Design complexity in termite-fishing tools of chimpanzees (Pan troglodytes)

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Adopting the approach taken with New Caledonian crows (Corvus moneduloides), we present evidence of design complexity in one of the termite-fishing tools of chimpanzees (Pan troglodytes) in the Goualougo Triangle, Republic of Congo. Prior to termite fishing, chimpanzees applied a set of deliberate, distinguishable actions to modify herb stems to fashion a brush-tipped probe, which is different from the form of fishing tools used by chimpanzees in East and West Africa. This means that ‘brush-tipped fishing probes’, unlike ‘brush sticks’, are not a by-product of use but a deliberate design feature absent in other chimpanzee populations. The specialized modifications to prepare the tool for termite fishing, measures taken to repair non-functional brushes and appropriate orientation of the modified end suggest that these wild chimpanzees are attentive to tool modifications. We also conducted experimental trials that showed that a brush-tipped probe is more effective in gathering insects than an unmodified fishing probe. Based on these findings, we suggest that chimpanzees in the Congo Basin have developed an improved fishing probe design.

Keywords: tool use; tool modification; cognitive template

1. INTRODUCTION

Wild chimpanzees (Pan troglodytes) and orang-utans (Pongo abelii) have long been held as the most sophisticated tool users in the natural world. However, few attempts have been made to assess their tool sophistication, and reports of tool use in some other species suggest ways of assessing it, which may help determine their cognitive abilities. Recent reports of the tool-using skills of New Caledonian crows (Corvus moneduloides) have shown a repertoire of several different tool behaviours, for instance some of which show evidence of design complexity (Hunt & Gray 2003; Hunt et al. 2006). Design complexity has been invoked when there are alternative forms of a tool, some of which involve manufacture steps that result in more complex material transformations than others (Hunt & Gray 2003; Hunt et al. 2006). New Caledonian crows manufacture tools from Pandanus leaves with varying numbers of stepped notches along their edge, but there is no evidence that complex tools are more effective than other variants. In this study, we examine whether chimpanzees perform deliberate modifications to fishing probes, which could increase their effectiveness in gathering termite prey.

Based on the chimpanzee tool assemblages recovered in Cameroon, it was suggested that chimpanzees deliberately manufactured “brush sticks” with frayed ends to dig termites from their earthen nests and may also have used flexible probes for termite fishing (Sugiyama 1985). Observations of wild chimpanzees, field experiments and archaeological analyses have shown that the frayed ends of brush sticks are not deliberately manufactured and do not have functional importance in termite gathering (Sanz et al. 2004; Takemoto et al. 2005; Heaton & Pickering 2006).

It remains unclear, however, whether other tool modifications, such as brush-tipped fishing probes, are by-products of repeated use or whether they represent deliberate design features of the tool. Brush-tipped probes are found across sites in central Africa and show striking similarity in form (length, diameter and brush modification) (Fay & Carroll 1994; Suzuki et al. 1995; Bermejo & Illera 1999). In contrast to East African chimpanzees who actively remove the frayed ends of termite-fishing probes (McGrew et al. 1979), brush tips were found on 81 per cent of termite-fishing tools recovered across six chimpanzee communities in the Goualougo Triangle, Republic of Congo (Sanz et al. 2004).

We investigated whether chimpanzees deliberately manufactured brush-tipped fishing probes by analysing when and how chimpanzees modified herb stems. Additionally, we experimentally assessed the effectiveness of probes with and without brushes. Our goal is to expand the discussion of design complexity in tool-using behaviours of wild chimpanzees, which, owing to an exclusive reliance on data on brush sticks, may have been prematurely dismissed in recent discussions of these topics.

2. MATERIAL AND METHODS

(a) Study site

The Goualougo Triangle is located within the Nouabalé-Ndoki National Park (16°51’–16°56’E; 2°05’–3°03’N), Republic of Congo. The study area covers 380 km² of evergreen and semi-deciduous lowland forest, with altitudes ranging between 330 and 600 m. Rainfall is bimodal, with a main rainy season from August to November and a short rainy season in May.

(b) Data collection

Between September 2003 and December 2006, remote video recording devices with passive infrared sensors were used to conduct surveillance at termite nests for chimpanzee visitation and tool-using behaviours. Detection of movement by the sensor caused the camera to record for 2 min intervals until triggers ceased (Sanz et al. 2004).

(c) Definitions

(i) Tool use in termite predation

Chimpanzees in the Goualougo Triangle use three different tools in termite predation, which occurs throughout the year at this site (Sanz et al. 2004). Termite fishing involves inserting a flexible herb stem into a termite nest to extract termites biting the invading object. A variation of the termite-fishing technique involves using a perforating tool to open the exit holes and then inserting a fishing probe into the nest. Extracting termites from subterranean (as opposed to elevated) nests involves inserting the length of a stout stick into the ground to create a long, narrow tunnel for the insertion of the fishing probe.
We scored whether brush manufacture occurred prior or during termite fishing, paying particular attention to whether the brush arose as a by-product of tool use. We determined that brush creation was deliberate when chimpanzees directed distinguishable modifications to the tip of the tool and that it arose as a by-product when no modifications were directed towards the tool. Cohen’s $\kappa$ was calculated to assess inter-observer agreement for tool modification behaviours observed during the transformation of an unmodified herb stem into a brush-tipped tool ($\kappa = 0.902$, $n = 54$ episodes) between C. Sanz and a research assistant who was blind to the experimental hypothesis.

