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## **Social learning and Culture in Monkeys**

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### Abstract

The first report of cultural behaviour in primates - potato-washing described in Japanese macaques - was the starter point for 70 years of investigation of social learning in wild animals and has laid the foundations of animal culture studies. In this chapter, we review key findings now accumulated for many different monkey species and using a wide array of methodologies including observations in the wild, controlled experiments in captivity, and field experiments. Both observational and experimental approaches highlight the existence of technical, feeding, and social traditions in monkeys. Recent advances in modelling techniques enable a better understanding of when social learning is used and if the pathways of transmission follow specific biases such as payoff bias, conformity or learning from specific group members like higher-ranked or successful individuals. Technologies including environmental DNA metabarcoding, GPS loggers and artificial intelligence are promising new tools in evidencing group-level differences. Combining all these examples, we illustrate the diversity of cultural behaviour found in monkeys, confirming the saying 'monkey see, monkey do'!

Key words: technical traditions; feeding traditions; social traditions; social learning experiments, learning biases, behavioural observations

## Introduction

In September 1953, on Koshima island in Japan, Satsuo Mito, the research assistant of the primatologist Kinji Imanishi from Kyoto University, witnesses a behavioural innovation that will soon become a great discovery. A young female Japanese macaque (*Macaca fuscata*), named Imo, took a sandy sweet potato and washed off the sand using water from a stream (see Rawlings & Reader, this volume, for further discussion of innovation). At this time, researchers were provisioning Japanese macaques with food on the beach in order to facilitate observation. More excitingly, this new behaviour spread to others gradually, within three months to two of Imo's playmates as well as her mother, and within four years, to other juveniles and their mothers. In a second phase of propagation, the behaviour spread from mothers to offspring, and nine years later 73.4% of monkeys above two years old displayed the habit, leading today to a deeply anchored behavioural tradition on Koshima island (Fig. 1A). Imanishi and his students, Kawamura and Kawai, described and studied the propagation of this 'newly-acquired pre-cultural behaviour' in detail (Kawai, 1965), laying the foundation of animal culture studies at a time when genetic transmission of animal behaviour was a predominant assumption (de Waal, 2003).

The study of animal cultures has received considerable attention over the last several decades, in part because it helps us to better understand what makes our human culture so unique. More precisely, it sheds new light on the evolutionary origins and the specific selection pressures that drove social learning strategies. Debates have revolved around how to define culture, what kinds of social learning mechanisms are involved and how best to interpret behavioural traditions. Social learning, defined as "learning facilitated by observation of, or interaction with, another individual (or its products)" (Heyes, 1994; Hoppitt & Laland, 2013), has aroused particular interest because it is considered as the basis for traditions and culture (see Wild & Hoppitt, this volume). A tradition has been defined as "a behavioral practice that is relatively enduring (i.e., is performed repeatedly over a period of time), that is shared among two or more members of a group, and that depends in part on socially aided learning for its generation in new practitioners" (Fragaszy & Perry, 2003, p12). We adopt here the definition of culture given by Laland & Hoppitt (2003, p151), "cultures are those group-typical behavior patterns shared by members of a community that rely on socially learned and transmitted information". Accordingly, a culture may be composed of several traditions (for further discussion see Schuppli & Lokuciejewski, this volume).

Cultural behaviours have been described in a great variety of animal species (Whiten, 2021) including local dialects in song birds (Marler & Tamura, 1964), tool use in crows (Holzhaidner et al., 2010), hunting

techniques in whales (Rendell & Whitehead, 2001) and in many primate species where numerous social conventions, extractive foraging techniques and manipulation behaviours have been reported (spider monkeys: Santorelli et al., 2011a; Japanese macaques: Leca et al., 2007, capuchins: Perry et al., 2003, orangutans: van Schaik et al., 2003, chimpanzees: Whiten et al., 1999; gorillas: Robbins et al., 2016; see other chapters in the Animal Cultures section of this volume). Most of the cultural behaviours documented in monkeys have been evidenced through long-term field observations. For example, the “group-contrasts method” compared the behavioural repertoire of different groups in which different innovations could have happened and socially spread while the “method of exclusion” attributed behavioural differences to social transmission only if they could not be explained by genetic or ecological differences (Hoppitt & Laland, 2013). However, experiments such as transmission chain studies and diffusion studies in captive settings and, more recently, in the wild, greatly contributed to our understanding of implied social learning biases – what, when and from whom to learn (see Kendal & Watson, this volume) - and mechanisms underlying how to learn. Such studies revealed surprising parallels with the social learning of humans. In this chapter, we i) provide an overview of cultural behaviours – technical, foraging and social - discovered through long-term observations; ii) present results from social learning experiments, both in captivity and in the wild, and iii) summarize suggested future directions for monkey culture studies.

