

RESEARCH ARTICLE

Extraction of honey from underground bee nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon: Techniques and individual differences

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A detailed analysis of tool use behaviors can disclose the underlying cognitive traits of the users. We investigated the technique used by wild chimpanzees to extract the underground nests of stingless bees (*Meliplebeia lendliana*), which represent a hard-to-reach resource given their highly undetectable location. Using remote-sensor camera trap footage, we analyzed 151 visits to 50 different bee nests by 18 adult chimpanzees of both sexes. We quantified the degree of complexity and flexibility of this technique by looking at the behavioral repertoire and at its structural organization. We used Generalized Linear Mixed Models to test whether individuals differed in their action repertoire sizes and in their action sequencing patterns, as well as in their preferences of use of different behavioral elements (namely, actions, and grip types). We found that subjects showed non-randomly organized sequences of actions and that the occurrence of certain actions was predicted by the type of the previous action in the sequences. Subjects did not differ in their repertoire sizes, and all used extractive actions involving tools more often than manual digging. As for the type of grip employed, the grip involving the coordinated use of hands and feet together was most frequently used by all subjects when perforating, and we detected significant individual preferences in this domain. Overall, we describe a highly complex and flexible extractive technique, and propose the existence of inter-individual variation in it. We discuss our results in the light of the evolution of higher cognitive abilities in the human lineage.

KEYWORDS

complexity, flexibility, individual differences, tool use

1 | INTRODUCTION

The occurrence of habitual tool use is relatively rare but spans across the animal kingdom (Shumaker, Walkup, & Beck, 2011). Based on evidence accumulated on an increasing number of taxa, from invertebrates to mammals, the earlier view of tool use as a uniquely human characteristic was dismissed. Applying a comparative framework, research thus focused on investigating to what extent cognition is involved in these behaviors by assessing their degree of complexity and flexibility, assuming that highly complex and flexible behaviors would be associated with higher cognitive abilities, such as the abilities of action sequencing, organizing, and planning (Coolidge & Wynn, 2001). Tool use requires the ability to relate one external object (i.e., the tool) to another (i.e., the target) to attain a goal, by integrating actions across space and time (Matsuzawa, 2008). The extent of complexity and flexibility involved is usually regarded as the degree of variation and recombination of the underlying organizational patterns

of these behaviors according to the properties of the object or the situation (Parker & Gibson, 1977). But how can we characterize these features? The repertoire size of unique functional actions and their structural organization have been used as indices of behavioral complexity (Byrne, Corp, & Byrne, 2001). The latter aspect is usually measured as the length of the sequences of actions executed and the occurrence of recurrent transitions between actions within the sequences (Byrne, 2002). Another approach assesses behavioral complexity by looking at the operational sequence of a technique, suggesting that complexity increases with the number of different actions required to reach a goal (Sellet, 1993). This method explicitly addresses the decisions made by the subject when using a tool to reach a goal, allowing for the recognition of the underlying cognitive requirements needed for success (i.e., mental organization; physical and causal understanding) (Carvalho, Cunha, Sousa, & Matsuzawa, 2008; Hayashi, 2015; Stokes & Byrne, 2001) and it can be coupled with a quantification of the transitions between actions (Tonooka, 2001).

Another source of complexity is the extent of bimanual coordination of hands and feet in performing an action, since bimanual and coordinated handling patterns are considered to be associated with higher neurological complexity (Leca, Gunst, & Huffman, 2011). On the other hand, flexibility has been characterized as the diversity of combinations of actions in a sequence and by the ability to apply one action to different contexts (Boesch, 2013).

Another aspect to consider is the possible individual variation in a behavior (Kappeler & Kraus, 2010). Several studies in the wild demonstrated that individuals specialized in or preferentially used alternative strategies, including dietary choices, employed techniques, handling patterns, or tool selection (dolphins: Mann et al. [2008]; sea otters: Tinker, Costa, Estes, & Wieringa [2007]; primates: Gruber, Muller, Strimling, Wrangham, & Zuberbühler [2009]; Gumert, Kluck, & Malaivijitnond [2009]; Gunhold, Massen, Schiel, Souto, & Bugnyar [2014]; Humle & Matsuzawa [2002]; Koops, Schöning, Isaji, Hashimoto [2015]; Leca, Gunst, & Huffman [2007]; Luncz & Boesch [2014]). These differences could be driven by ecological, individual (e.g., life history), or social factors (Reader & Laland, 2003; Sargeant, Wirsing, Heithaus, & Mann, 2006; van Schaik, Fox, & Fechtman, 2003), and belong to a specific age- or sex-class within a population (Agostini & Visalberghi, 2005; Boesch & Boesch, 1981; Ottoni & Mannu, 2001; Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011) or characterize certain individuals (Byrne & Byrne, 1993; Mann & Sargeant, 2003; van de Waal, Krützen, Hula, Goudet, & Bshary, 2012).

Special emphasis has been given to the study of great apes' object manipulation patterns, considered as a precursor of tool use (Byrne & Suomi, 1996; Takeshita & Walraven, 1996), and tool use behaviors. In fact, among tool-using species, chimpanzees and Sumatran orangutans present the richest repertoire of techniques (McGrew, 2013; van Schaik, Ancrenaz et al., 2003), and given their phylogenetic closeness to humans they represent a crucial model with which to infer the evolution of higher cognitive abilities in our lineage (Byrne, 2007; Krützen, Willems, & van Schaik, 2011; Wynn, Hernandez-Aguilar, Marchant, & McGrew, 2011).

Here, we investigated the extractive techniques employed by members of one community of wild central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon, to extract honey from underground nests of stingless bees (*Meliplebeia lendliana*) (Boesch, Head, & Robbins, 2009). Chimpanzees exploit bee nests across their range, employing a variety of behaviors, with or without tools. Such behavioral variety is likely linked to the diversified nesting behaviors of the bees, which forces chimpanzees to adjust their strategy according to a highly variable task (Boesch et al., 2009; McGrew, 1992; Sanz & Morgan, 2009). In the specific case of underground nests the challenge is even greater given that the nests are not directly visible (the only sign of their presence being a tiny waxy entrance tube protruding only few millimeters above ground), and that the underground chamber (where honey and brood are contained) is deeply interred (Boesch, 2013; Roubik, 2006). Indeed, we demonstrated that bee nests' structure significantly constrains chimpanzees' success (Estienne, Mundry, Kühl, & Boesch, 2017). In this study, we focused on adult individuals under the assumption that they would display the complete species- or individual-specific repertoire for this

honey extraction technique. We defined "technique" as the ordered sequence of discrete behavioral elements (here referred to as "actions") (Byrne & Byrne, 1993) performed by one individual. Additionally, we specifically looked at the different patterns of bimanual coordination used (here referred to as types of "grips"). First, we characterized the complexity and flexibility of this technique by looking at the behavioral repertoire size, in terms of number of unique actions and grips employed, and the frequencies of usage of different actions and grips; we also analyzed the structural organization of this behavior by quantifying the length of the sequences and the variety of transitions observed, and we tested whether actions were non-randomly organized. Then, we investigated individual differences in technique. We tested whether subjects differed in the number of different actions used during a visit, whether they used preferred transitions between actions, and whether they preferred using certain actions or grips over others available in their repertoire. We predicted that all members of the community would have the same action repertoire and that the use of actions would be more likely dictated by nest-specific environmental challenges (i.e., soil hardness) rather than by individual preferences. Therefore, we did not expect differences among individuals in this domain. On the contrary, we hypothesized that, if alternative grips were available to perform one action, then individuals could perform it in different ways and, thus, we predicted the existence of individual differences in the grip used.

