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Animal behaviour

The effects of tradition on problem solving by two wild populations of bearded capuchin monkeys in a probing task

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The effects of culture on individual cognition have become a core issue among cultural primatologists. Field studies with wild populations provide evidence on the role of social cues in the ontogeny of tool use in non-human primates, and on the transmission of such behaviours over generations through socially biased learning. Recent experimental studies have shown that cultural knowledge may influence problem solving in wild populations of chimpanzees. Here, we present the results from a field experiment comparing the performance of bearded capuchin monkeys (*Sapajus libidinosus*) from two wild savannah populations with distinct toolkits in a probing task. Only the population that already exhibited the customary use of probing tools succeeded in solving the new problem, suggesting that their cultural repertoire shaped their approach to the new task. Moreover, only this population, which uses stone tools in a broader range of contexts, tried to use them to solve the problem. Social interactions can affect the formation of learning sets and they affect the performance of the monkeys in problem solving. We suggest that behavioural traditions affect the ways non-human primates solve novel foraging problems using tools.

1. Introduction

Cultural primatologists attribute the status of culture to population-specific behavioural differences maintained in groups of wild primates over generations through learning opportunities due to the activities of conspecifics [1]. In humans, culture influences the way in which people perceive and categorize their environment, but in non-human animals, few studies have addressed the possible influence of culture on cognitive domains [2]. Comparative studies on behavioural differences between ape populations suggest potential traditions as explanations for their distinct toolkits [3]. Wild chimpanzee populations differ in the techniques they employ to solve a foraging task and how they perceive objects as potential tools in accordance with their respective traditions, suggesting that cultural knowledge channels how apes approach new foraging problems [4,5]. Here, we examine how different traditions can affect the performance of wild bearded capuchin monkeys in tool-aided problem solving.

Tufted capuchin monkeys (*Sapajus* sp.) are known for their manual dexterity and ability to solve problems involving tools under laboratory conditions [6]. However, in the wild, only populations living in savannah-like environments show habitual tool use, whereas populations inhabiting rainforests do not [7]. The degree of terrestriality seems an appropriate explanation for this difference [8]. The use of lithic tools to crack open nuts or seeds is widespread

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among those savannah populations, but the use of stick probes is rare. In some cases, ecological (or genetic) differences may be sufficient to explain the presence or absence of tool use among wild populations, or differences between their toolkits [7]. Field studies with wild and semi-free groups, though, have yielded corroborating evidence on the role of social cues in the ontogeny of tool use in capuchin monkeys [9,10]. In short, variation in the toolkits of wild capuchin populations may reflect, along with potential genetic factors or environmental constraints, different behavioural traditions.

We investigated if wild bearded capuchin monkeys from two populations that differed in their toolkits, especially with respect to the use of stick probes, would approach a probing task with the customary tools used by each of these groups. We expected that probe users would approach the problem using sticks, while habitual stone tool users would attempt to solve the problem using stones.

2. Material and methods

(a) Subjects and study sites

The populations of bearded capuchin monkeys (*Sapajus libidinosus*) studied here inhabit two locations in northeastern Brazil, 350 km apart (electronic supplementary material, figure S1). The 'Chicão' group lives in the dry woodland (*cerrado*) at Fazenda Boa Vista (FBV), and customarily uses stones to crack very hard palm nuts; long-term observations [11] provide reliable negative evidence of customary use of probe tools. At the time of the study, the FBV group consisted of 16 monkeys, excluding infants (table 1).

The 'Pedra Furada' group inhabits the even drier *caatinga* at Serra da Capivara National Park (SCNP). The SCNP population exhibits the broadest toolkit reported for wild capuchin monkeys, using stone tools for a variety of purposes [12], and stick probes to reach insects in nests, or lizards in rock crevices ([13], see electronic supplementary material, table S1 for more details). At the time of the study, the SCNP group consisted of 23 monkeys, excluding infants (table 1).

We did not register the behaviour of infants (less than 2 years) towards the boxes because they did not use either sticks or stones (as expected at this age) and their exposure to the task was just a passive consequence of the mother's engagement with it.

Both groups are partially provisioned with maize and bananas during the dry season and are habituated to human presence. Neither of those groups had previous experience with the proposed task. In both locations, the experiment was carried out in a place visited daily by the monkeys.

