# Acquisition of a complex extractive technique by the immature chimpanzees of Loango National Park, Gabon

Vittoria Estienne [a, *], Benjamin Robira [a, b], Roger Mundry [c], Tobias Deschner [a], Christophe Boesch [a]

[a] Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany
[b] Institut de Biologie de l'Ecole Normale Supérieure (IBENS), Ecole normale supérieure, CNRS, INSERM, PSL Research University, Paris, France
[c] Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

The relative importance of individual and social learning in acquiring complex technological skills in animals is debated, especially the influence of processes allowing high copying fidelity (namely, imitation and teaching). We investigated how immature wild chimpanzees, *Pan troglodytes troglodytes*, acquired the technique for extracting underground honey. This technique is interesting because (1) adults perform exploration, pounding and perforation in nonrandom but highly flexible action sequences to locate underground bee nests, (2) they have individual preferences for how to perforate the ground and (3) the nests are deeply buried and concealed, making success difficult to achieve. We analysed the behaviour of 16 immatures recorded by camera traps at 50 sites, and tested the influence of individual attributes (namely, age and sex) and maternal behaviour; we also tested whether mothers provided learning opportunities for their offspring. We found that, as they aged, immatures of both sexes progressively matched adults' behaviour in action sequences and observed their social models more continuously. Immature males used the most common grip type used by adults for perforating (namely, the coordinated use of hands and feet) progressively more as they aged, but no effect of maternal preferences was detected. Thus, the adult technique was probably acquired via a combination of physical maturation (i.e. increased body strength and motor coordination) and observational learning, although individual learning could not be completely ruled out. Finally, the proportion of time mothers spent inactive at bee nest sites was high when they were accompanied by young daughters and decreased as daughters aged, while the opposite pattern was found for sons. Mothers may thus stimulate learning by immatures by adjusting their behaviour according to their offspring's sex and age. Overall, we showed that immature chimpanzees acquired this complex tool use behaviour via a combination of social and nonsocial learning processes, including potential maternal stimulation.

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The process of cumulative culture has been proposed to be uniquely human, sustained by processes that allow high-fidelity transmission of behavioural traits leading to the emergence of complex technological skills (Dean, Vale, Laland, Flynn, & Kendal, 2014). To explain the evolutionary roots of this process, researchers have focused on understanding the relative contributions of individual learning and social influences in the transmission of specific behaviours in animals, particularly in our closest living relatives. Social learning, defined as the ability to learn from others' behaviour or from the resulting products (Galef & Laland, 2005;

Heyes, 1994), is widespread across the animal kingdom (Fragaszy & Perry, 2008), and several underlying processes are involved (Hoppitt & Laland, 2008; Rendell et al., 2011; Whiten, Horner, & de Waal, 2005). Previous studies have shown that animals can learn simply by being attracted to a certain part of the environment by the activity of others (that is, learning by local or stimulus enhancement; Galef & Giraldeau, 2001) or by observing the relationship between stimuli disclosed by the behaviour of another individual (i.e. observational learning; Heyes & Dawson, 1990). Animals can also copy the actions of others. The term 'copying' can refer to two different processes: reproducing the results of another individual's action, denoted as 'emulation', or reproducing the action itself, which has been termed 'imitation' (Tomasello & Call, 1997). It has now been extensively shown that, depending on the

* Correspondence: V. Estienne, Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Deutscher Platz 6, 04103 Leipzig, Germany.
*E-mail address:* vittoria_estienne@eva.mpg.de (V. Estienne).