2 | METHODS

2.1 | Study site and data collection

Details on ecological parameters at our field site in Loango NP, Gabon (2°04'S, 9°33'E) were described elsewhere (Head, Boesch, Makaga, & Robbins, 2011). The focal chimpanzee community, called Rekambo (Head et al., 2013), was not fully habituated to human observers during this study.

Video data were collected between April 2009 and March 2014. We used remote-sensor camera traps (Sony Handycam with trail-master 700V, Scoutguard 550, and Bushnell Trophy Cam) to monitor opportunistically found underground nests of the stingless bee *M. lendliana* ($N = 50$ nests). Sony cameras recorded continuously until no movement was further detected within a 2-min interval; Scoutguard 550 and Bushnell Trophy Cam recorded 1-min clips, and were re-activated as long as movement persisted. Inter-clip intervals varied between 1 s and few minutes, due to possible malfunctioning of camera re-trigger. Footage from cameras was collected every 2 weeks. This non-invasive study was conducted in compliance with the regulations of the Centre National de la Recherche Scientifique et Technique of Gabon, and adhered to the American Society of Primatologists principles for the ethical treatment of primates.

We defined "visits" as all instances when one or more chimpanzees attempted to dig out an underground bee nest, either by manually digging or by using tools. A visit started when a subject arrived at the nest and ended when he/she departed from it. If the arrival or the departure was not recorded (due to a delayed trigger of

the camera trap), a visit comprised all the time a chimpanzee was recorded at the nest. A visit could comprise one or more clips recorded with intervals between them of no more than 15 min. Chimpanzees' behavior was coded using INTERACT 9 (Mangold, 2010). We recognized three main phases: (1) an exploratory phase; (2) a tool manufacture phase, comprising tool making (i.e., when the subject created a new tool) and tool modification (i.e., when the subject modified a tool that was previously used by himself/herself or by another chimpanzee); and (3) an extractive phase, possibly including tool use (*sensu* Shumaker et al. [2011]). The overall operational sequence showing all coded actions is depicted in Figure 1, and all operational definitions used for coding are in Table 1. For each action, we coded the "grip" used by the subject as one of the following, mutually exclusive types (Figure 2): "hands only," when the subject exclusively used one or two hands; "feet only," when the subject exclusively used one foot or two feet; and "both," when the subject used hands (one or two) and feet (one or two) simultaneously. Moreover, we coded the occurrence of a specific grip modifier, which we named "amplify strength," referring to when the subject held on to a support while exerting weight on the tool, thus applying a greater force to the action. Inter-observer reliability was assessed by comparing the observations coded by two raters in 18 different video clips (one per individual chimpanzee). In particular, we tested reliability for the number of occurrences of digging, pounding, and perforating (Spearman's $\rho = 0.7, 0.8, \text{ and } 0.8$, respectively), the type of grip used during perforations (Cohen's Kappa: $\kappa = 0.8, N = 76, p < 0.001$), and the occurrence of "amplify strength" for each perforation ($\kappa = 0.5, N = 76, p < 0.001$). These results show there were no problems with inter-observer reliability. From footage, we individually identified a total of

22 adult females, 11 adult males, and 37 immature chimpanzees (infant or juveniles and adolescents; age classes categorized following Boesch & Boesch-Achermann [2000]). Here, we focused on a subset of adult individuals (10 females and 8 males), for which we recorded a minimum of three visits each; our sample comprised 151 individual visits (Table 2).

2.2 | General features of the technique

We quantified the following features: observed repertoire size of actions and grips and their respective frequencies of usage, length of action sequences, and variety of transitions between two subsequent actions in a sequence. We defined a "sequence" as any instance where at least two actions occurred between the arrival and the departure of an individual to and from a bee nest (or between the beginning and the end of a visit, if arrival and departure were not recorded); if gaps in the footage occurred during a visit (due to malfunctioning of camera traps; maximum time gap = 14.2 s), the actions before and after these gaps were treated as separate sequences. Since our focus was the extractive technique, we lumped all exploratory actions into one category ("explore"), and we did the same for all actions involved in tool manufacturing, while we kept separate the actions involved in extraction (namely, manual digging and all tool use actions). The actions "extract," "lick," and "eat" were ignored in this analysis since they necessarily occurred only when chimpanzees successfully extracted the nest and are thus irrelevant with regard to the extractive technique.

We used a permutation test to assess whether individuals showed preferred action patterns in the sequence of actions. Sequences

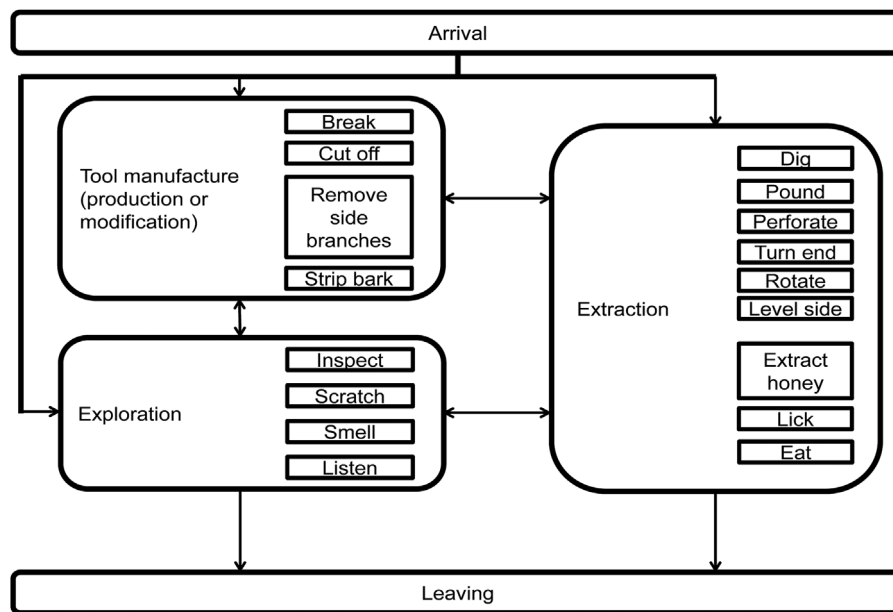


FIGURE 1 Operational sequence performed by chimpanzees to extract honey from underground bee nests in Loango NP, Gabon. Here, we indicated all possible actions that could occur within each phase, and arrows indicate all possible successions between different phases: upon arrival, one individual can manufacture a tool, explore, or attempt the extraction. Each phase can be followed by any other phase; transitions between actions that belong within the same phase are not specified here, given the high number of possible different transitions (see text for details about variation in transitions and action sequencing)

TABLE 1 Ethogram used for coding the behavior performed during attempted extractions of underground honey by chimpanzees in Loango NP, Gabon

