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Elemental variation in the termite fishing of wild chimpanzees (*Pan troglodytes*)

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Chimpanzee tool behaviours vary dramatically in their complexity and extent of geographical distribution. The use of tool sets with specific design features to gather termites extends across a large portion of central Africa. Detailed examination of the composition and uniformity of such complex tool tasks has the potential to advance our understanding of the cognitive capabilities of tool users and processes underlying the maintenance of technological skills. In this study, we examined variation in chimpanzee tool use in termite gathering from video-recorded sequences that were scored to the level of functionally distinct behavioural elements. Overall, we found a high degree of similarity in tool-using techniques exhibited by individuals in this population. The number of elements in each individual's repertoire often exceeded that necessary to accomplish the task, with consistent differences in repertoire sizes between age classes. Adults and subadults had the largest repertoires and more consistently exhibited element strings than younger individuals. Larger repertoires were typically associated with incorporation of rare variants, some of which indicate flexibility and intelligence. These tool using apes aid us in understanding the evolution of technology, including that of our human ancestors, which showed a high degree of uniformity over large spatial scales.

Keywords: technology; Congo Basin; tool use

1. INTRODUCTION

Tool-using behaviours are typically defined in terms of tool form, action and target. An alternative approach involves identifying the distinct components (elements), which comprise a task, such as has been undertaken for the thistle processing of mountain gorillas, and the nut cracking and the use of leaves to drink water by chimpanzees [1–4]. Byrne [5] has suggested that careful study of the intricate complexity of skilled behaviour patterns may be a more direct method to detect 'cultures' than current exclusionary approaches, in that elemental variation may provide clues into the cognitive underpinnings of behaviours and a means to examine the abilities of species to socially transmit information between generations. When ecological and genetic differences are accounted for, social learning can generate detectable levels of homogeneity in behaviours within groups [6]. Alternatively, Tennie *et al.* [7,8] assert that these behaviours could be within the species' existing repertoire and generated by founder effects, individual learning and emulative processes. In this study, we examine the tool use of wild chimpanzees to determine: (i) if there is meaningful variation in element repertoires of different individuals, (ii) whether the expression of these elements is consistent within and between individuals in the same population, and (iii) if the structuring of element sequences differs between mature and immature individuals. We expected to find a certain degree of variation within and between individuals as they responded to different ecological or social conditions. However, analysis of repertoire composition and homogeneity provides an indication of whether individuals are exhibiting exploratory use of elements or potentially drawing upon behaviours exhibited by others in this context. As we gather more information from apes at this site, we hope to test whether degree of similarity in repertoires between individuals is correlated with genetic distances or social associations.

Termite fishing is one of the most widespread tool using behaviours shown by chimpanzees, having been observed in several populations ranging from west to east Africa [9,10]. This task involves inserting a flexible probe into a termite nest and extracting the insects that attack the tool by biting the fibres with their mandibles. The use of tool sets in termite predation by chimpanzees in central Africa represents a more complex variant of this behaviour, involving multiple tools with specific design features such as particular modifications and high degree of selectivity for certain raw materials [10,11]. At epigeal termite nests, chimpanzees use a small twig to perforate the surface of the nest and then insert a brush-tipped fishing probe to extract the termites from the nest. Termite nest puncturing is another variant, which involves creating a tunnel into a subterranean termite nest with a stout stick, which is then followed by the use of a brush-tipped fishing probe. These tool sets represent some of the most complex material technology that has been observed in the wild [12].

In this study, we set out to examine variation in a complex form of termite gathering by wild chimpanzees, with the hopes of advancing our understanding of the technological capacities of these apes and how these technologies are maintained in natural settings. Comparisons of the element composition and variation associated with particular tasks and across species may aid in elucidating the evolutionary origins of particular tool-using skills.

2. MATERIAL AND METHODS

(a) *Study site*

The Goualougo Triangle is located in the southern sector of the Nouabalé-Ndoki National Park (16°51′ – 16°56′ N; 2°05′ – 3°03′ E), Republic of Congo. The study area covers 380 km^2 of evergreen and semi-deciduous lowland forest, with altitudes ranging between 330 and 600 m.

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(b) ***Data collection***
Between September 2003 and 2007, remote video-recording devices with passive infrared sensors were used to conduct surveillance at termite nests for chimpanzee visitation and tool-using behaviours [10].

