



Memory, transmission and persistence of alternative foraging techniques in wild common marmosets

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Experimental studies on traditions in animals have focused almost entirely on the initial transmission phase in captive populations. We conducted an open diffusion field experiment with 13 groups of wild common marmosets, *Callithrix jacchus*. Seven groups contained individuals that were already familiar with the task ('push or pull' box) and thus served as potential models for naïve individuals. Additionally, in four groups one individual was trained for one of the two possible techniques and in two control groups no skilled individuals were present. First, we investigated whether experienced individuals would remember how to solve the task even after 2 years without exposure and whether they would still prefer their learned technique. Second, we tested whether naïve individuals would learn socially from their skilled family members and, more importantly, whether they would use the same technique. Third, we conducted several test blocks to see whether the individual and/or group behaviour would persist over time. Our results show that wild common marmosets were able to memorize, learn socially and maintain preferences of foraging techniques. This field experiment thus reveals a promising approach to studying social learning in the wild and provides the basis for long-term studies on tradition formation.

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One of the defining features of human societies is the sophistication in social information transmission, resulting in the accumulation of behavioural traditions and its adaptive modification over time (Tomasello, Carpenter, Call, Behne, & Moll, 2005). Representing a nongenetic inheritance system, this form of social or cultural information transmission has major evolutionary implications (Whiten, 2005): it not only allows the rapid spread of adaptive information through groups, but may also modify selective pressures acting on populations and therefore may influence genetic evolution (Boyd & Richerson, 1985, 2005; Laland, Odling-Smee, & Feldman, 2000).

In the last few decades, several nonhuman animals have been found to be capable of socially transmitting information (Galef, 1976; Heyes, 1994; Laland, 2004; Price & Whiten, 2012; Whiten & Mesoudi, 2008). The first block of findings come from laboratory studies, using a dyadic setting in which one trained model demonstrates a specific behaviour and a single naïve individual (usually termed observer) is allowed to watch, and learn, from the demonstrations (Bugnyar & Huber, 1997; Campbell, Heyes, & Goldsmith, 1999; Galef, Manzig, &

Field, 1986; Heyes & Dawson, 1990; Voelkl & Huber, 2000). The focus of these studies is centred on differentiating between possible underlying learning mechanisms, such as enhancement, observational conditioning, imitation or emulation. More recently, studies have tested directly for information transmission in captive social groups by seeding alternative behavioural patterns in different subgroups and observing the spread of these patterns (Bonnie, Horner, Whiten, & de Waal, 2007; Crast, Hardy, & Frigaszy, 2010; Dindo, Whiten, & de Waal, 2009; Hopper et al., 2007; Whiten et al., 2007). Although these studies experimentally show the formation of traditions, they are constrained by various factors of captivity and only roughly simulate the species' social structure under field conditions (Galef, 2004; Kendal, Galef, & van Schaik, 2010).

Field studies using the 'ethnographic approach' on nonhuman animals show population differences in various contexts that are considered to be independent of genetic and ecological influences (Leca, Huffman, & Gunst, 2007; Ottoni & Izar, 2008; Perry et al., 2003; Rendell & Whitehead, 2001; van Schaik et al., 2003; Whiten et al., 1999). However, since the origin of these differences is often unclear, it is difficult to determine the role of social learning in establishing the behavioural variants (Galef, 2004; Laland & Janik, 2006). Recently, attempts have been made to bridge the gap between the population-level studies under

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naturalistic settings and the controlled experimental designs in captivity (Reader & Biro, 2010; Whiten & Mesoudi, 2008), testing social/cultural information transmission in free-living animals via so-called ‘open diffusion experiments’ in which a certain behaviour is experimentally seeded into groups and the spread is tracked and recorded (Kendal, Custance, et al., 2010; Schnoell & Fichtel, 2012; Thornton & Malapert, 2009a; van de Waal & Bshary, 2011; van de Waal, Claidière, & Whiten, 2013).

The majority of experimental studies on cultural transmission have focused on the transfer of information, whereas questions concerning the maintenance of the socially acquired information have received limited attention (Hopper, Schapiro, Lambeth, & Brosnan, 2011; Lindeyer & Reader, 2010; Pesendorfer et al., 2009; Thornton, Samson, & Clutton-Brock, 2010). Most of our knowledge come from mathematical models that simulate and/or analyse transmission patterns over several generations and/or investigate the interplay of several factors such as task affordances, social dynamics and memory capacities for the establishment of new behavioural variants in social groups or subgroups (Acerbi, Jacquet, & Tennie, 2012; Allen, Weinrich, Hoppitt, & Rendell, 2013; Claidière & Sperber, 2010; Claidière & Whiten, 2012; Franz & Matthews, 2010; Franz & Nunn, 2009; Hoppitt, Kandler, Kendal, & Laland, 2010; Hoppitt & Laland, 2011; Kendal, Kendal, Hoppitt, & Laland, 2009). For the stability of behavioural variants within a group, conformity (Efferson, Lalive, Richerson, McElreath, & Lubell, 2008) and conservatism/habit formation (Pesendorfer et al., 2009) have been proposed as potential mechanisms. The former has received support mainly from two studies on captive groups of chimpanzees, *Pan troglodytes* (Hopper et al., 2011; Whiten, Horner, & de Waal, 2005) and one study on wild vervet monkeys, *Chlorocebus pygerythrus* (van de Waal, Borgeaud, & Whiten, 2013); the latter has been shown in two studies on captive chimpanzees (Hrubesch, Preuschoft, & van Schaik, 2009; Marshall-Pescini & Whiten, 2008) and in wild groups of common marmosets, *Callithrix jacchus* (Pesendorfer et al., 2009) and may be characterized by a high likelihood of being ‘washed out’ after a short time period (Thornton & Malapert, 2009b). To our knowledge, there are hardly any experimental tests on the stability of socially learned behaviours over a time span longer than a few months.