Phase	Action	Operational definition
Exploration	Inspect ^a	Subject inserts the hand into the hole without removing anything (e.g., ground, honey, leftovers, dirt)
	Smell ^a	Subject brings an object (finger or stick or tool) to the nose
	Scratch ^a	Subject scratches the ground or the hole with hand or finger but no ground or dirt is evidently removed
	Listen	Subject directs the head towards the ground and moves it from side to side
Tool manufacture	Break ^a	Subject creates a new tool by detaching an object (e.g., branch or sapling) from a substrate (e.g., tree or ground)
	Strip bark ^a	Subject removes the bark from a sapling or tool
	Remove side branches ^a	Subject removes leaves or side branches from a sapling or tool
	Cut off ^a	Subject cuts one of the end of a sapling or tool in a sharp way
Extraction	Dig ^{a,b}	Subject removes ground or dirt from the hole or from around the entrance tube of the bee nest
	Pound ^{a,b}	Subject strikes a tool against the ground repeatedly
	Perforate ^a	Subject inserts a tool into the ground and applies a pressure so that it penetrates into the ground
	Turn end ^a	Subject turns a tool upside-down
	Rotate ^a	Subject keeps a tool inserted into the ground and moves it in circles or from side to side
	Level side ^a	Subject keeps a tool inserted into the ground and applies lateral pressure on it
	Extract ^a	Subject inserts a hand into the hole and extracts honey
	Eat ^{a,b}	Subject chews honeycombs or honey extracted from the nest
	Lick ^a	Subject licks honey from hand or tool

^aActions for which the “grip” was specified, as one of the following categories: “hands only,” “feet only,” or “both”.

^bActions coded as “bouts,” defined as continuous periods of time during which the subject acted accordingly; a bout ended when the subject either stopped for >2 s, dropped the tool or changed grip or body posture (Humble & Matsuzawa, 2009; Sousa, Biro, & Matsuzawa, 2009).

comprised exploration, tool manufacturing, digging, and tool use (i.e., pounding and perforating). For each individual, we first made a transition matrix detailing the frequency of each transition between two specific sequential actions (i.e., the rows corresponded to the first action type, the columns to the second action type, and each entry was the observed frequency of a transition between the first and second action types). Next, we ran a X^2 test on the transition matrix, in effect testing whether the observed transitions occurred randomly. Then, we ran X^2 tests on transition matrices obtained from randomized sequences (randomization without replacement, within each sequence; $N = 1000$ permutations, one of which was the observed data; R-function provided by R. Mundry). We finally compared the X^2 value calculated from the observed transition matrix with the X^2 values calculated from all randomized transition matrices. The p value was taken to be the proportion of randomizations revealing a X^2 at least as large as that of the observed sequences. We conducted this test twice per subject, once randomizing the sequences including repetitions of the same actions and once while keeping the number of repetitions constant throughout all permutations (i.e., testing only transitions between different actions).

2.3 | Individual preferences

We tested whether individuals differed in their action repertoire sizes across phases (model 1), in their action sequencing (models 2a–d), and in their preference for using different extractive actions (model 3) or grips (models 4a,b). We defined an individual as having a preference

for one or more types of extractive actions or grip types if there was a significant difference in the frequencies of usage among all types of actions or grips (e.g., if one individual used more often “pound” and “perforate” over “dig” then this individual had a preference for the former two actions).

In model 1, we tested the effects of sex, soil hardness at nest site at the time of the visit and the random slopes of “phase type” and “soil hardness” within “subject” on the number of different actions used during a visit by fitting a Generalized Linear Mixed Model (GLMM, Baayen [2008]; $N = 327$, each data point corresponds to the number of different actions used, per phase, by the subject in a visit) with Poisson error structure and log link function (McCullagh & Nelder, 1996). Soil hardness, expressed as centimeters of penetration of a stick into the soil, was obtained for each nest site at the time of each visit from a predictive model based on repeated measures taken at 29 nests (see Estienne et al. [2017] for details about the implementation of this predictive model). We controlled for “phase type” (three levels: exploration, extraction, and tool manufacture), and for the cumulative digging time at the nest prior to the visit (see Estienne et al. [2017] for how this variable was calculated). We included the random effects of nest site (37 levels), subject (18 levels), and visit identity nested in subject (accounting for the non-independence of actions performed during the same visit by one or more subjects; 109 levels), and all other necessary random slopes (Barr, Levy, Scheepers, & Tily, 2013), namely “cumulative digging time” within “subject” and “phase type” within “nest site.” Finally, we included the total number of actions performed during a visit as an offset term.



FIGURE 2 Snapshots captured from camera trap footage illustrating two examples for each of the three different grip types used by chimpanzees in Loango NP (see main text for detailed description of each): (a) “hands only”; (b) “both”; and (c) “feet only.” In addition, the occurrence of the grip modifier “amplify strength” is visible in b (left) and c (both pictures)

In models 2a,d, we tested the effect of previous action on the likelihood for a certain action to occur in the sequence (e.g., the likelihood of an action to be “pound” could be higher when the previous action was “dig”) as well as individual preferences for specific transitions. We fitted four GLMMs with binomial error structure and logit link function ($N = 1684$ transitions). The response variables were whether or not an action was pounding, perforating, digging, and exploring (models 2a–d, respectively); we ignored the actions “level side” and “rotate” because of being too rare in our sample ($N = 5$ and 6 , respectively), while “turn end” was ignored because it was more likely related to the ongoing wear of the used tool rather than to a functional need to reach the nest. We tested the effect of the immediate previous action (pounding, perforating, digging, or exploring) and the random slopes of “previous action” and “soil hardness” within “subject.” We controlled for sex of the subject, transition number (accounting for when, within a sequence, a transition occurred) and soil hardness at nest site at the time of the visit. We also included as random effects nest site (46 levels), subject (18 levels), and visit identity (nested in subject; 124 levels) and the following additional random slopes: “transition number” within “subject,” “previous

action” and “transition number” within “nest site,” and “previous action” and “transition number” within “visit identity”.

Finally, we used two GLMMs (both with Poisson error structure and log link function) to investigate the factors affecting the use of different actions and grips (models 3 and 4). In model 3, we focused on the three most commonly used extractive actions (i.e., digging, pounding, and perforating; $N = 294$). We tested the effects of soil hardness, type of action (three levels) and the random slopes of “action” and “soil hardness” within “subject” on the number of times an action was performed during a visit. We controlled for the sex of the subject and for the cumulative digging time at the nest prior to the visit. We included the random effects of nest site (34 levels), subject (18 levels), and visit identity (nested in subject; 98 levels), and the additional random slopes of “cumulative digging time” within “subject” and “nest,” as well the random slope of “action” within “visit.” We also included the duration of the extraction (calculated as the total duration of digging and tool use during a visit) as an offset term.