(b) Experimental procedure

Both groups were exposed to the same apparatus; a transparent Plexiglas box with a slit at the top, containing a dispenser with 400 ml of sugarcane molasses (electronic supplementary material, figure S2). Thus, the molasses was not directly accessible for the monkeys, but could be obtained through the insertion of probes longer than 5 cm through the slit. To avoid monopolization of the apparatus by high-ranking males, we simultaneously presented two identical problem-boxes (hereafter 'boxes'), attached to trees 8 m apart. All individuals were free to engage with the boxes (thus individuals contributed differently to our sample).

All activity towards or in the vicinity of the boxes was recorded by two video cameras. We registered, for each visiting monkey, the frequency and duration of each visit to the box and all occurrences of tool use, the frequency of probing (i.e. insertion of a stick into the slit of the box) and the outcome (success or failure in molasses' extraction).

After the failure of FBV monkeys to solve the problem in the same conditions as the SCNP group (which did not involve any facilitation), we gave the FBV group the opportunity to engage with boxes with 10 pre-inserted sticks made from surrounding trees' branches (length: 150 mm; diameter: 0.5 mm). We replenished the boxes with new sticks whenever the last one had been removed from the box, at least 120 s after the last visit by the monkeys.

3. Results

The SCNP group was exposed to the boxes for 5 consecutive days. All 23 non-infant capuchins visited the boxes (mean = 213 visits/days of presentation; standard deviation (s.d.) = 55). We analysed 1067 individual visits. The FBV group was exposed to the same problem for 13 consecutive days; this resulted in 376 individual visits (mean = 29 visits/days of presentation; s.d. = 12). Except for two peripheral individuals, all non-infant monkeys visited the boxes (14 out of 16). The FBV group spent less time engaging with the boxes than the SCNP group (table 1).

Most male monkeys in the SCNP group readily used probes and solved the task (10 out of 14 in the first session), but no female did it. We observed 428 visits made by males carrying sticks to the boxes (electronic supplementary material, table S2). They used (sometimes re-used) most of the 704 transported sticks as probing tools to obtain molasses ($N = 617$ sticks) (figure 1). We counted 6423 probing events—5836 of them successful. Except for the three youngest probe users, all males succeeded in above 90% of their attempts to obtain molasses (figure 2). Most of the sticks were collected close to the boxes; a few were detached from trees by the monkeys themselves.

FBV monkeys, on the other hand, never tried to use probes to access the molasses. They seemed interested in the resource—most of them repeatedly tried to reach it by inserting their fingers through the slit (table 1). After 6 h (over three daily sessions) of exposure to the original task (3.6 h of direct engagement), they were exposed to pre-inserted sticks available in the boxes. In general, though, the monkeys just pulled the sticks out of the slit, licked the molasses and discarded them. In the same way, when they retrieved abandoned sticks from the ground, they just licked the tips and dropped them or carried them away. In short, the FBV monkeys never reinserted any pre-inserted stick in the boxes.

FBV monkeys also did not try to use stones (their customary nut cracking tools) to crack open the boxes. They seldom carried objects to the boxes, and when some juveniles did it (palm nuts: $N = 4$; sticks: $N = 3$) they never contacted the object with the box surface. Some individuals from the SCNP group did, though (table 1; electronic supplementary material, table S3), but they never succeeded in gaining access to the molasses this way, and—in the case of males—eventually turned to the probing approach (electronic supplementary material, Movie S1).

4. Discussion

FBV monkeys did not succeed in the probing task, even after they had the opportunity to manipulate pre-inserted sticks. Similar to the SCNP females, they only extracted and licked them—but never *reinserted* them. Analogous performances have been observed with wild non-probe user populations of

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Table 1. Summary of the performances of the monkeys (of the SCNP and FBV group) engaging in the task. 'mode' refers to behaviours towards the boxes: F, finger insertion; P, probe use; S, stone use. Tool use was scored (yes or no). no. visits = number of visits. Both length of direct engagement with the task and the time spent per visit are shown in seconds. (FBV: mean time = 75 s, s.d. = 75 s, median = 48 s, range = 648 s; SCNP: mean time = 156 s, s.d. = 176 s, median = 92 s, range = 1398 s) (Mann–Whitney test: $Z = -4541$, $p < 0.0001$, two-tailed).