(c) ***Definitions and data analysis***
Elements were defined as functionally distinct behavioural units, which were assumed to have biological meaning owing to their seamless execution ([13]; see also [2]). Ethograms from previous studies at other chimpanzee study sites were taken into consideration when defining behavioural elements ([14]; W. C. McGrew 2010, personal communication). Strings were defined as groupings of elements, which consistently occurred within tool-using bouts. For example, the element string associated with the direct mouthing technique of gathering termite prey involves three steps: (i) straighten the brush, (ii) insert/extract the probe, and (iii) eat the termites directly from the probe. Strings were initially identified in structural analysis of first-order element transitions in tool-using behaviours [13].

The electronic supplementary material contains operational definitions of behavioural elements and detailed information on statistical analyses.

3. RESULTS

Between 2003 and 2007, a total of 130 identified chimpanzees (adult males = 41, adult females = 41, subadult males = 5, subadult females = 11, juveniles = 23, infants = 9) exhibited tool-using behaviours at sites monitored with remote video cameras. Most of these individuals were observed on multiple occasions (average = 9.32 visits, median = 5, range = 1, 67) with individual observation time ranging between a few seconds to 5.44 h (individual average, 46 min).

After controlling for observation time, we found significant differences among age classes in repertoire size at epigeal tool sites (Kruskal–Wallis $\chi^2_3 = 10.9829$, p-value = 0.0118) and a similar trend at subterranean sites (Kruskal–Wallis $\chi^2_3 = 6.9091$, p-value = 0.0748). Overall, mature chimpanzees had larger repertoires of tool-using elements in both epigeal (adult average = 9.9, median = 9; subadult average = 11.3, median = 11) and subterranean settings (adult average = 8.9, median = 8.5; subadult average = 13.2, median = 12) than juveniles (epigeal average = 10.2, median = 9.5; subterranean average = 6.8, median = 5) and infants (epigeal average = 4, median = 2; subterranean average = 3, median = 3). Adult and subadult repertoires consistently included more elements than those fundamentally essential to accomplishing these tasks (five essential elements at epigeal sites and seven essential elements at subterranean sites, based on [13]; figure 1).

Adult chimpanzees more consistently exhibited element strings (figure 2), than juveniles who tended to repeat elements until reaching a particular criterion or goal. Infants and juveniles showed a higher frequency of repeated brush straightening to prepare the modified end of the fishing probe for insertion than adults and subadults. By contrast, older individuals achieved a higher proportion of successful fishing probe insertions. We found significant differences between individuals with regard to preferences for particular element strings at epigeal nests ($\chi^2 = 324.6543$, $p = 0.026$). Juveniles and infants more often consumed termites directly from the tool than adults, who exhibited a more coordinated sweeping technique in termite fishing.

Larger element repertoires were typically associated with incorporation of rare variants, which individually