For the grips (models 4a,b) we focused on perforations, as this action was the one where most of the variability in the use of the modifier “amplify strength” occurred. In one model (model 4a; $N = 357$), we tested the effects of soil hardness, grip type (three

TABLE 2 Extraction of underground honey in Loango chimpanzees; for each individual are listed sex, number of visits to bee nests, number of successful extractions, number of different nests visited, total duration (in minutes) of recorded time, tool use and digging behaviors, number of different actions used (that is, the action repertoire size), number of recorded tool manufacture instances, average, and range of number of visits recorded per nest

Subject ID	Sex	N tot visits (successes)	N visited nests	Duration (min)			N different actions	N tool manufacture	N visits/nest	
				Visit	Tool use	Dig			Mean	Range
ARO	F	4 (0)	3	4.77	1.38	0.00	8	8	1.33	1–2
CHY	F	4 (2)	4	16.57	2.66	0.57	10	6	1.00	1–1
EMM	F	16 (0)	9	36.13	13.67	3.33	12	21	1.78	1–5
IDA	F	11 (2)	10	29.29	6.77	1.28	11	19	1.10	1–2
IKO	F	14 (1)	10	28.88	10.81	2.28	13	14	1.40	1–3
LOL	F	17 (0)	10	14.40	5.41	0.95	10	5	1.70	1–4
ONO	F	4 (0)	3	1.17	0.49	0.00	6	0	1.33	1–2
PEM	F	3 (1)	3	9.07	3.75	0.67	9	5	1.00	1–1
SUZ	F	5 (0)	4	12.38	3.00	1.37	7	2	1.25	1–2
VER	F	4 (1)	3	8.91	2.08	0.38	9	3	1.33	1–2
CHE	M	14 (2)	9	33.06	9.41	2.67	12	16	1.56	1–3
CHI	M	7 (1)	5	12.67	2.74	0.64	12	12	1.40	1–3
CHU	M	5 (1)	4	9.95	1.22	0.87	10	4	1.25	1–2
EBA	M	7 (2)	7	26.71	1.15	2.41	10	10	1.00	1–1
EMI	M	7 (0)	7	7.65	3.66	0.17	8	8	1.00	1–1
JAC	M	4 (0)	3	6.67	1.39	0.17	9	6	1.33	1–2
OBO	M	8 (0)	6	13.80	3.38	0.25	10	11	1.33	1–3
SHA	M	17 (0)	12	24.36	7.60	2.44	13	29	1.42	1–3

levels: “hands only,” “feet only,” “both”) and the random slopes of “grip type” and “soil hardness” within “subject” on the number of times a grip was used. We controlled for sex of the subject and included the random effects of nest site (45 levels), subject (18 levels), and visit identity (nested in subject; 119 levels). We included the additional random slopes of “soil hardness” and “grip” within “nest” as well as “sex” within “nest.” We tested the effects of the same predictors listed above on the number of times “amplify strength” occurred for each grip type used while perforating (model 4b; $N = 238$). In this model, the variable “grip” comprised only two levels (“hands only” and “both”), since when using “feet only” subjects must necessarily hold a support on which they exert force while perforating. We controlled for sex of the subject and included the same random effects and random slopes as above. Finally, we included the total number of times each grip was used as an offset term.

2.4 | Model implementation

All analyses were conducted in R (version 3.1.0) (R Core Team, 2014) and GLMMs were fitted using the function `glmer` of the package `lme4` (Bates, Maechler, Bolker, & Walker, 2015). Correlations between random slopes and random intercepts were not included to avoid overly complex models, and since omitting them does not increase the risk of type I error (Barr et al., 2013). We inspected Variance Inflation Factors (VIF) (Field, 2005) derived using the function `vif` of the package `car`, based on standard linear models excluding the random effects, and

concluded that collinearity among predictors was not an issue (max. VIF = 1.151). For Poisson models, overdispersion was not detected in any of the models (models 1, 3, 4a, and 4b: dispersion parameters = 0.78, 0.85, 0.38, 0.66, respectively). Model stability was assessed by comparing the estimates derived from a model based on all data with those obtained from models based on subsets obtained by excluding levels of the random effects one at a time and no issues were found. In all cases, we tested the significance of the test predictors (Forstmeier & Schielzeth, 2011) by comparing the full model with a null model comprising only the control predictors and the offset term (if present) using a likelihood ratio test (function `anova` with argument test set to “Chisq”). All covariates were z-transformed, and the offset terms were log-transformed before fitting the models.

3 | RESULTS

3.1 | General features

Overall, we identified 14 distinct actions occurring in the repertoire of our subjects. All individuals performed the exploratory actions “scratch” and “smell”; manual inspection was performed by seven females and four males, whereas “listen” was observed in only two females. All subjects but one female manufactured tools: in particular, the action “cut off” was used by all tool manufacturers; whereas “break” was used by seven females and seven males, “remove side

branches" was used by five females and seven males, and "strip bark" was used by five females and five males. During the extractive phase, only two males and one female exhibited the complete action repertoire, while most of the subjects used only four different actions. In particular, all subjects performed "perforate" and "pound," whereas "level side" and "rotate" were rare (the first used only by two females and two males, the latter used by one female and three males); two females were never observed digging with hands (although their sample is relatively small). Overall, the average number of different exploratory actions used by females was comparable to that used by males (range of averages for females: 1.00–2.00 different actions; range for males: 0.86–1.71); the same applied for the tool manufacturing phase (range for females: 0.00–1.67; range for male: 0.60–1.57). Nevertheless, females performed on average a slightly lower number of different actions in the extractive phase as compared to males (range for females: 1.25–3.00; range for male: 2.14–3.00).

When perforating, all individuals used the grip types "both" and "hands only," whereas only three subjects (two females and one male) used "feet only," and one individual used it with comparatively higher frequency than others (10 out of 14 total observations belonged to PEM; Figure 3). The longest observed sequence included 280 actions. For successful visits, the number of actions ranged between 3 and 186. Overall, we observed 109 different transitions between actions.

The permutation test including sequences with repetitions showed that ten individuals (six females and four males) used non-random sequences of actions (range p : 0.001–0.055); when analyzing sequences that disregarded repetitions, these results held for five females and two males (range p : 0.001–0.037). Individuals that used sequences significantly different from random showed a more consistent use of specific transitions as compared to individuals for whose observed sequences did not significantly differ from randomized sequences. These specific transitions were those between exploratory actions and one of the three most common extractive actions ("pound," "perforate," or "dig"; Figures 4 and 5; see Table S1 for the results of the permutation test).

3.2 | Individual preferences

The action repertoire size employed during a visit was significantly affected by soil hardness (model 1; full vs. null model: $X^2 = 65.874$, $df = 7$, $p < 0.001$; Tables S2), with individuals using a bigger action repertoire when the soil was harder (estimate \pm SE: -0.168 ± 0.064 ; $X^2 = 5.779$, $df = 1$, $p = 0.016$). We also found a trend for the effect of sex, with males performing more different actions than females (estimate \pm SE: 0.256 ± 0.140 ; $X^2 = 3.268$, $df = 1$, $p = 0.071$). Neither the effect of phase nor the effect of soil hardness differed significantly among individuals (Tables S2). Our models showed that, in a sequence, the occurrence of specific actions was significantly affected by the type of the action immediately preceding them (Figure 6). In particular, pounding was more likely to occur after exploration and digging (model 2a; full vs. null model: $X^2 = 35.834$, $df = 8$, $p < 0.001$; effect of "previous action": $X^2 = 23.235$, $df = 3$, $p < 0.001$; Table S3). The occurrence of pounding, in turn, significantly increased the probability of perforating to occur (model 2b; full vs. null model: $X^2 = 26.490$, $df = 8$, $p = 0.001$;

effect of "previous action": $X^2 = 19.524$, $df = 3$, $p < 0.001$; Table S3). Digging was more likely to be preceded by digging than by any other action (model 2c; full vs. null model: $X^2 = 25.361$, $df = 8$, $p = 0.001$; effect of "previous action": $X^2 = 24.199$, $df = 3$, $p < 0.001$; Table S3). Finally, exploring was most likely to occur after perforation (model 2d; full vs. null model: $X^2 = 34.438$, $df = 8$, $p < 0.001$; effect of "previous action": $X^2 = 20.018$, $df = 3$, $p < 0.001$; Table S3). Nevertheless, the effects of previous action and soil hardness were consistent across individuals (results of the tests for the random slopes for models 2a–d are summarized in Table S4).