### Long-term observations revealed cultural behaviours

#### *Material and technical traditions*

The most prominent evidence of primate culture is provided by behavioural variations involving tool use between chimpanzee groups reviewed in a seminal paper by Whiten and colleagues in 1999 (Whiten et al., 1999; see Whiten, this volume). Five years later, habitual tool use was also reported in wild capuchins (Fragaszy et al., 2004; Moura & Lee, 2004) making chimpanzees not the only primates renowned for their material culture. We adopt here Beck’s definition of tool use as “the external employment of an unattached environmental object to alter more efficiently the form, position or condition of another object, another organism, or the user itself” (Beck, 1980). Bearded capuchins (*Sapajus libidinosus*; Fig. 1B), yellow-breasted capuchins (*Sapajus xantosternos*) and, more recently, white-faced capuchins (*Cebus capucinus*) are the main capuchin species known to use stone tools in the wild to crack open nuts (Barrett et al., 2018; Canale et al., 2009; Fragaszy et al., 2004; Moura & Lee,

2004). Reports of tool use by wild capuchins mainly come from studies of two populations of bearded capuchins in north-eastern Brazil, Piauí State: one in Fazenda Boa Vista (FBV: Fragaszy et al., 2004) and one in the Serra da Capivara National Park (SCNP: Moura & Lee, 2004). Bearded capuchins at FBV use as hammers stones that weigh almost as much as themselves (Spagnoletti et al., 2011) to open resistant palm nuts and softer cashew nuts (Fragaszy et al., 2004; Spagnoletti et al., 2011). Compared to FBV, capuchins at SCNP exhibit an enhanced tool kit, using stones not only to crack hard-shelled nuts but also as digging tools to access roots and tubers. They also use sticks as probing tools to access insects, honey or vertebrate prey (Mannu & Ottoni, 2009). Evidence for social learning in tool use comes from observations of semi-wild capuchins at the Tietê Ecological Park, São Paulo, Brazil, where observers preferentially watch the more skilled nutcrackers (Ottoni et al., 2005). Young capuchins do not simply observe socially close partners during nut-cracking events but bias their attention towards older, proficient and dominant individuals (Coelho et al., 2015).

Capuchins are not the only monkeys that use tools to process encased food. The first report of long-tailed macaques (*Macaca fascicularis*) using stone tools to open oysters dates from 134 years ago (Carpenter, 1887). This behaviour has been later described in long-tailed macaques living on several islands within Laem Son National Park (Malaivijitnond et al., 2007; Gumert et al., 2009) and Khao Sam Roi Yot National Park in Thailand (Tan et al., 2015; Luncz et al., 2017; Tan, 2017). Long-tailed macaques use two different forms of hammering to crack molluscs: axe hammering and pound hammering (Fig. 1C). Axe hammers consist of stone tools used to open oysters that cannot be moved from the substrate they attach to such as boulders, while pound hammers consist of other stone tools used to crack unattached foods such as crabs or seashells (Tan et al., 2015). Different action patterns in tool use techniques along with frequency of use have been reported between the different troops inhabiting the two national parks (Tan et al., 2015). While these differences might be explained by availability of prey in each habitat (Tan et al., 2015), some macaques select smaller stones to prey on the same species, and this is not explained by available stone tools on each island (Luncz et al., 2017). Tool use develops over several years and young macaques first display simple manipulations that become more complex and combinatory over time (Tan, 2017). Young macaques stay in proximity to tool users, and especially older tool users, giving them opportunities for social learning (Tan et al., 2018).

The longest studied and best documented cultural behaviour in monkeys is stone handling (Fig. 1D) in captive and free-ranging Japanese macaques (Huffman, 1984, 1996; Leca et al., 2007). First reports of stone handling were described only in infants and juveniles in Takagoyama Prefectural Natural Park