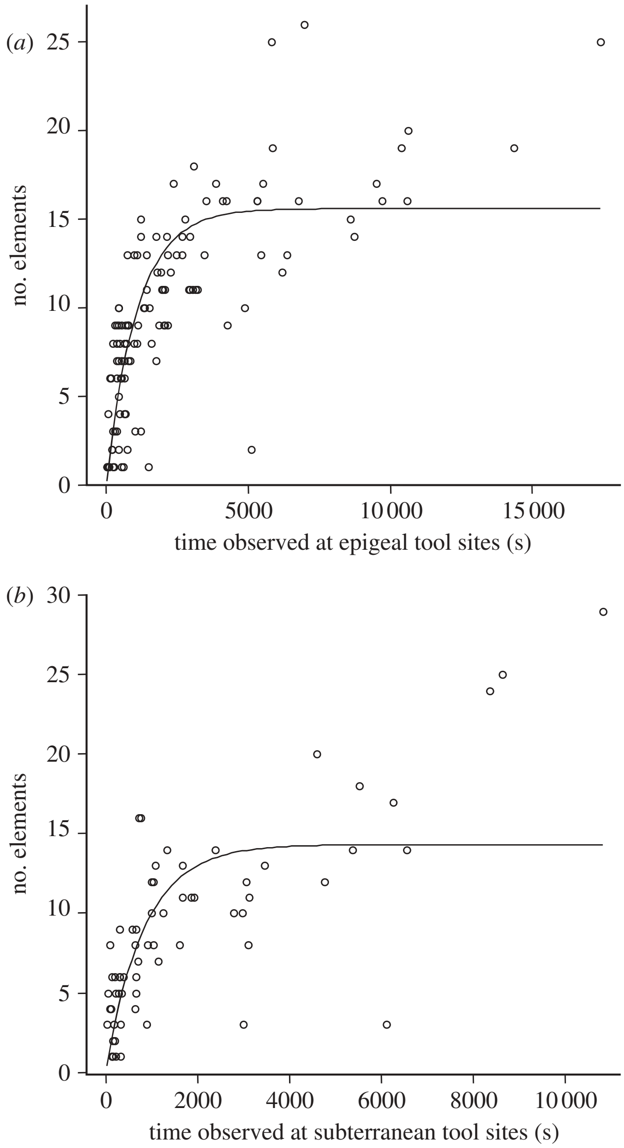

Figure 1. Cumulative element repertoire size by the total time observed in the tool using context for each individual subject (*a*) at epigeal and (*b*) subterranean termite nests.

comprised less than 1 per cent of all elements. These included tool modifications during the tool-using sequence, manufacture of a second tool and the use of tool for another function. Mature chimpanzees were observed invoking rare elements to solve problems encountered while termite gathering. For example, several chimpanzees ($n = 25$) were observed to change the orientation of their brush-tip fishing tool to use the unmodified end of the probe as a perforator (total of 63 observations) in response to a blockage of a fishing tunnel. Although we do not yet have information on the development of the use of these tool sets, we observed that two adult females accounted for a third of these observations among females (21 observations, $n = 11$ females), and their three sons accounted for 29 per cent of the behaviours exhibited by males (42 observations, $n = 14$ males).

Homogeneity of tool sequences was strongest within those shown by the same individual, but the basic elements necessary to accomplish tool use in termite predation were also consistent between individuals in this population. We found significant differences

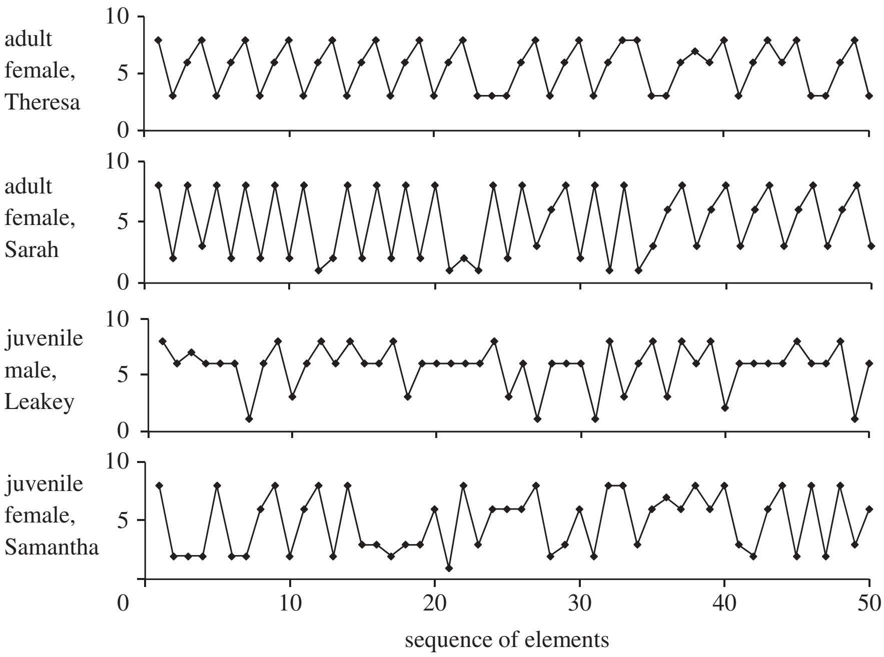

Figure 2. Sequence of elements exhibited by chimpanzees in termite fishing. The horizontal axis indicates progression of elements in a tool using sequence. The vertical axis represents different behavioural elements which are numbered from 1 to 10 (1, termite gathered by hand; 2, termite swept from tool; 3, termite eaten directly from tool; 4, fray end of tool to brush; 5, reduce length; 6, straighten brush fibres; 7, failed insertion; 8, insert/extract fishing probe; 9, probe to perforate; 10, reverse orientation of tool). The arrangement and repeated cycles of element strings can be seen in the adult sequences (Theresa, Sarah). Theresa exhibited strings of elements associated with the direct mouthing technique to gather termites, whereas Sarah repeated strings associated with the sweeping technique. Although the same behavioural elements are present in the sequences of their juvenile offspring (Leakey, Samantha), the execution of element strings is not as consistent.