In terms of frequencies of usage of extractive actions, all individuals used on average the actions "perforate" and "pound" more often than "dig" (model 3; full vs. null model: $X^2 = 93.636$, $df = 8$, $p < 0.001$; effect of "action": $X^2 = 72.671$, $df = 2$, $p < 0.001$; Table S5). Soil hardness had no significant effect. Subjects did not significantly differ in their relative frequency of use of different actions (Table S5; Figure S1), and this result held for soil hardness, as well (Table S5). We also found significant differences in the frequencies of usage of grips during perforations (model 4a; full vs. null model: $X^2 = 124.244$, $df = 7$, $p < 0.001$). In particular, all individuals used the grip "both" on average more often than any of the other two grip types (effect of "grip": $X^2 = 47.755$, $df = 2$, $p < 0.001$; Table S6), whereas the grip "feet only" was generally strongly avoided (Figure 3). Moreover, subjects significantly differed in their preference for using different grips (test for the random slope of "grip" within subject: $X^2 = 25.514$, $df = 2$, $p < 0.001$) whereas soil hardness did not significantly affect the response and this was consistent across individuals (Table S6). Regarding the usage of the modifier "amplify strength," we found that all individuals used it more often when perforating using only hands as compared to when using hands and feet simultaneously (model 4b; full vs. null model: $X^2 = 19.654$, $df = 5$, $p = 0.001$; predictor variable "grip": estimate \pm SE = 0.637 ± 0.104 ; $X^2 = 17.568$, $df = 1$, $p < 0.001$; Table S7). However, no differences among individuals were found with regard to the effects of grip or soil hardness, nor was there an effect of soil hardness in general (Table S7).

4 | DISCUSSION

Our analyses revealed that the extraction of underground honey as performed by chimpanzees in Loango NP involved a high number of distinct functional elements, sorted in long sequences that included a large variety of combinations of actions. Despite such potential diversity in action sequencing, some of the individuals in our sample showed non-randomly organized sequences; whereas the lack of significant results for other individuals is likely linked to a limited number of observations. In particular, we found that all subjects recurrently switched between the exploratory and the extractive phases. As predicted, individuals did not differ in their relative repertoire sizes across phases, or in how they sequenced extractive actions and exploration, indicating that these features were a shared, necessary component of this technique. Interestingly, the action repertoire used during a visit was affected by local conditions: as penetration into the soil became easier, chimpanzees used a less

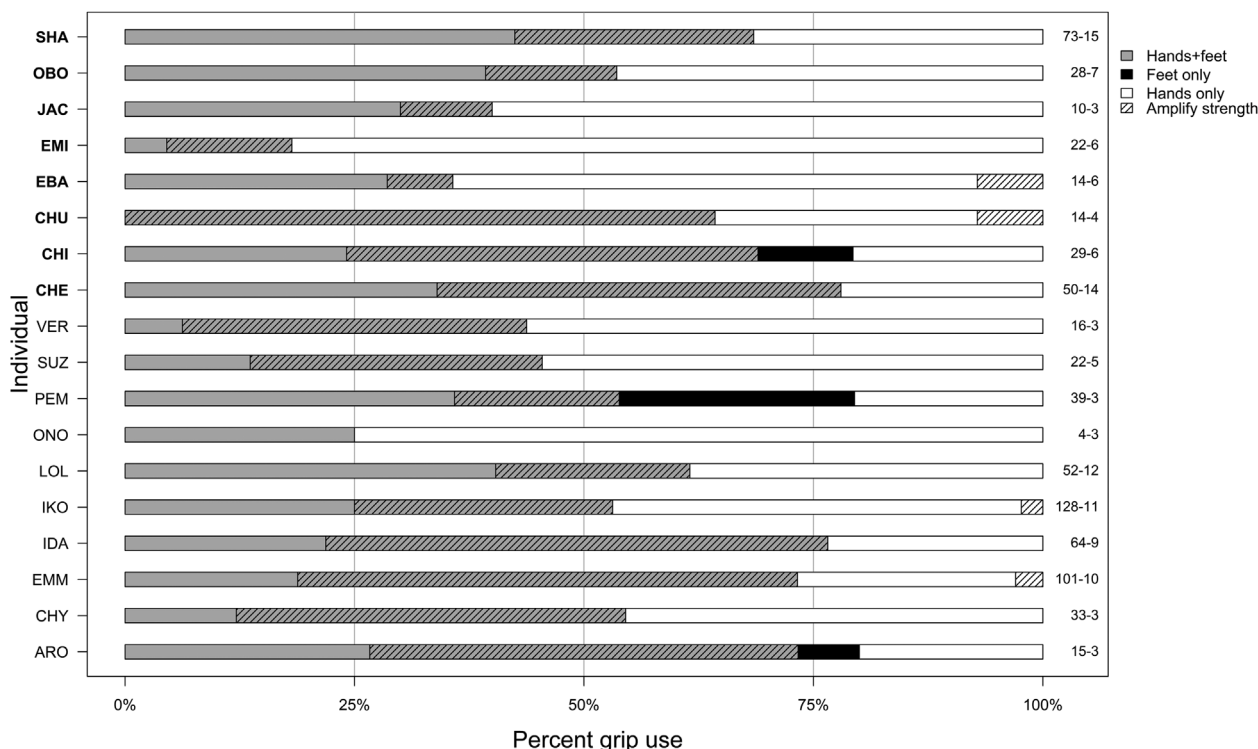


FIGURE 3 Individual variation in the percentage of times different grips (with or without the occurrence of the modifier “amplify strength”) were used by chimpanzees in Loango NP when perforating in order to extract underground honey; subjects are listed on the left side of the plot, and sorted by sex (males indicated in bold); on the right, we report the number of perforations and the number of visits considered, respectively

diverse repertoire. Males tended to use a more varied repertoire than females. This seemed to contradict the general view that female chimpanzees would be more skilled tool users (Boesch & Boesch, 1981; Gruber, Clay, & Zuberbühler, 2010). Our data showed that action repertoire sizes were comparable between males and females for the exploratory and tool manufacturing phases, but males used, on average, a greater number of different actions in the extractive phase. In particular, more males than females used the actions “level side” and “rotate.” This could be due to the fact that males, having a bigger body size than females, needed to enlarge the holes more in order to insert their hands and reach the bee nests. Alternatively, in line with previous findings, females could be seen as being better tool users as compared to males: that is, they would need a less variable technique to obtain results comparable to those achieved by males. In fact, contrary to what has been found in other tool use techniques (i.e., nut cracking; Boesch & Boesch [1981]) the number of successes was comparable between sexes (Table 2). This suggests that neither physical strength nor other sexually dimorphic characters affected success, although our small sample of successes precluded statistical testing.