(Hiraiwa, 1975) and in the Arashiyama troop at the Iwatayama Natural Park in Japan (Huffman, 1984) and reported later in adults as well as in nine other geographically isolated troops across Japan (Leca et al., 2007; Nahallage & Huffman, 2007). Stone handling was innovated by a juvenile female and then spread to young relatives and playmates, the behaviour being transmitted later to younger individuals as these individuals aged (Huffman, 1984). Forty-five different stone handling patterns have been described and classified into five categories according to their motor patterns: 1) investigative activities (e.g. cradle one stone for a few seconds), 2) locomotive activities (e.g. carry a stone cuddled in one's hand from one place to another), 3) collecting and gathering activities (e.g. gather stones into a pile in front of oneself), 4) sound-producing activities (e.g. clack stones together) and 5) manipulation of stones together with other objects (e.g. wrap stones in leaves; groom somebody with a stone). No single individual in the troops exhibited all 45 behavioural variants and some were specific only to juveniles or adults (Nahallage & Huffman, 2007). Stone handling seems to be a cultural behaviour since there are significantly greater similarities in stone handling patterns within troops compared to between troops (Leca et al., 2007). Inter-troop variability in the form of stone handling does not appear to be explained by ecological factors since stones and substrates are available at all sites. Moreover, genetic determinants are unlikely to account for the observed inter-troop variability in the form of stone handling because different subspecies display the behaviours.

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Insert Figure 1 about here

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#### *Foraging and feeding traditions*

The sweet potato washing behaviour observed in 1953 in Japanese macaques did not spread randomly to every group member but through a specific transmission pattern. For monkeys that were born before 1956, the propagation of the behaviour occurred through playmates' relations and through kinship. More precisely, the transmission occurred from youngster to mother and, within kinship, from younger to older brothers and sisters. However, none of the older males acquired this behaviour. For infants that were born after 1958, sweet potato washing behaviour was accepted as a normal feeding behaviour, naturally spreading from mothers to infants (Kawai, 1965). These two stages of transmission, where first the juveniles are usually the most interested individuals, and sometimes the innovators, and second where the adults are the most proficient individuals, have later been reported for stone handling in

Japanese macaques and nut-cracking in capuchins (Huffman, 1996; Coelho et al., 2015). The Koshima troop displayed another 'cultural behaviour': wheat-washing behaviour consisting of throwing grains of wheat into water to separate the grains from sand, also innovated by Imo. This followed the same transmission pathways as sweet potato washing behaviour (Kawai, 1965). In the same troop, adult males started to eat raw fish in 1979 and the habit spread through most of the group over the next 6 years with dominant adult females as vectors, and juveniles learning it last (Watanabe, 1989).

Researchers working at three geographically close and ecologically similar field sites in Costa Rica; Lomas Barbudal Biological Reserve, Palo Verde National Park and Santa Rosa National Park, investigated potential foraging traditions in white faced capuchins (Panger et al., 2002). They found that of the 61 overlapping foods, 20 were processed differently by capuchins across sites. Most of the processing differences involved differences in manipulative behaviour – “object-use” behaviour (e.g. pounding or rubbing an object against a fixed substrate; fulcrum use), tool-use (e.g. “leaf-wrap” against a fixed substrate) and other manipulative behaviours (e.g. tap fingertips against an object; “army ant following” to catch insects; Panger et al., 2002). Another survey documented behavioural variation in spider monkeys (*Ateles geoffroyi*) at five long-term field sites: Barro Colorado Island in Panama, Corcovado National Park and Santa Rosa National Park in Costa Rica, Runaway Creek Nature Reserve in Belize and Punta Laguna Reserve in Mexico (Santorelli et al., 2011a). The authors used the method of exclusion in a similar way as previously done with chimpanzees (Whiten et al., 1999). The authors classified each behaviour as customary, habitual, present or absent due to ecological explanation, or unknown. They found that 22 behaviours out of 62 showed variation in their occurrence across the study sites, that had no ecological explanation. Seven of these behaviours were food-related behaviours and consisted in consuming specific fruits, leaves, caterpillars and their larvae, mushrooms or rocks. Four other behaviours were related to water (e.g. drink from waterhole, lick water off palm; Santorelli et al., 2011a). The same team tested for differences in the proportional use of behavioural variants across three of these communities (two neighbouring communities in Punta Laguna Reserve in Mexico and one in Santa Rosa National Park in Costa Rica) in a follow-up study (Santorelli et al., 2011b). They reported that one community in Mexico and one community in Costa Rica preferentially extracted fruits with their hands rather than mouths in contrast to the second community in Mexico, suggesting that this preference might be maintained by social learning (Santorelli et al., 2011b). Similarly, our team studied the diet composition of six neighbouring groups of vervet monkeys (*Chlorocebus pygerythrus*) with strong gene flow between groups which all lived under similar ecological contexts at Loskop Dam Nature Reserve, in South Africa (Tournier et al., 2014). Although differences in tree diet composition between

groups were strongly linked to differences in the local abundance of tree species, some differences were not explicable by habitat and availability variables measured, suggesting socially learned preferences (Tournier et al., 2014).

