressful environmental circumstances. Despite its significance to a broad range of research disciplines, the topic of behavioural innovation in animals is widely neglected in the evolutionary literature (Sol, 2003).

15 Box.2 Tool-use innovations in non-human primates

A multitude of tool-use innovations have been reported in the primate literature. Wild chimpanzees (*Pan troglodytes*) are known to innovate at a relatively high rate in the domain of spontaneous tool-use (sensu Beck, 1980), including aimed object throwing as an agonistic display, leaf-clipping as a courtship display and leaf-spooning/folding/sponging as ways to get access to water sources located in the hollows of trees (see Nishida *et al*., 2009 for a review). Health maintenance, a sub-division of self-medicative behaviour (Huffman, 2007), in the form of the use of twigs as 'toothpicks' has been reported in great apes, including chimpanzees (McGrew and Tutin, 1973), bonobos, *Pan paniscus* (Ingmanson, 1996) and orang-utans, *Pongo pygmaeus* (Russon *et al*., 2009). Although macaques are not frequent tool-users (Beck, 1980; but see Malaivijitnond *et al*., 2007; Leca *et al*., 2008a), dental flossing behaviour has been reported in long-tailed macaques, *Macaca fascicularis* (Watanabe *et al*., 2007). The spontaneous use of tools in hygienic contexts, such as stones in allo-grooming and sticks as vaginal probes, has been occasionally reported in this genus (Weinberg and Candland, 1981; Sinha, 1997).

Despite the numerous examples of socially transmitted tool use innovations in several non-human primate species, it should be noted that only a subset of such innovations becomes traditions. Many new tool-use behaviours have been reported to appear in primate troops, but were either idiosyncratic, or independently adopted by very few individuals, or their performance was restricted to a small class of the population, and for some reason, they never widely spread within the group by social means, and disappeared after the death of their few performers (Nishida *et al*., 2009).

However, the role of the importance of these behaviours to the performers themselves in the likelihood to innovate has received little attention (Kummer and Goodall, 1985). Surprisingly, few attempts have been made to address the factors that could favour or constrain the spontaneous appearance of novel tool use patterns (Reader and Laland, 2003). As Huffman (1996) pointed out, it is critical to know the history of a behavioural innovation in order to assess how environmental factors and social influences may enhance or limit its propagation within a group.

15 Box.3 Dental flossing behaviour as a tool-use and grooming-related innovation

In an effort to encourage the compilation of relevant data on the determinants of tool use innovations in non-human primates, I report the first case of dental flossing (DF) behaviour in Japanese macaques (*Macaca fuscata*). From June to October 2008, I collected video-recorded focal data on a 14-year-old middle-ranking female (named Chonpe-69–85–94, hereafter 'the innovator') living in the free-ranging Arashiyama E troop of at the Iwatayama Monkey Park, Arashiyama, Kyoto. I systematically documented her frequent and spontaneous use of hair as dental floss to remove food remains stuck between her teeth, and I examined the initial conditions that may have favoured this tool-use innovation (cf. Leca *et al*., 2010).

I distinguished three different DF techniques or variants. First, the 'stretching with mouth' technique consisted of stretching its own hair or another individual's hair by clenching its lips onto the basal part of the hair, inserting the hair between the front teeth by slightly pulling its head downwards, and pulling the head backwards while gradually moving the lips to the distal end of the hair and performing repeated teeth-chattering. Second, the 'stretching with hand' technique consisted of stretching its own hair or another individual's hair by grasping and pulling the tip(s) of the hair between the thumb and forefinger of one hand, moving the mouth to the hair, and inserting the hair between the front teeth by performing repeated teeth-chattering (Figure 15 Box.1a). Third, the 'plucking' technique consisted of pulling out its own hair with one hand, holding the hair horizontally by grasping and pulling the tips of the hair between the thumb and forefinger of both hands, taking the hair to the mouth, and inserting the hair between the front teeth by performing repeated teeth-chattering (Figure 15 Box.1b).

The innovator's dependence on this form of tool use was shown by the fact that in all DF episodes, she used hair to floss her teeth and never used her fingers alone. Although DF may serve to remove food remains stuck between the teeth, there was no significant difference in the DF frequency between post-feeding and non-feeding focals. Regarding the context of occurrence, the DF behaviour was always associated with self- or allo-grooming activity.