We here investigated the formation and persistence of an experimentally introduced foraging tradition in common marmosets under natural conditions. We took advantage of the study by Pesendorfer et al. (2009), in which two alternative behavioural patterns were established in family groups of wild marmosets by using an artificial fruit apparatus (push-or-pull box, Bugnyar & Huber, 1997). Note that this initial study was not designed to test for social learning but for the maintenance of initial personal preferences in a group setting. However, it resulted in the majority of monkeys per family group preferring one over the other technique. In the present study, we made use of this situation and tested (1) the long-term memory of experienced monkeys, (2) the information transmission from experienced to naïve group members (that have been born and/or immigrated in the 2 years since the original study) and (3) the persistence of socially learned techniques over several test blocks conducted in the course of 9 months. We expected (1) experienced individuals to remember the task and show a preference for their previously learned technique and (2) naïve individuals to learn socially from skilled family members to solve the task using the same technique. Concerning (3), we did not have a clear expectation since the learned behaviours might persist over time or collapse at a certain point, that is, the preference for a technique would fade and the distribution of both alternative techniques become random.

In addition to the groups used in the Pesendorfer et al. study (2009), we incorporated six further groups. In four of the groups we trained one individual on one of the two possible techniques (two

individuals learned to pull and two to push). This allowed us to see whether the presence of just one skilled individual would be sufficient to get the transmission going and establish a group ‘norm’ and, in comparison to groups with experienced subjects from the previous study, whether recently trained individuals would use the trained technique more reliably than those relying on long-term memory. Furthermore, two other (untrained) groups served as additional controls.

METHODS

Study Site and Population

The study was conducted between September 2009 and May 2010 on wild common marmosets in an area of 32 ha, part of a ca. 100 ha fragment of mixed primary and secondary Atlantic Forest, 40 km west of Recife in the state of Pernambuco, northeast Brazil (see Souto, Bezerra, Schiel, & Huber, 2007 for a description of the study site).

Thirteen family groups (comprising 4–15 individuals each) participated in our experiments (Table 1). Six groups were naïve to the task, but seven groups contained individuals that participated in the study by Pesendorfer et al. (2009) and were therefore already familiar with this experiment (henceforth ‘experienced groups’). Nevertheless, in the meantime (the time span without exposure to the task was about 2 years) the composition of these groups had changed because of births, deaths and individuals dispersing to other family groups. Hence, these groups also included naïve individuals (see section Experimental Conditions for further details). All subjects could be identified individually (see the Appendix and Schiel, Souto, Bezerra, & Huber, 2008 for procedure) and were assigned to four different age categories (adults/subadults: >11 months; juveniles: 5–10 months; older infants: 3–4 months; young infants: 0–2 months; Schiel & Huber, 2006). For detailed group compositions see Table A1. This study complied with Brazilian law.

Apparatus

We used the same apparatus as in the study by Pesendorfer et al. (2009), a replica of the push-or-pull box (20 × 10 × 10 cm) designed by Bugnyar & Huber (1997). Prior to the experiments, all family groups were habituated to the experimental set-up by food provisioning (apples and bananas). The wooden box could be manipulated in two different ways, by either pushing or pulling an opaque flap door on one side to gain access to the rewards inside (Fig. 1a, b). Details of the experimental set-up are described in the Appendix (see also Fig. A1).

Experimental Conditions

Depending on their condition in the pilot study (Pesendorfer et al., 2009), the experienced groups were divided into three corresponding experimental conditions, namely pull (groups A and T), push (groups L and W) and free condition (groups F, H and S; see Table 1). Importantly, although the free condition groups included individuals with preferences for either technique, tendencies for one favoured technique could be observed at the group level. In addition, in four of the six new groups we trained one dominant individual (always the dominant male, except for group P) to perform the pull or the push technique (pull: C and P; push: B and E; the conditions were randomly chosen). The training phase of the model lasted for 10 sessions (one session per day with 10 trials each) consisting of 100 demonstration trials in sum (see the Appendix for details of the training procedure). Note that in the experienced groups no individuals were trained, but that in these groups the experienced individuals served as potential models for

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