### *Social traditions*

In the early 1980s, some males of a troop of olive baboons (*Papio anubis*) living in the Masai Mara Reserve in Kenya started to exploit a garbage dump at a tourist lodge. Those males were the most aggressive and least socially affiliated to the troop. In 1983, an outbreak of bovine tuberculosis, due to contaminated meat in the garbage dump, occurred and resulted in the deaths of all the males of the troop that foraged in the dump (Sapolsky & Share, 2004). The female-to-male ratio in the troop shifted in favour of females and the remaining adult males were particularly affiliative and unaggressive. The adolescent males of the troop along with new immigrant males adopted this pacific social style that persisted for decades and remains a key example of culture transmission of social behaviour in primates (Sapolsky, 2006).

Another famous example of social traditions is found in white-faced capuchins. Perry and collaborators (2003) described five social conventions found across 13 social groups over 13 years at four field sites, ecologically similar and geographically close, in Costa Rica. One of these social conventions is “hand-sniffing” consisting of an individual taking the hand or feet of another individual and deeply inhaling (Fig. 1E) and/or sticking a finger up their nose or in their mouth. Another convention consists of sucking some body parts of another individual for a lengthy period of time. White-faced capuchins are also involved in different kinds of games, putting their fingers in the mouth of another individual (finger-in-mouth game), biting hair from each other (hair game) and pulling non-food objects from each other’s mouth (toy game). The hypothesis is that such social conventions are used by capuchins to test the quality of their relationships. The authors found that some conventions were present at some field sites and not at others and that some of them were invented in identical form at multiple disconnected field sites, suggesting that they were socially transmitted (Perry et al., 2003). Another comparative study across 11 groups of white-faced capuchins from three field sites in Costa Rica reported variation in interspecific interactions between capuchins and other species across sites (Rose et al. 2003). The authors reported variation in interactions with prey species, with potential predators, competitors and with other monkey species including howler and spider monkeys. As an example, Lomas Barbudal capuchins encounter



squirrels less often than Santa Rosa capuchins but are more likely to hunt and kill them by biting the squirrel's head or neck. Capuchins from only one group, out of four studied groups at one site, have been observed grooming spider monkeys, suggesting this habit may be socially transmitted (Rose et al. 2003). In another species of capuchin, the bearded capuchin monkey, females have been observed to throw stones at males during sexual displays, in only one of two studied groups in Serra da Capivara, Brazil (Falótico & Ottoni, 2013). This courtship behaviour, restricted to only one group in the wild, although observed in captive females (Mucury Filho et al., 2021), and with an increasing number of females performing it, invites researchers to assume social learning plays an important role in its transmission (Falótico & Ottoni, 2013).

Social traditions have also been reported in spider monkeys. On average, 57% of the traditions identified by Santorelli and collaborators (2011a) were in the social domain, maybe because the fission-fusion dynamics of this species, in which individuals split and merge into sub-groups of varying composition, make social behaviour variants linked to community identity important. The authors notably reported different kinds of greetings with the greeting variant "kiss" being absent in one population and habitual in two others (Santorelli et al., 2011a; 2011b). The behaviour "rub with *Ficus* root" is performed by several individuals in only one community and only two populations out of five groom individuals from another species (Santorelli et al., 2011a).

There is also some evidence in howler monkeys. Briseño-Jaramillo and collaborators (2015) observed for the first time a communication signal not yet reported in any howler monkey species in Palenque National Park in Mexico. Some adult and sub-adult males placed one hand in front of their mouths while vocalizing, a behaviour they called 'hand-front-mouth'. Nineteen groups of black howler monkeys (*Alouatta pigra*) have been observed in three different geographical areas in Mexico: Palenque National Park, Palenque fragmented forest and Yucatan peninsula, and only a subset of the groups, geographically close to each other, produced hand-front-mouth behaviour. Individuals in six of the eight Palenque National Park groups and in one of the seven studied groups in the Palenque fragmented forest displayed hand-front-mouth behaviour while none did so in captive groups in the Yucatan peninsula. This behaviour, reported only in geographically close groups, which may therefore share hand-front-mouth knowledgeable migrants, and are more genetically dissimilar than more distant groups, has been qualified as a tradition (Briseño-Jaramillo et al., 2015).