group	ID	sex	age group	mode	use of tools	no. visits	length of direct interaction(s)	time spent per visit(s) (±s.d.)
FBV	JTB$^{\alpha}$	male	adult	F	no	38	1647	43 (±26)
FBV	MSN	male	adult	F	no	10	625	62 (±70)
FBV	TEI	male	adult	F	no	20	1162	58 (±41)
FBV	CAT	male	juvenile	F	no	48	3169	66 (±60)
FBV	PAT	male	juvenile	F	no	24	2507	104 (±90)
FBV	CNG	male	juvenile	F	no	11	757	69 (±59)
FBV	COC	male	juvenile	F	no	38	3475	91 (±68)
FBV	TOM	male	juvenile	—	—	—	—	—
FBV	DIT	female	adult	F	no	59	3012	51 (±47)
FBV	CHU	female	adult	F	no	50	4336	87 (±85)
FBV	PSS	female	adult	F	no	18	948	53 (±45)
FBV	AMR	female	adult	F	no	7	827	118 (±62)
FBV	TEN	female	adult	—	—	—	—	—
FBV	DOR	female	juvenile	—	no	7	215	31 (±14)
FBV	PAM	female	juvenile	F	no	20	2325	130 (±111)
FBV	PAS	female	juvenile	F	no	18	2601	129 (±143)
SCNP	TOR	male	adult	P, S	yes	53	7715	146 (±118)
SCNP	BEI	male	adult	F, P, S	yes	35	9974	285 (±275)
SCNP	ZAN	male	adult	F, P	yes	63	10 663	168 (±147)
SCNP	NIC	male	adult	P, S	yes	42	11 793	281 (±207)
SCNP	ZEN	male	adult	F, P,	yes	38	6513	171 (±128)
SCNP	CLA	male	adult	P	yes	27	5570	206 (±198)
SCNP	BLP	male	sub-adult	P, S	yes	34	9010	265 (±327)
SCNP	CAP	male	juvenile	F, P, S	yes	47	9504	202 (±233)
SCNP	LIM	male	juvenile	F, P, S	yes	53	9659	182 (±208)
SCNP	COR	male	juvenile	F, P	yes	27	6219	230 (±277)
SCNP	VOL	male	juvenile	F, P, S	yes	64	9201	144 (±157)
SCNP	PAD	male	juvenile	F, P, S	yes	59	8175	139 (±130)
SCNP	DES	male	juvenile	F, P, S	yes	66	7281	110 (±126)
SCNP	CIN	male	juvenile	F, S	yes	77	7043	91 (±118)
SCNP	GOR	female	adult	F, S	yes	56	7040	126 (±139)
SCNP	MAC	female	adult	F, S	yes	69	8730	126 (±148)
SCNP	BEM	female	adult	F, S	yes	58	7850	135 (±140)
SCNP	CAN	female	adult	F	no	27	4804	178 (±181)
SCNP	NIN	female	adult	F	no	17	977	57 (±66)
SCNP	LIC	female	adult	F	no	30	3514	117 (±142)
SCNP	ALI	female	adult	F, S	yes	42	5131	122 (±147)
SCNP	VES	female	adult	F	no	16	2373	148 (±109)
SCNP	BAT	female	sub-adult	F	no	67	7944	119 (±117)

white-faced [14] and black [15] capuchins, and chimpanzees [4]. Foraging behaviour in non-human primates, particularly for generalist species, is influenced by ecological features and previous experience with problems in the environment, which may differ between populations [5,7,16]. Regarding probe use, the overall performance of our subjects in the task

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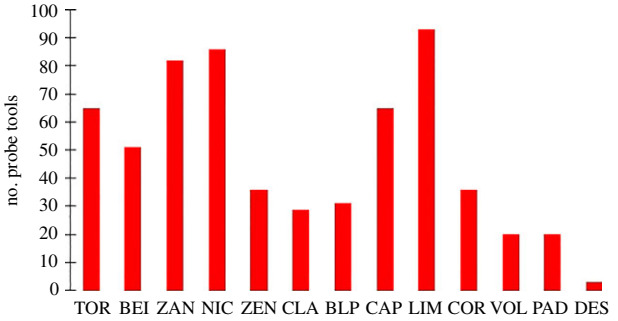

Figure 1. Number of sticks used by each monkey of the SCNP group. All males; females did not use probes. (Online version in colour.)