between the average correlation coefficients of within-subject and between-subject tool sequences at both epigeal ($\rho = 0.0009$, $p = 0.001$) and subterranean nests ($\rho = 0.0013$, $p = 0.026$). The same result was found when we compared the median correlation coefficients of within- and between-subject tool sequences ($\rho_{epg} = 0.0007$, $p = 0.004$; $\rho_{sub} = 0.0013$, $p = 0.025$). At epigeal nests, correlation coefficients were slightly higher within the sequences of the same individual (mean $= 0.57 \pm 0.16$, median $= 0.58$) compared with tool sequences of different individuals (mean $= 0.53 \pm 0.18$, median $= 0.54$). The same pattern of higher correlations within-subject sequences (mean $= 0.72 \pm 0.12$, median $= 0.74$) compared with between-subjects comparisons (mean $= 0.67 \pm 0.14$, median $= 0.69$) was found at subterranean termite nests.

4. DISCUSSION

We examined elemental variation in the tool sequences of a wild chimpanzee population known to exhibit complex tool-using behaviours. Adult and subadult chimpanzees exhibited the largest repertoires of tool-using elements and more consistently exhibited element strings. Juveniles and infants had smaller repertoires and tended to repeat elements until reaching a particular goal, rather than experiment with extraneous elements. The highest degree of homogeneity was found in tool-using sequences exhibited by the same individual, but tool-using behaviours exhibited by different individuals were also similar in their basic element composition. The observed homogeneity in both individual- and group-level execution of this task may be convergence to optimal solutions or effective social transmission. Further studies of the tool-using behaviour of living apes will inform us about the processes and circumstances in which technology evolves.

Within the chimpanzee population of the Goualougo Triangle, we found a high degree of similarity in element repertoires and execution of tool-using sequences. However, there were notable differences in the expression of particular elements, particularly between immature and mature individuals. On the obvious and straightforward interpretation, trial and error learning would show a developmental trajectory from exploration, with many elements used gradually towards execution, when the repertoire has narrowed to a smaller set of efficient elements. We found the opposite, a change from few elements used by juveniles to an increasingly large repertoire in older chimpanzees. One possible explanation for these data could be social acquisition of new elements. Longitudinal studies have the potential to reveal strong evidence of social learning, by following the transmission of distinctive elements from one individual to another.

Closer examination of particular elements also provides a window into an animal's understanding of the tool task. For example, an argument can be made for goal-directedness in a chimpanzee's manufacture and actions to maintain a brush-tip on one end of their fishing probe, which increases efficiency in gathering prey [11]. A potential indication of insight was found in the rare observations of chimpanzees reversing the orientation of their brush-tip fishing probes to use the blunt end to clear an obstruction, realizing that their fishing probe could be used for a second function.

Transport of both puncturing and fishing tools to a termite nest may indicate planning or anticipation. Longitudinal studies of the ontogenetic trajectory of termite gathering techniques could provide information about how such rare variants arise, while homogeneity is maintained within populations.

Long-term behavioural monitoring and video data collection are critical aspects of this research, which enabled us to overcome many obstacles (such as habituation effects, low frequency of observation and sample size) often associated with the limitations of observational conditions in the wild. Future research on chimpanzee traditions could adopt the approach taken to analyse song type sharing among nightingales, in which researchers simulated models of song acquisition and the cultural evolution of the population's repertoire [15]. We concur with Byrne [5] in that studies of the element composition and structure of complex tasks have the potential to facilitate more informative cross-site comparisons and provide a more precise approach to examining cognitive capacities in the wild.

This field research was conducted in accordance with wildlife research protocols and ethical standards of the Wildlife Conservation Society of the USA, the Ministry of Science and Technology of the Republic of Congo, and the Ministry of Forest Economy of the Republic of Congo.

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