15 Box.4 Determinants of the dental flossing innovation

Because they are provisioned with food several times a day, Arashiyama E troop members have 'free time on their hands', and this environmental opportunity

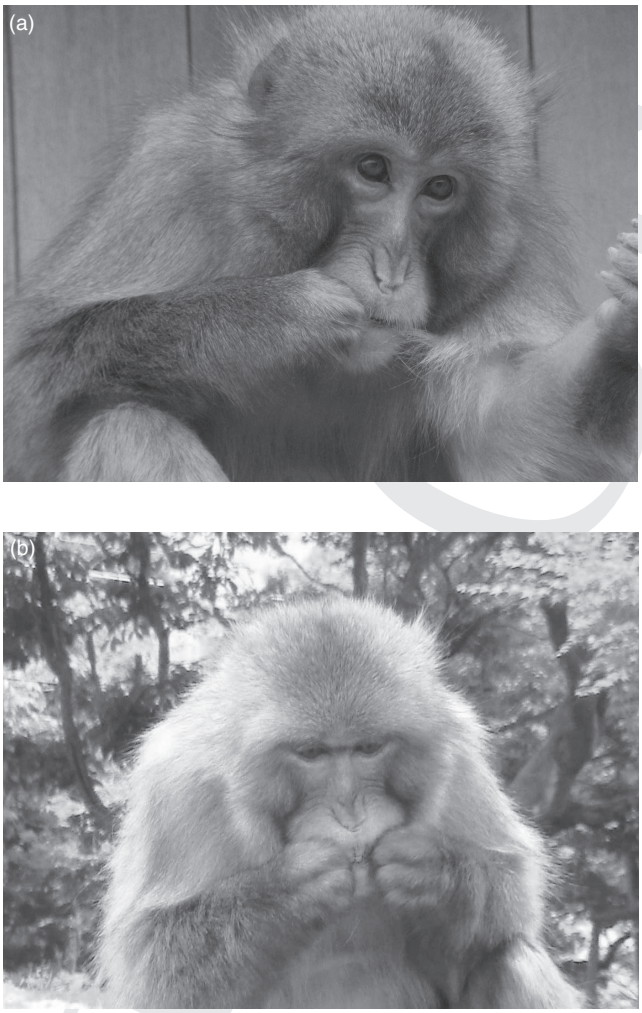

Figure 15 Box.1. Chonpe-69–85–94 performing two dental flossing techniques: (a) 'Stretching with hand' technique during self-grooming; (b) 'Plucking' technique (photos by J.-B. Leca).

could lead them to further explore various objects and incorporate them into feeding activities (Leca *et al*., 2008b). These artificial conditions are likely to enhance the appearance of food-related tool use, such as the use of dental floss. Provisioning has relaxed selective pressures on foraging, and created favourable environmental conditions under which various behavioural innovations by Japanese macaques may occur (Leca *et al*., 2007c, 2008c).

Since DF is always grooming-related, the behaviour is more likely to appear in frequent groomers, i.e. central group members, than in individuals less involved in grooming interactions, i.e. peripheral group members (cf. Nakamichi and Shizawa, 2003). Thus, it is not surprising that the innovator was a central individual. As an adult female, the current age of the innovator was consistent with most studies, whereas the sex was not. It has been found that innovators were more frequently males and adults than females and non-adults (see Reader and Laland, 2001 for a review). However, previous observations suggest that the innovator may have started performing the DF behaviour from the age of 2 years (Zamma, pers. comm.). This is consistent with previous research showing that most Japanese macaque innovators are juvenile females (Itani and Nishimura, 1973; Huffman, 1984; Kawai *et al*., 1992).

Finally, Chonpe-69–85–94 might have temperamental traits that made her prone to behavioural innovation. Despite extensive observation of most troop members in a study of stone-handling behaviour, she has been the only individual observed repeatedly rolling small stones on the palm of her hand while intensively grooming her palm and presumably trying to remove a spine stuck into it (Leca, pers. obs.). This first report in Japanese macaques on an apparent attempt to use stones in a health-maintenance context is suggestive of a generally inventive temperament. Sinha (2005) suggested the role of temperament in bipedal begging innovation by bonnet macaques (*Macaca radiata*).