Additionally, individuals did not differ in their relative use of different types of actions, but we found a general preference to use tool-aided extractive actions (i.e., perforating and pounding) rather than manual digging, supporting the idea that tools would aid chimpanzees in their proficiency in digging out the underground bee nests (Estienne et al., 2017). On the contrary, while the grip involving hands and feet together was the most frequently used by all subjects during perforations, we also found that individuals differed in their

preferences in this domain. In particular, the grip “feet only” was used by only three individuals, and most consistently by one of them (PEM). Interestingly, environmental conditions (i.e., soil hardness) had the same effect on the behavior of all individuals, strengthening the view that our results reflected individual idiosyncrasies.

The extraction of underground bee nests has been reported for chimpanzees across their range, but all data derived from indirect evidence (*P. t. troglodytes*: Deblauwe [2006]; Fay & Carroll [1994]; Hicks, Fouts, & Fouts [2005]; *P. t. vellerosus*: Fowler & Sommer [2007]; *P. t. schweinfurthii*: Kajobe & Roubik [2006]; McLennan [2011]; Yamagiwa, Yumoto, Ndunda, & Maruhashi [1988]). Thus, a direct comparison of behavioral repertoires for this technique is impossible. Nevertheless, our results suggested a remarkable degree of complexity and flexibility for this technique as compared to other tool use techniques reported for wild chimpanzees. In fact, the action repertoire size of underground honey extraction exceeded the ones described for both termite and honey gathering techniques in Goulougo, considered as the most complex tool use techniques among those used by chimpanzees there (Table 3). This holds true even when comparing only the number of strictly extractive actions considered in our study (five in total) with the number of extractive actions reported for Goulougo (two and three for termite and honey gathering respectively), excluding thus the actions involved in exploratory behaviors, tool manufacturing, and resource consumption, which can be accounted for in different ways depending on the degree of detail of the study. The repertoire size described in our study is also larger than the ones reported for nut cracking and leaf sponging

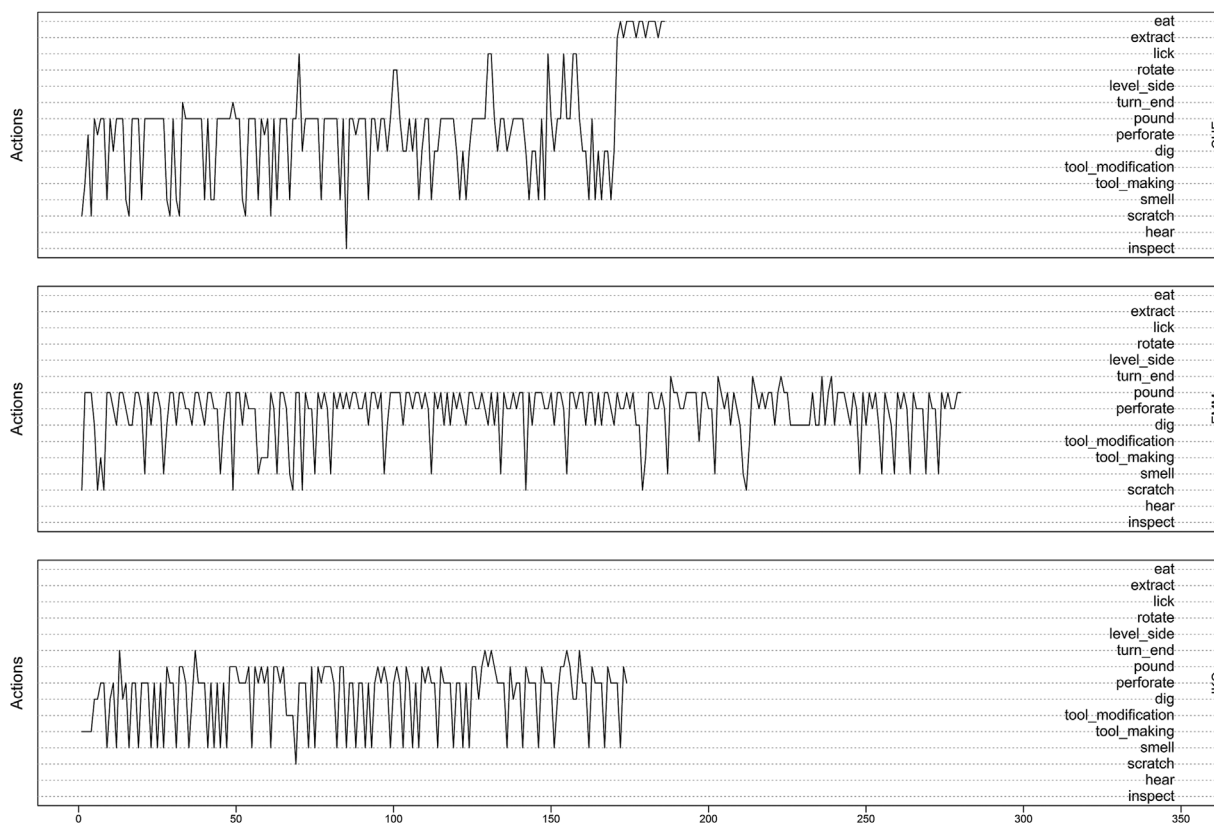


FIGURE 4 Three examples of the sequences of actions to extract underground bee nests by chimpanzees in Loango NP: actions are listed on the right side of the plot, with the name of the subject attempting the extraction; the line shows the sequence of actions; the top most plot represents a successful extraction after performing *ca.* 180 actions, whereas the other two (middle and bottom) were unsuccessful attempts. Notice the recurrent transitions between one of the exploratory actions (in particular, “smell”) and the extractive actions (in particular, “dig,” “perforate,” or “pound”)

(Table 3). Significantly larger repertoires were recorded only for food processing techniques of wild mountain gorillas (Byrne & Byrne, 1993), counting 20 distinct actions. This number increases to include hundreds of different elements when the definition used to characterize unique elements accounts for the precise grip and fingers used while performing an action (222 elements for thistle processing, 78 for gallium, and nettle leaves; Byrne et al. [2001]).