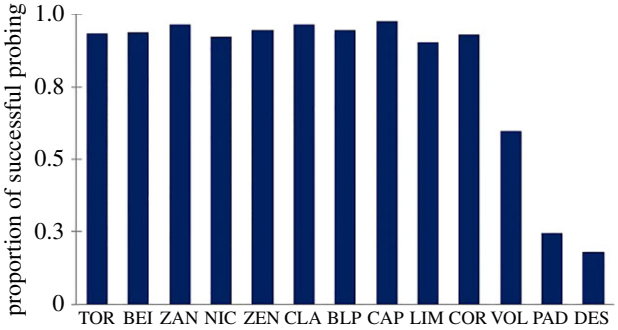

Figure 2. Proportions of successful probing by each monkey of the SCNP group. All males; females did not use probes. (Online version in colour.)

reflected their respective toolkits (the absence of probing in FBV group and among SCNP females). In this respect, our results resemble those found with wild chimpanzees [4,5]. The lack of customary probe use may explain the failure of FBV monkeys and Sonso chimpanzees in the probing tasks.

Females can use probing tools in natural contexts, although it is much less frequent than in male adults [13]. As young capuchin monkeys tend to adopt the foraging techniques of their close associates (in the case of females, their mothers) [17,18], females may differ from males with respect to opportunities to observe others using sticks. Although the SCNP females had plenty of opportunities to observe other monkeys using sticks in our experiment, their lack of previous experience with probing tools may have prevented them from learning how to solve the problem.

An unexpected result was the absence of attempts by FBV monkeys to gain access to the molasses using stones to break the box, because the stone-aided cracking of palm nuts is customary in this group. By contrast, SCNP monkeys did try (unsuccessfully) to use stones in their early attempts to solve the task—even those who were customary probe users. A possible explanation might be found in the difference in potential 'hammer' stones availability, abundant in SCNP, but scarce in the whole FBV area. However, our experiment was carried out (in FBV) near a talus where sandstone pieces and pebbles are abundant [19]. This suggests that only the difference in the immediate availability of stones cannot satisfactorily explain the difference observed between the two groups in the box-directed use of stone tools.

The monkeys of the two populations customarily use stone tools, but they differ in the breadth of their usage. In SCNP, the abundant stones are customarily used by monkeys of both sexes for several purposes, while FBV monkeys' use of stones is usually restricted to processing palm and cashew nuts (electronic supplementary material, table S1). We suggest that this broader scope of stone tools usage made it more easily generalizable to the new context.

5. Conclusion

Gruber and co-workers [2] suggested that species with different behavioural traditions may differ not only in terms of their cultural behaviour (e.g. apply culturally acquired tool use behaviour to a novel problem) but also at a cognitive level (e.g. how they represent their toolkits and solve problems). Nevertheless, this cognitive level is itself limited by the cognitive abilities of the species studied, particularly their capacity to access the mental representations of their cultural knowledge. Our results can also be discussed at a more strictly behavioural level, in terms of learning sets (learning how to learn efficiently the general solution to new problems recognized as belonging to a class of similar problems [20]) in accordance with their own behavioural traditions, and the degree of previous flexibility and generalization associated with each item in their toolkits. As tool use behaviours by wild non-human primates seem to constitute behavioural traditions, maintained over generations by mechanisms of socially biased learning that channel the individual experiences of novice tool users, it is reasonable to expect an effect of traditions on their problem solving abilities.

Ethics. All procedures were previously authorized by Instituto Chico Mendes de Conservação da Biodiversidade (permission no. 26549-1) and are in accordance with Brazilian laws.

Data accessibility. We provide supporting data in the electronic supplemental material. Dataset available from the Dryad repository: http://dx.doi.org/10.5061/dryad.10940 [21].

Authors' contributions. E.B.O. and R.M.C conceived and designed the experiment. R.M.C performed the experiment. R.M.C. and E.B.O analysed the data and wrote the paper. Both authors approved the final version and are accountable for all aspects of the work.

Competing interests. The authors declare they have no competing interest.

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