Animal Behaviour 80 (2010) 955–964

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Inducing traditions in captive capuchin monkeys (*Cebus apella*)

Jessica Crast [a,*], Jessica M. Hardy [b,1], Dorothy Fragaszy [c,2]

[a] Department of Psychology, University of California, Los Angeles
[b] Odum School of Ecology, University of Georgia
[c] Department of Psychology, University of Georgia

ARTICLE INFO

Article history:
Received 25 February 2010
Initial acceptance 31 March 2010
Final acceptance 25 August 2010
Available online 2 October 2010
MS. number: A10-00131R

Keywords:
capuchin
Cebus
conformity
foraging
habit formation
skill acquisition
socially mediated learning
tradition

Potential foraging and social traditions have been identified in groups of wild capuchin monkeys (*Cebus* spp.). Verification of traditions requires documentation that socially mediated learning contributes to acquisition by new practitioners. We investigated the emergence and maintenance of a foraging tradition in two generations of infant tufted capuchins (*Cebus apella*) in captive social groups. In baseline, we provided the first cohort of infants with a foraging apparatus that dispensed juice via two methods inside a small enclosure away from adult interference (the crèche). Later in phase 1, we provided a second apparatus to all group members with only one method of solution available (in the group setting); the crèche apparatus, with both methods available, remained accessible to infants only. Two years later (phase 2), we replicated phase 1 with a new cohort of infants from the same social groups. As adult activity and expertise with the apparatus increased across baseline (no adult activity), phase 1 (initially unskilled) and phase 2 (initially skilled), the proportion of infants in each cohort that acquired the foraging skill increased and their latency to skill acquisition decreased. Despite ambiguous evidence that the infants conformed to the specific method of solution common in their group, the social context clearly contributed to the development and maintenance of a general foraging tradition. The results provide support for the existence of traditions in wild capuchin groups.

In many group-living species, specific behaviour patterns are shared among group members. A shared behaviour pattern is a tradition if adoption by new practitioners is facilitated by socially mediated learning and persists over time (Fragaszy & Perry 2003). Early suggestions that nonhuman species might have traditions came from observations that different populations of wild animals show behavioural differences that are not readily explained by genetic inheritance or ecological variation, but appear to be transmitted between individuals though nongenetic means; for example, song learning and migration-route learning in birds (e.g. Bonner 1980). The method of identifying potential traditions by tracking differences in behaviour between groups is referred to as the ethnographic approach (Rendell & Whitehead 2001; Leca et al. 2007) and group contrast method (Fragaszy & Perry 2003). Candidate traditions identified using this approach in wild populations include behaviours related to foraging, social interactions, tool use and vocal communication in species as diverse as birds (e.g. Hunt & Gray 2003), cetaceans (e.g. Rendell & Whitehead 2001) and nonhuman primates (e.g. Whiten et al. 1999, 2001; Panger et al. 2002; van Schaik et al. 2003). However, apparent traditions may reflect genetically predisposed behaviours (e.g. Kenward et al. 2005) and/or homogeneous but individually discovered solutions to shared ecological conditions (Galef 1980, 1992). For this reason, verifying that socially mediated learning supports an individual's acquisition of a behaviour is crucial to confirm that any behaviour is a tradition (Fragaszy & Visalberghi 2004).

Field studies investigating the behavioural ontogeny of potential traditions provide stronger evidence for the social contribution to skill acquisition and diffusion among group members (e.g. macaques: Huffman 1996; Leca et al. 2010; rats: Terkel 1996; chimpanzees: Biro et al. 2003; Humle et al. 2009; capuchins: Perry et al. 2003). To complement longitudinal field studies, controlled laboratory research can provide corroborating evidence that traditions can emerge and be sustained within captive groups of the species in question (see Whiten & Mesoudi 2008). A good example is provided by studies that have effectively induced traditions and arbitrary social conventions in groups of captive chimpanzees (e.g. Horner et al. 2006; Bonnie et al. 2007; Whiten

* Correspondence: J. Crast, Department of Psychology, University of California, Los Angeles; Wake Forest University Primate Center, Winston-Salem, NC 27127, U.S.A.
E-mail address: jessicrast@gmail.com (J. Crast).
[1] J. M. Hardy is at the Odum School of Ecology, University of Georgia, Athens, GA 30602, U.S.A.
[2] D. Fragaszy is at the Department of Psychology, University of Georgia, Athens, GA 30602, U.S.A.

0003-3472/$38.00
doi:10.1016/j.anbehav.2010.08.023

et al. 2007). Providing empirical evidence for the role of socially mediated learning in the acquisition and maintenance of a behaviour pattern among group members strengthens the claims for traditions in wild populations of chimpanzees. In addition, controlled laboratory studies can clarify the social-learning mechanisms underlying behavioural transmission between individuals, which can help guide longitudinal field studies aimed at verifying traditions in natural settings.