Recently, a population-specific interaction with humans has been reported in free-ranging long-tailed macaques living around the Uluwatu Temple in Bali, Indonesia (Leca et al., 2021). These long-tailed

macaques spontaneously engage in token-mediated bartering interactions with humans after having stolen objects such as glasses, hats, or bags from temple visitors (Fig. 1F). The macaques have been observed using the stolen objects as tokens by returning them to tourists in exchange for food rewards provided by the temple staff. This behaviour is suspected to be cultural as it has not been observed in other Balinese temples, and it has been established in this population for at least 30 years (Brotcorne et al. 2017; Leca et al., 2021).

### Controlled experiments confirm social learning and claims for culture in wild monkeys

In parallel to long-term field observations, many social learning experiments have reported evidence of social learning in various monkey species, supporting the conclusion that monkeys are able to transmit knowledge via cultural transmission. Initially, primatologists conducted social learning experiments with captive individuals, particularly chimpanzees (see Whiten, this volume), but later also on different monkey species. These experiments consisted initially of dyadic designs (i.e. trained individual A is isolated and tested with naïve individual B; Voelkl & Huber, 2000), then of transmission chains (i.e. trained individual A is paired with naïve individual B, individual B is then paired with naïve individual C and so on; Dindo et al., 2008), and finally at the group level with seeded models (van de Waal et al., 2013a) or open diffusion paradigms with no trained demonstrator (Canteloup et al., 2020; see Mesoudi, this volume, and Wild & Hoppitt, for further information on such experimental methods). It is only during the last decade that researchers adapted such methodologies used in captivity to test wild monkeys. By contrast with the concentration of captive work on apes, monkeys have been studied more frequently in field experiments than chimpanzees or other great apes, mainly due to their non-endangered status and less neophobic nature. Here, we first describe experiments testing for the occurrence of social learning and the mechanisms involved (ranging from low-fidelity social learning mechanisms such as enhancement to high-fidelity social learning such as imitation or emulation; see Wild & Hoppitt, this volume), and then present examples of experiments on social learning biases (see Kendal & Watson, this volume), testing when, what and from whom monkeys learn socially.

A first social learning experiment investigated if social style in macaques was socially learnt (de Waal & Johanowicz, 1993). The researchers conducted a co-housing experiment with mixed groups of juvenile rhesus macaques (*Macaca mulatta*), a despotic species, housed with stump-tail macaques (*Macaca arctoides*), a more tolerant species. This study reported an increase of reconciliation after fights as an

apparent result of the exposure of juvenile rhesus monkeys to a more conciliatory model species, the stumptail macaque.

Later on, the experimental paradigms used to test for the mechanisms involved in social learning were mainly 'artificial fruits' (i.e. a puzzle box with alternative solutions to open it to retrieve a food reward designed for experiments initially with chimpanzees and humans (Whiten et al., 1996)). This method has the advantage that a model can easily be trained on one solution while the other one is blocked, thus introducing different seeded techniques into several study groups. In an experiment testing dyads of captive common marmosets (*Callithrix jacchus*), Voelkl and Huber (2000) showed that the subjects would match manual *versus* oral techniques they had observed models use to remove film canister lids to gain access to the food inside. Using the same setup with captive vervet monkeys, we tested four groups with one model trained to open the artificial fruit in each group (van de Waal and Whiten, 2012). Most individuals used the mouth to open the fruit, but in a group with a model showing manual opening, this method spread to be more common and, in a group using a cord to pull the 'fruit' apart, this spread likewise. Using a novel foraging task, sufficiently challenging that only just over half of brown capuchins (*Cebus apella*) tested successfully gained food from it, researchers compared the performance of participants working either alone, or in a social condition (Dindo et al., 2009). When participants could observe an actively feeding conspecific in an adjacent chamber, their latency to solve the task was threefold reduced, thus revealing social learning in this dyadic context. To test social diffusion of behaviour, researchers conducted a transmission chain study with captive brown capuchins using a pull-slide artificial fruit (Dindo et al., 2008). They found that each method was transmitted along the respective chains with high fidelity, echoing similar results that were available then only for chimpanzees and children.

Recently, new types of transmission experiments were conducted using touchscreen technology along chains in captive guinea baboons (*Papio papio*) (Claidière et al., 2014). Using a fully automated experimental station, baboons interacted freely with computers. Previous transmission chain studies showed that cultural transmission can lead to the progressive emergence of systematically structured behaviours in humans (Kirby et al., 2008). Based on this work, researchers used a pattern reproduction task using pixels on touchscreens to develop transmission chains in baboons. They implemented an iterated learning procedure, in which the behavioural output of one individual, meaning the four squares touched on a grid containing 16 squares and during a set of 50 grids, became the target behaviour for the next individual. They found that baboons exhibited three fundamental aspects of

human cumulative cultural evolution: a progressive increase in performance, the emergence of systematic structure and the presence of lineage specificity (Claidière et al., 2014; see further discussion in Caldwell, this volume). In another transmission chain experiment run with the same population of captive baboons, individuals observed and produced visual patterns composed of four squares on touchscreen devices (Saldana et al., 2019). To be rewarded, monkeys had to avoid touching squares that were touched by the previous participant (i.e. they were rewarded for innovation rather than copying). Results revealed fundamental properties of cumulative culture: i) an increase over generations in task performance, and ii) emergence of systematic structure. Interestingly, high-fidelity social learning was not necessary for the emergence of this cumulative culture.