C. Sanz and D. Morgan conducted experimental trials to evaluate the effectiveness of unmodified versus brush-tipped tools. Five local guides were asked to fish with an unmodified (no-brush) and a brush-tipped tool at three to five nests (20 attempts for each guide per tool type at each nest). A tool of each type was manufactured to specifications resembling a chimpanzee fishing probe. Order of tool type was balanced for each nest, and the same fishing hole was used for brush and no-brush trials. Each probe was inserted for $3\text{ s}$ (similar to chimpanzee termite fishing), and experimenters counted the number of termites extracted after each fishing attempt. Non-parametric statistics were used to evaluate the yield of termites between conditions.

3. RESULTS

Brush manufacture occurred prior to contact with the termite nest in 96 per cent of observations (52/54). In the two other observations, an adult female and subadult male used the blunt end of the stem to contact the termite exit holes, possibly to test whether the hole was open. Both of these individuals subsequently manufactured a brush and then began termite fishing. We observed five different types of modification to herb stems during brush manufacture: fray end by pulling through teeth (75% of modifications); split probe lengthwise (16%); separate

fibres by biting (3%); clip probe length (2%); and remove extraneous vegetation (3%). Brush-tipped tool manufacture consisted of $3.2 \pm 1.7$ modifications (range: 1–10; total: 175 modifications) and lasted $7.9 \pm 6.4$ s (range: 2.0–29.6; $n = 54$ observations).

After 93 per cent of brush manufacture observations (50/54, involving AF/SAF = 11, AM/SAM = 12, JUV = 4), chimpanzees were observed to pull the brush tip through a partially closed fist to compact (or straighten) brush fibres for insertion into the nest (for more detailed information about ‘brush straightening’ within termite-fishing sequences, see Sanz & Morgan in press). If the fishing probe was not successfully inserted, the chimpanzees often repeated the straightening action until the brush fibres were appropriately arranged for insertion into the nest. Chimpanzees also took measures to maintain the brush during termite fishing. In contrast to brush manufacture, maintenance consisted of fewer modifications (1.3 $\pm 0.5$; range: 1–2; total: 14) that occupied less time (2.2 $\pm 1.9$ s, range: 0.6–6.5; $n = 11$) and were aimed at refining tool dimensions or repairing the brush tip.

Chimpanzees consistently not only used the modified end of the tool for termite fishing, but we also observed four chimpanzees reverse the tool orientation and use the blunt end for a different function. In the midst of termite fishing, these individuals (AF, AM, SAM, JUV) were each observed to change the tool orientation and then use the unmodified end temporarily as a perforating tool to clear debris from a fishing hole. After the obstruction had been cleared, the chimpanzee immediately reoriented the tool to resume fishing with the brush tip.

Termite-fishing trials conducted by local guides showed that brush-tipped fishing probes were significantly more effective in gathering termites ($\chi^2_{6} = 83.60, p < 0.001$) than unmodified probes. Seventy-six per cent of fishing attempts with a brush were successful in gathering termites, compared with only 18 per cent success during attempts without a brush. Humans gathered an average of $4.90 \pm 5.92$ termites per attempt with a brush-tipped tool ($n = 420$ attempts), compared with only $0.27 \pm 0.71$ termites per attempt with an unmodified tool ($n = 420$ attempts).

4. DISCUSSION
Chimpanzees in the Goualougo Triangle deliberately modified herb stems to fashion a brush tip prior to termite fishing. The absence of this behaviour in several other chimpanzee populations suggests that this is a skill acquired during ontogeny, not necessarily a species-specific trait. Experimental trials showed that the tools with brush modifications are more effective in gathering insects than unmodified tools. Based on these findings, we suggest that these chimpanzees have developed an improved fishing probe design.

The brush-tipped fishing probe is not inherent in the structure of the herb stem, but rather arises from transformation of the raw material that shows evidence of being deliberate. In particular, the lengthwise pulling of the probe through partially closed teeth is a behaviour that was not observed in other contexts and was often repeated several times during brush manufacture. These transformations also increased the effectiveness of these tools. Our results indicate that chimpanzees have a mental template of the tool form, which is employed in crafting the tool prior to use and refining it during use, which expands on Boesch & Boesch’s (1990) finding that chimpanzees show specificity in the length of different types of tools. Furthermore, other chimpanzee and orang-utan populations have been reported to use tools with similar design features for particular foraging applications (Tutin et al. 1995; Fox et al. 1999). This makes it likely that simple tool technologies (involving a single unmodified tool) were the precursors of techniques with more tool modifications and more complex tool sets. For example, multiple tool use involving a puncturing tool followed by a brush-tipped fishing probe is likely to have arisen as an elaboration of the basic fishing approach that involved simply an unmodified herb stem. Increased effectiveness in gathering termites could promote adoption of such a tool set or modification.

A hallmark of human cultural traditions is that they change over time, with some showing an accumulation of modifications, which improves their functionality (Boesch & Tomasello 1998). Although the technology of chimpanzees is relatively simple when compared with humans, we have shown that certain chimpanzee populations modify their termite-fishing probes into a determined shape that has the potential to markedly enhance tool-using performance. These findings prompt further research to examine the prevalence and maintenance of cumulative modifications in the tool-using behaviours of great apes.

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