The goal of the present study was to lend credence to claims of behavioural traditions in wild capuchin monkey populations by showing that traditions can develop and persist over time in groups of captive capuchins (*Cebus apella*). Interpopulation and within-group differences in various foraging and social behaviours have been identified as candidate traditions in groups of wild capuchins. For example, groups of capuchins vary in their use of specific food selection and processing behaviour and the social context appears to contribute to acquisition and maintenance of skills by new practitioners (e.g. Panger et al. 2002; Fragaszy et al. 2004; O'Malley & Fedigan 2005a; Ottoni & Izar 2008; Perry 2009). In addition, groups of white-faced capuchins, *Cebus capucinus*, at various sites in Costa Rica engage in idiosyncratic social behaviours ('games') that involve extracting items from one another's mouth and placing fingers inside one another's nose and/or mouth (Perry et al. 2003). Numerous field and captive studies suggest that capuchins experience a general support from the social context when learning a new behaviour pattern (e.g. Visalberghi & Fragaszy 1995; Bonnie & de Waal 2007; Meunier et al. 2008; Gunst et al. 2008). For example, mere proximity to others' foraging appears to influence acquisition of sex-typical foraging behaviour in black-capped capuchins, *Cebus nigritus* (Agostini & Visalberghi 2005). Stimulated by the social context to explore individually, capuchins may develop idiosyncratic ways of performing a particular behaviour or achieving a particular goal. Alternatively, capuchins may be influenced by particular groupmates to learn a specific form or technique of a behaviour pattern, one that is similar to that of others in their group (e.g. Perry 2009).

To determine whether traditions could be induced in captive capuchins, we provided a foraging apparatus to several socially housed groups of capuchins. Two different action sequences could be used to obtain juice from the apparatus (each action sequence will hereafter be referred to as a 'method of solution'). The behavioural tradition of interest was performance of the foraging skill, which was operationally defined as obtaining juice from the apparatus using at least one method of solution. We examined the acquisition of the foraging skill and subsequent use of the apparatus by infants (ages 7–18 months) of two cohorts (i.e. generations), first in a baseline phase and later in experimental phases separated by 2 years (phase 1 and phase 2). During baseline and the experimental phases, the foraging apparatus was provided inside a small wire-mesh enclosure within the group's outdoor enclosure (termed the 'crèche') that permitted entry only to infants and juveniles (see Fig. 1). Inside the crèche, infants could use both methods of solution to obtain juice; thus they had the opportunity to discover both methods of solution in an area that was within the group's enclosure (hereafter, the 'group setting') but removed from interference by adults. During phase 1 and 2 experimental sessions, all group members could access a second identical foraging apparatus in the group setting with only one method of solution baited with juice (one method of solution was pre-assigned to each group; Fig. 1). Thus, the first cohort of infants encountered the foraging apparatus without adult demonstrators (baseline sessions), and later encountered the apparatus in the presence of initially unskilled adults (phase 1 experimental sessions). In phase 2, the second cohort of infants first encountered the apparatus in the presence of skilled adults. This experimental design allowed us to disentangle the effects of experience with the foraging apparatus from the effects of the social context.

In this study, individuals within each group could discover a novel behaviour pattern (i.e. operation of the foraging apparatus) without specific training by experimenters. In addition, the emergence of a 'group norm' for method of solution was facilitated by baiting only one method in the group setting. Accordingly, we tested the following hypotheses: (1) that adult presence and proficiency with a particular behaviour pattern supports learning by new practitioners and (2) that the particular form, or technique, used by proficient group members biases new practitioners

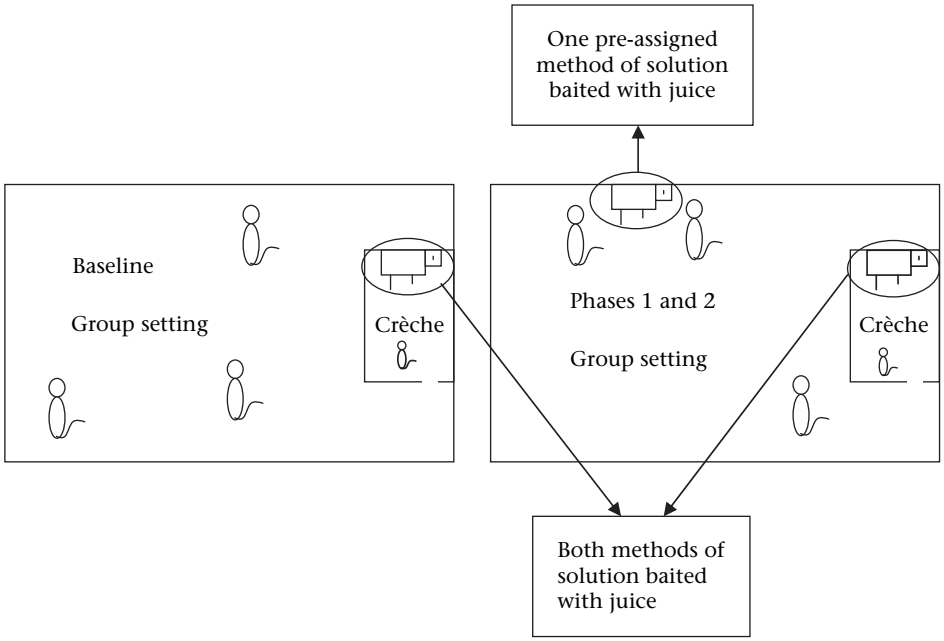

Figure 1. Generalized aerial view of the testing set-up (not drawn to scale; positions of crèche and apparatuses varied across groups). Baseline sessions: both methods available in the crèche; phases 1 and 2 experimental sessions: both methods available in the crèche and one method available in the group setting.