Most social learning experiments conducted on monkeys were conducted at the group-level with a trained model. Researchers found evidence for socially learned behaviour in group-seeded artificial fruit experiments in one species of Catarrhini monkey, vervet monkeys (van de Waal et al., 2010, 2013a, 2015; Bono et al., 2018) and in different Platyrrhini monkey species (common marmosets: Gunhold et al. 2014a, 2014b; squirrel monkeys (*Saimiri boliviensis*): Hopper et al., 2013; brown capuchins: Crast et al., 2010). Although it is not entirely within the scope of our chapter, it is relevant to report that more distantly related primates, lemurs, also learned socially in similar field experiment set-ups (ring-tailed lemurs (*Lemur catta*): Kendal et al., 2010; redfronted lemurs (*Eulemur rufifrons*): Schnoell and Fitchel, 2012). Another type of group-level social learning paradigm is open-diffusion, where no models are trained to solve the task. This enables researchers to observe who innovates and how the knowledge spreads in the group. Many groups of different zoo-housed callitrichids species were tested with an open-diffusion setup using multiple two-action foraging tasks, the findings were ambiguous with only some of the experiments highlighting innovation socially transmitted through the group (Day et al. 2003, Kendal et al. 2007, 2009). Dean and colleagues (2012) used this method with an artificial fruit with three escalating levels of difficulty, each rewarded to test for cumulative problem solving in capuchins, chimpanzees and humans. The success of the children, but not of the chimpanzees or capuchins, in reaching higher-level solutions was strongly associated with a package of sociocognitive processes (notably teaching, imitation and prosocial behaviour) that were observed only in humans. A recent open-diffusion experiment with free-ranging Barbary macaques revealed that in a complex foraging task, they employed a social learning strategy of copying the most successful demonstrator observed (Garcia-Nisa et al. 2023).

In the wild, we conducted two open-diffusion experiments with vervet monkeys: one involving an artificial fruit (Fig. 2A; Canteloup et al., 2020) and one involving a novel food needing to be extracted (peanuts in shells: Canteloup et al., 2021). We analysed data from these experiments with two different modelling approaches: Network Based Diffusion Analysis (Fig. 3; NBDA: Hoppitt, 2017) for the artificial fruit experiment and Experience Weighted Attraction Models (EWA: Barrett et al., 2017) for the peanut experiment (see Wild & Hoppitt, this volume, for discussion of these methods). While NBDA allows us to test only for the acquisition of a new behaviour, EWA analyses the whole behavioural sequence, i.e. the acquisition and the maintenance of behavioural preferences. Both techniques simultaneously test for different transmission pathways which represent social learning biases (eg. age bias), assessing the weight of each. In both cases, we found that vervet monkeys socially learnt how to access the reward. All the above-mentioned experiments were foraging tasks involving a food reward and social learning paradigms in other contexts remain rare in primatology. Nevertheless, a very nice example concerns dialects that are socially learnt during the co-housing of common marmosets of different origins (Zürcher et al., 2019).

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Insert Figure 2 about here

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The focus of social learning experiments on monkeys has shifted from mechanisms to biases. Now that it is known that many monkeys do learn socially, researchers have focused their investigations more on when and from whom cultural transmission happens, and what traits are transmitted. These strategies appear to vary during the ontogeny of primates, with a first phase of infants commonly learning exclusively from their mother (known as vertical transmission), then juveniles widening their attention to other group members, and a final phase happening after dispersal with immigrants learning from residents, or residents learning from immigrants (Whiten and van de Waal, 2018). Field experiments on vervets have revealed vertical social learning of foraging techniques (van de Waal et al., 2012, 2014) and foraging choice (van de Waal et al., 2013b). Beyond vertical transmission, experiments have revealed different context-based social learning biases such as learning from central individuals in squirrel monkeys (Claidière et al., 2013), from high-ranking individuals (Canteloup et al., 2020; 2021) in vervets; but also the importance of the content and context of actions, with experiments showing payoff biased learning (capuchins: Barrett et al., 2017; vervets: Bono et al., 2018, Canteloup et al., 2021; see further

discussion in Kendal & Watson, this volume). Considering dispersal, immigrant vervet monkeys conformed to local food preferences (van de Waal et al., 2014b) but were also the vector of novel foraging habits (Dongre et al., preprint). The variability and complexity of these findings, often revealing multiple social learning biases within a species and even within the same experiment (Bono et al., 2018; Canteloup et al., 2021) highlight the need to replicate the experiments in more populations, taking into account the different classes of individuals (age, sex, rank, kinship) and developing more tasks in non-foraging contexts.