Since chance may account for a good number of behavioural innovations (Reader and Laland, 2003), and DF was always associated with grooming activity, we suggest that the DF innovation is an accidental by-product of grooming. Thus, the following is a reasonable scenario: during regular grooming episodes, Japanese macaques sometimes bite into hair or pull it through their mouths to remove external parasites, such as louse eggs (Tanaka and Takefushi, 1993). Due to particular anatomical constraints such as diastema (i.e. gaps between incisors), pieces of hair may accidentally have stuck between the innovator's teeth, and as she drew them out, she may have noticed the presence of food remains attached to them. The immediate reward consisting of licking the food remains off the hair may have encouraged her to repeat the behaviour for the same effect in the future, by actively inserting the hair between her teeth.

Therefore, the DF innovation could be a transformation of grooming patterns via the running of hair between the teeth to remove louse eggs. These scenarios are consistent with the 'perception-action' perspective on the development of tool use and foraging competence in monkeys, apes and humans, postulating that skilled actions are acquired through the routine generation of species-typical exploratory actions, coupled with learning about the outcomes and affordances of each action that generates directly perceptible information (Lockman, 2000).

Besides possible proximate causes, the problem arises about why the DF behaviour has been maintained by its innovator for several years. A first parsimonious explanation for this behaviour is that the flosser may simply enjoy the interaction between the hair and its teeth, and apparent pleasurable feedback potentially gained from the activity may be an immediate reinforcement (cf. Leca *et al*., 2007b). Second, DF could alleviate the possible physical annoyance caused by a piece of food stuck between the teeth. A third beneficial consequence of DF could be an improvement in the teeth condition. Flossing one's teeth would be a form of health maintenance, which is considered a level of self-medication (Huffman, 2007). Since all self-medicative behaviours are driven by some quest for comfort, these interpretations are congruent with the classification of the tooth-pick behaviour in orang-utans as a 'comfort innovation' (Russon *et al*., 2009). Since DF was not more frequent in post-feeding than non-feeding periods, we doubt that the DF innovation had a significant or even any survival value, through the very small amount of extra food the flosser can obtain from its behaviour.

15 Box.5 A scenario for the emergence of new dental-flossing variants

Although the present data did not allow us to accurately determine the order of appearance of the different DF techniques, past observations and a comparative analysis of the behavioural patterns support the view that the 'plucking' technique was acquired later than the two other DF variants. First, previous long-term behavioural observations of this group showed that Chonpe-69–85–94 had been using the 'stretching with hand' and the 'stretching with mouth' techniques for at least four years (Leca, unpublished data; Vasey, pers. comm.; Zamma, pers. comm.). Although the 'plucking' technique was not noticed before 2008, its absence remains speculative. Second, several elements show a higher level of complexity in the 'plucking' technique relative to the two other variants: (1) the former consists in the manipulation of a detached object (pluck hair) whereas hair is attached to the skin in the latter, (2) the former requires both hands to be used whereas only one hand is used in the latter, (3) hair selection was more frequent in the former than in the latter, and (4) since the former necessitates hair to be pulled out, it is more invasive than the latter.

Likewise, the 'stretching with hand' technique, that requires the use of hand and mouth can be considered more complex, in terms of sequence of actions, than the 'stretching with mouth' technique, in which only the mouth is used. Although we cannot determine the exact timeline, we propose the following order in the emergence of DF techniques: first the 'stretching with mouth' technique, then the 'stretching with hand' technique, and last the 'plucking'

technique. In long-tailed macaques, there was a generalisation of the DF behaviour with hair to the use of coconut-shell fibres for the same purpose (Watanabe *et al*., 2007). In Japanese macaques, even non-instrumental object manipulation can undergo a major 'transformation' process over time, with an increase in the diversity and complexity of the behavioural patterns exhibited (Leca *et al*., 2007a, 2008a).

This is one of the rare studies to document the spontaneous appearance of tool-use behaviour in Japanese macaques under natural conditions (see also Leca *et al*., 2008a). The lack of report on DF in other troops of Japanese macaques and the idiosyncratic presence of the behaviour in this troop may reflect possible intra- and inter-troop variations in (1) the likelihood of behavioural innovation, (2) the social constraints on the early dissemination and long-term maintenance of such inventions and (3) appropriate social and/or environmental reinforcement for the emergence, propagation and continued practice of this behaviour. When a behaviour is restricted to one or very few group members, it is likely to disappear at the group level (Leca *et al*., 2007c; Nishida *et al*., 2009). Further investigation, including experimentally elicited DF, may help to determine more accurately the conditions of appearance of this novel behaviour, and to elucidate why it has not spread within the group (cf. Watanabe *et al*., 2007; Leca *et al*., 2008a).

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