The technique investigated here also exhibited a higher degree of flexibility as compared to other tool use techniques, as shown by the variety of possible transitions between actions (Table 3). Again, greater flexibility was described only for gorillas' food processing techniques (256 action sequencing patterns for thistle processing; Byrne et al. [2001]). Our study also highlights chimpanzees' behavioral flexibility, denoted as the ability to use similar strategies across different contexts presenting analogous challenges, which is considered an index of understanding of causal relationship between different external objects (Boesch, 2013). In particular, the extraction of underground bee nests presents some striking similarities with termite gathering at subterranean nests rather than other honey gathering techniques. In fact, the puncturing behavior reported from the Goulougo Triangle (Sanz, Morgan, & Gulick, 2004) resembled the perforating behavior in Loango NP. Puncturing sticks (also called perforating or digging sticks) were reported in the context of termite consumption for other

populations of central African chimpanzees (Congo and Central African Republic: Bermejo & Illera [1999]; Suzuki, Kuroda, & Nishihara [1995]; Cameroon: Deblauwe, Guislain, Dupain, & van Elsacker [2006]; Muroyama [1991]; Equatorial Guinea: Sabater Pí [1974]; Gabon: McGrew & Rogers [1983]), and our observations support that perforation could be a distinctive element of the repertoire of this subspecies (Sanz et al., 2004). Nevertheless, the function of the same action seemed to differ according to the nature of the resource: termite nests are more widely dispersed underground, thus chimpanzees need to create an access point from which to fish the insects; on the contrary, underground stingless bee nests are more circumscribed, requiring a different strategy to access them. Similarly, the flexible use of the same action across contexts can be discussed for “pounding,” described as a widespread behavior for honey extraction in central African chimpanzees. In our study this action seemed to act as a way to smooth the earth within the hole and enlarge it, rather than directly access the hive (Sanz & Morgan 2009); it resembles more the pounding used by capuchins to enlarge cavities when trying to reach small prey (Falótico & Ottoni, 2016).

An additional feature increasing the level of complexity and flexibility shown by this behavior is that one action could be performed with different grips, also involving the simultaneous use of hands and feet. Such a coordinated grip used when perforating resembled the

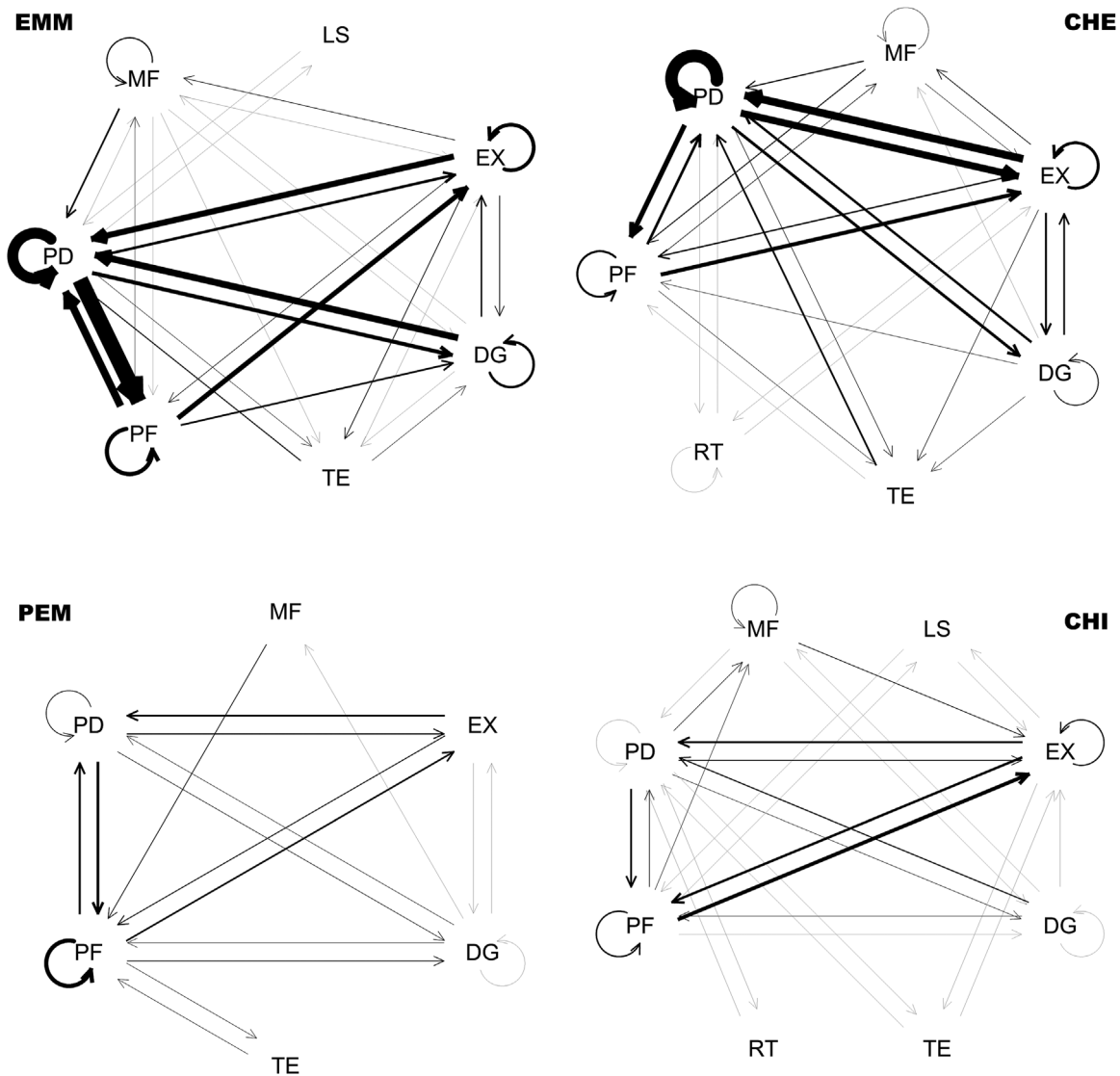


FIGURE 5 Examples of transitions occurring during attempts to extract underground honey by chimpanzees in Loango NP; in particular, the figure depicts the transitions of one female (top left; EMM) and one male (top right; CHE) showing significant non-random sequences, and of one female (bottom left; PEM) and one male (bottom right; CHI) showing sequences that are not significantly different from random sequences (see results of the permutation test in Table S1); lines represent transitions between two actions, while the line thickness represents the number of occurrences for each transition (total *N* of transitions per subject = 395, 316, 98, and 109 for EMM, CHE, PEM, and CHI, respectively); the actions in the figure are coded as follows: DG = dig, EX = explore, LS = level side, MF = tool manufacture, PD = pound, PF = perforate, RT = rotate, TE = turn end. Individuals that performed sequences different from random (EMM and CHE) used more consistently transitions between exploratory actions (EX) and extractive actions (DG, PF, and PF) as compared to individuals whose sequences did not differ from random (PEM and CHI)

one previously described for the perforation of termite mounds (Sanz et al., 2004). It was proposed that this type of grip could increase the force of the action, and this would explain why, in our study, all subjects seemed to prefer such a grip as compared to the others. We also observed the occurrence of the grip modifier “amplify strength,” which could further increase the strength applied to the tool. Moreover, since we found that individuals differed in their grip preference, the use of this modifier could serve as an alternative strategy to increase the force of the action when a grip different than the coordinated use of hands and feet was preferred. Since individuals did not obviously differ in the use of the grip modifier, this seemed to be a common strategy in this community. As found for the techniques

used for leaf processing in gorillas (Byrne & Byrne, 1993), it seems that, when different but equally effective options are available in the repertoire, then individuals do exert a choice.