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Insert Figure 3 about here

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### Perspectives & Conclusion

To understand more about monkey social behaviour, we urge researchers to continue long-term field observations as it is the only way to explore the persistence over time of the cultural behaviours exhibited. We also encourage primatologists to start long term field sites on other monkey species as currently capuchins, macaques and vervets are overrepresented in studies. We also wish to highlight the importance of studying multiple neighbouring groups of the same study population, as it enables researchers to set aside the environmental and genetic variables influencing behavioural variation and thus better deduce whether the observed variation is cultural or not (van de Waal, 2018). Concerning social learning experiments, there is still a need for replication studies to increase sample sizes as well as to validate the findings, and it will be important to conduct them on a broader array of species.

Researchers should consider collaborative projects such as ManyPrimates (ManyPrimates et al., 2019; 2020) to conduct comparative studies and reach a powerful sample size. Furthermore, new modelling approaches (Network Based Diffusion Analysis: Hoppitt, 2017, Experience Weighted Attraction models: Barrett et al., 2017; see Wild & Hoppitt, this volume) are promising in uncovering social learning biases and transmission pathways of new behaviours and should be more widely used. Finally, the rise of novel technologies opens totally new perspectives for primatological research. For example, using DNA metabarcoding data allows more fine-grained analysis of diet variation (Taberlet et al., 2012; Brun, 2019; Brun et al., 2022, Schneider et al. 2023), biologgers with voice recorders (Fig. 2B) will enable researchers to discover if wild monkeys have dialects, camera traps at nutting trees combined with artificial intelligence facial recognition should offer new avenues to observe transmission of nutcracking

behaviour in wild capuchins, and touchscreen technology (Fig. 2C) will offer more control over field experiments. The field of cultural primatology is already vibrant; but we believe that much remains to be discovered. It is important that conservation efforts enable us to protect wild monkeys, their cultures, and their environments for many more generations (Brakes et al., 2019; see Greggor, this volume and Gruber, this volume).

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## Figure legends

Figure 1. Illustrations of some traditional behaviours in monkeys: A) Potato-washing behaviour in Japanese macaques on Koshima island in Japan. Picture credit: Lucie Rigaiil. B) nut-cracking in bearded capuchins at the EthosCebus project in Brazil. Picture credit: Elisabetta Visalberghi. C) axe hammering in long-tailed macaques in Thailand. Picture credit: Amanda Tan. D) stone handling in mother and infant Japanese macaques at Arashiyama in Japan. Picture credit: Jean-Baptiste Leca. E) hand-sniffing in white-faced capuchins in Costa Rica. Picture credit: Chelsea Holman copyright of the Lomas Barbudal Monkey Project. F) robbing-bartering interaction between long-tailed macaques and human staff at the Uluwatu Temple in Bali. Picture credit: Axel Michels.

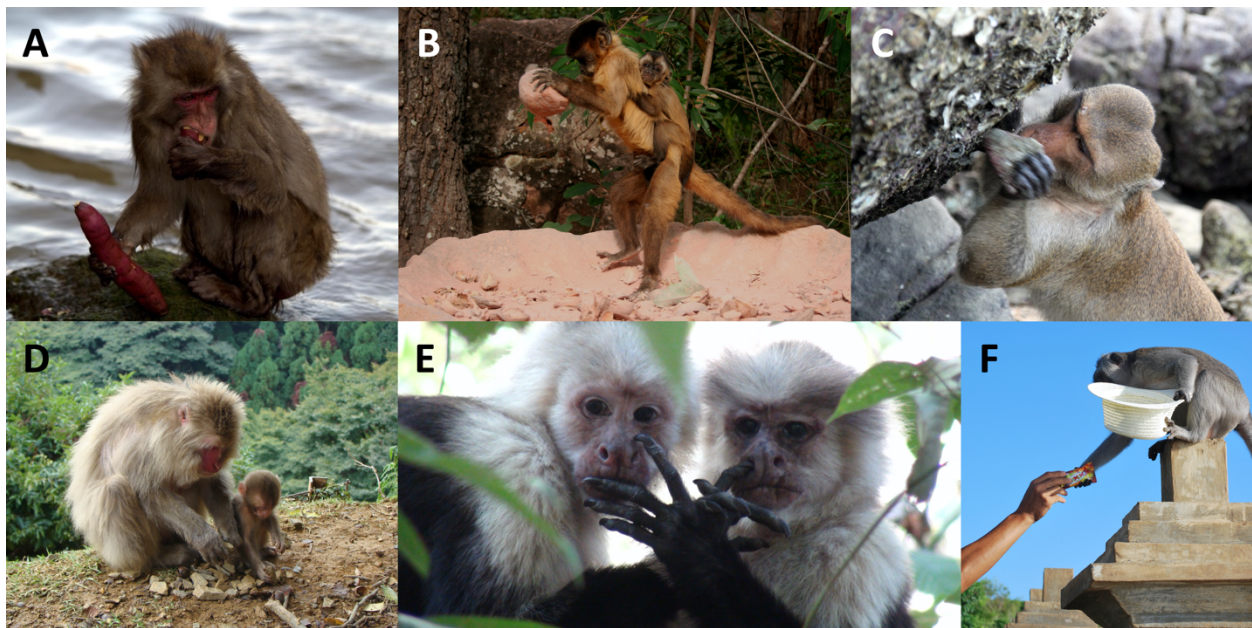


Figure 2. A) vervet monkey using the 'lift' technique to open the artificial fruit used in the Canteloup et al. (2020) open diffusion experiment. Picture credit: Charlotte Canteloup. B) vervet monkey with a biollogger. Picture credit: Morgane Alvino. C) vervet monkey using a touchscreen in a cognitive experiment in the field. Picture credit: Erica van de Waal.

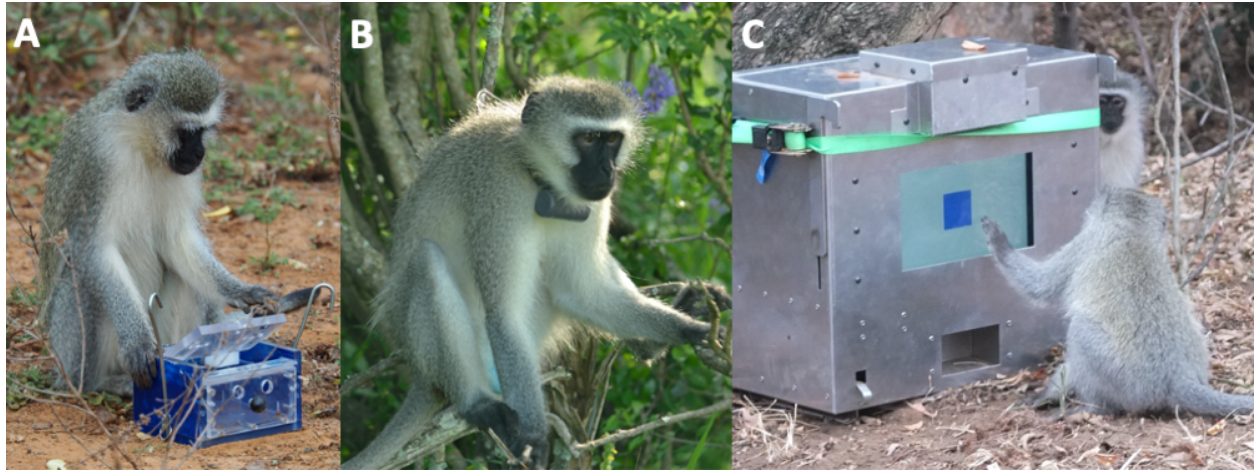


Figure 3. Social network depicting the transmission pathway of box opening techniques in Noha group from Canteloup et al. (2020). Each node (circle) represents an individual labeled by its social rank (1= highest rank; written in red for females and yellow for males). Dark blue nodes represent higher-ranked individuals while light blue nodes represent lower-ranked individuals. Numbers above the nodes, written in bold black italic underlined correspond to the order of acquisition of the ‘pull’ technique, while the other numbers correspond to the order of acquisition of the ‘lift’ technique. The larger the node, the earlier an individual learnt the task. Edges (connecting lines) between individuals represent the average rate of observation of an individual by another while naïve. The arrow signifies the direction of the observation. The thicker the edge is, the greater the average rate of observation is. Redrawn from data in Canteloup et al. (2020).