The assessment of the degree of complexity and flexibility expressed in a tool use behavior could give insight into the evolution of key cognitive abilities in the human lineage (Ardila, 2008), such as the ability to organize goal-directed sequences of actions, possibly for a delayed reward (Coolidge & Wynn, 2001). We found evidence for the ability of chimpanzees to deliberately organize their actions to extract the underground bee nests, as showed by the fact that the sequences they performed were neither strictly determined nor random (Gadbois, Sievert, Reeve,

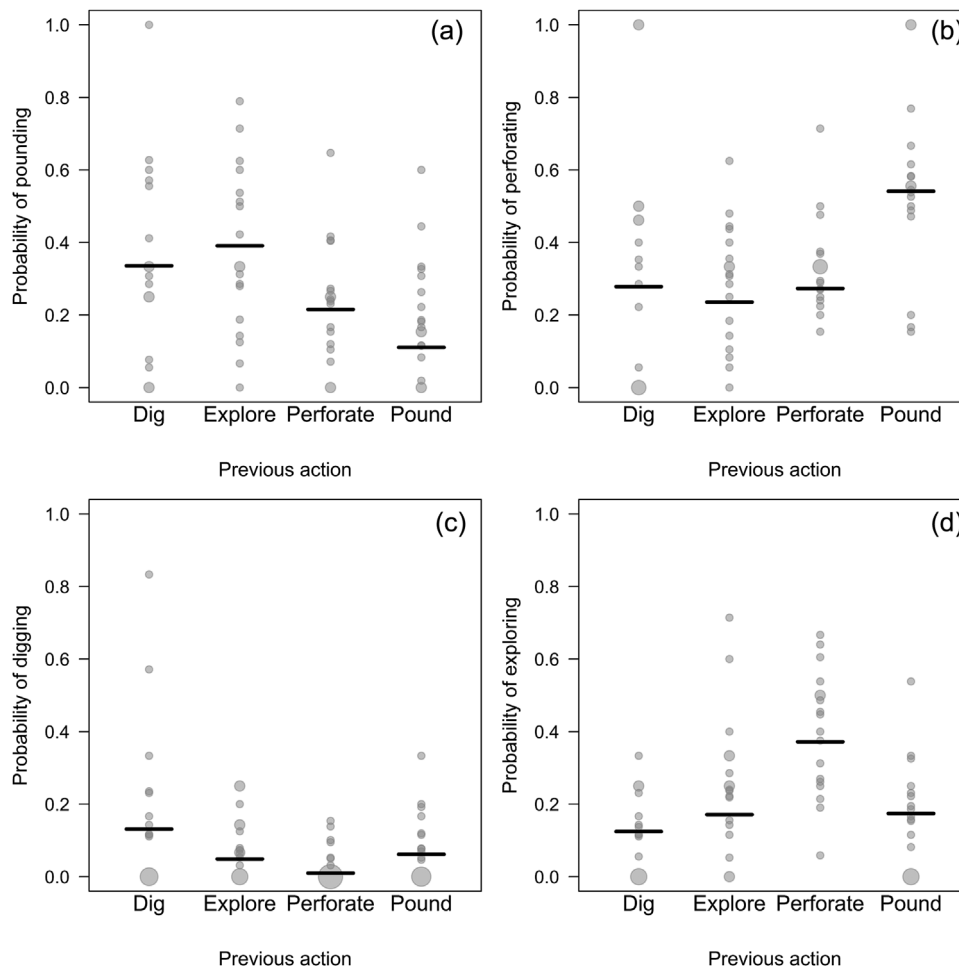


FIGURE 6 Effect of the type of action preceding pounding (a), perforating (b), digging (c), and exploring (d) on the probability of each of these actions to occur in the sequence, during an attempt to extract underground bee nests by chimpanzees in Longo NP; the area of each circle represents the frequency of occurrence of a certain action to occur in the sequence, and horizontal lines show the fitted probabilities from the GLMM (models 2a,d; $N = 1842$ in all models)

Harrington, & Fentress, 2015). The ability to sequentially organize different behavioral elements has been already described for termite fishing and honey gathering (Sanz & Morgan, 2010, 2011). Nevertheless, the technique that we investigated is particularly interesting given the structure of the targeted bee nests. In fact, the apes had to reach a resource that they cannot directly perceive given that the only cue they can use to detect the presence of a bee nest is the protruding wax tube (but this is not indicative of the actual nest's location) (Boesch, 2013). Furthermore, reaching the bee nests can potentially require a prolonged effort, as showed by the high number of actions performed during the visits to the nests. Solving problems encompassing high spatio-temporal distance between their perception and their solution has been proposed to underlie higher cognitive abilities (Haidle, 2010). Our data showed that chimpanzees consistently explored following perforations, mostly by smelling the same tool previously used (86% of the exploratory cases), supporting the hypothesis that the tube served as an indirect index for tracking the hidden resource (Boesch, 2013). Therefore, in this technique, the use of tools would aid chimpanzees not only in the physical domain, but also by

mediating the flow of information needed to locate the nest chamber (St Amant & Horton, 2008).

Overall, our results showed that wild chimpanzees used a complex technique to extract an out-of-sight resource, showing evidence of action organization coupled with the ability to flexibly adjust their behavior depending on local circumstances. Our study adds evidence that the exploitation of insects and their products would have had a relevant role in the evolution of technological abilities and associated cognitive traits during human evolution (McGrew, 2014; Sutton, 1995). Moreover, our study reinforces the call for including the nature of the task and the environment in the analysis of a tool use behavior (Mangalam & Frigaszy, 2016) and highlights the occurrence of significant inter-individual differences in the tool use domain, as recent studies have pointed out (Gruber, 2016; Massen, Antnides, Arnold, Bionda, & Koski, 2013). This aspect has been increasingly recognized as having potentially relevant implications in shaping ecological and evolutionary processes (Bolnick et al., 2003; Meulman, Seed, & Mann, 2013), and our results add to the growing body of evidence that suggests considering this dimension in the analysis of behavioral traits.

TABLE 3 Comparison of repertoire sizes and variability in action sequencing occurring in different tool use techniques used by chimpanzees

Technique	Action repertoire size (N fundamental actions)	N different transitions	Field site	Reference
Underground honey extraction	14 ^a	3 (explore–pound–perforate)	Loango	this study
Arboreal honey gathering	13 (5) ^{a,b}	3 (pound-hive inspection-honey gathering)	Goulougo triangle	Sanz and Morgan (2010)
Leaf sponging	4 (3) ^{a,b}	2 (insert-suck)	Goulougo triangle	Sanz and Morgan (2010)
	2 [+4] ^a	NA	Bossou	Sousa et al. (2009)
	4 [+3] ^a	2 (suck-take out)	Bossou	Tonooka (2001)
Nut cracking	4 ^b	3 (collect nuts-crack-eat)	Taï	Boesch and Boesch (1982)
	21 (5) ^b	NA	Bossou	Inoue-Nakamura and Matsuzawa (1997)
Termite fishing (elevated nests)	3	NA	Mahale	Nishida and Hiraiwa (1982)
	8 (5) ^{a,b}	2 (strengthen brush-insert probe)	Goulougo triangle	Sanz and Morgan (2010)
Termite fishing (subterranean nests)	9 (7) ^{a,b}	3 (strengthen brush-insert probe-gather termites)	Goulougo triangle	Sanz and Morgan (2010)

^aIncluding tool manufacture.

^bIncluding resource consumption.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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