species and context, primacy may rely on a number of social learning processes, such as local and stimulus enhancement, direct and indirect social facilitation and observational learning (Gunst, Boinski, & Fragaszy, 2008; Hobaiter, Poisot, Zuberbühler, Hoppitt, & Gruber, 2014; Inoue-Nakamura & Matsuzawa, 1997; Jaeggi et al., 2010; Lonsdorf, 2005; Perry, 2009; Price, Lambeth, Schapiro, & Whiten, 2009; Schuppli et al., 2016). Nevertheless, studies in captivity have found no evidence for the occurrence of imitation in great apes (Call, Carpenter, & Tomasello, 2005; Tennie, Call, & Tomasello, 2006) and thus have suggested that apes acquire behavioural patterns through a combination of emulative learning and individual trial-and-error (Tennie, Call, & Tomasello, 2009). However, a more complete consideration of the data has led others to propose that chimpanzees, *Pan troglodytes*, could also learn via imitation of conspecifics (Whiten, Horner, Litchfield, & Marshall-Pescini, 2004; Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). In addition, a number of studies have looked at the transmission of techniques used to obtain and process food, showing that primates are capable of motor imitation in copying single actions (e.g. marmosets, *Callithrix jacchus*: Voelkl & Huber, 2000; vervet monkeys, *Chlorocebus aethiops*: van de Waal & Whiten, 2012) as well as the structural organization of complex sequences of actions (e.g. chimpanzees: Whiten, 1998; mountain gorillas, *Gorilla beringei*: Byrne, 2002, 2003; Byrne & Russon, 1998; Byrne, Hobaiter, & Klailova, 2011).

Another key process allowing high-fidelity transmission of behaviour is teaching, whereby changes in the behaviour of skilled individuals facilitate learning by naïve individuals. Teaching is more likely to occur when other learning processes would be insufficient due to the complexity of the task involved (Boesch, 2013; Kline, 2015). Comparative psychologists advocate that teaching relies on psychological processes that are unique to the human species (Tomasello, Kruger, & Ratner, 1993), as demonstrators must be capable of understanding the lack (or the degree) of knowledge in naïve individuals and communicative intentions (that is, they must possess a full-blown theory of mind; Tomasello, Call, & Hare, 2003; Kaminski, Call, & Tomasello, 2008), so that they can intentionally transmit information to others. Nevertheless, more recent evidence from experiments conducted in the wild has shown that chimpanzees intentionally share information about danger with ignorant group members, in noncompetitive contexts (Crockford, Wittig, Mundry, & Zuberbühler, 2012). On the other hand, evolutionary biologists propose a behavioural-based approach, in which teaching interactions may be identified by considering their functional aspects, thus accounting for the relative costs and benefits involved for both the demonstrator and the naïve individual (Caro & Hauser, 1992). Adopting this approach, convincing evidence for functional teaching has been found in a few, taxonomically widely distributed, species (i.e. meerkats, *Suricata suricatta*: Thornton & McAuliffe, 2006; pied babblers, *Turdoides bicolor*: Raihani & Ridley, 2008; tandem running ants, *Temnothorax albipennis*: Franks & Richardson, 2006). These results showed that demonstrators intentionally create teaching contexts for their observers, which in turn can learn via a variety of processes (Hoppitt et al., 2008). Two studies have proposed potential forms of functional teaching in wild chimpanzees. First, early observations suggested that mothers enhance the learning of nut cracking by their offspring using different strategies, including regular and age-specific stimulation, facilitation and possibly (although rarely) active teaching (Boesch, 1991; Boesch & Boesch-Achermann, 2000). Second, a recent study has proposed that tool transfer mediates the learning of termite fishing (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016). Nevertheless, teaching is considered unlikely to occur in chimpanzees since naïve individuals are highly exposed to the activity of

experienced conspecifics; thus, skill acquisition can occur via inadvertent social learning (Hoppitt et al., 2008).

Within this framework, we investigated how immature wild chimpanzees (*P. t. troglodytes*; aged between 0 and 15 years) in Loango National Park, Gabon, acquire the technique for extracting honey from the underground nests of stingless bees, *Meliplebeia lendliana*. We analysed how age and sex affected the development of this technique and specifically asked whether immatures imitated their mothers' technique, since mothers are known to represent the main model for young chimpanzees (Boesch & Boesch-Achermann, 2000; Goodall, 1968; Lonsdorf, 2005). Because our data consist of camera trap footage recorded at a limited number of underground bee nest sites, we reasoned that 'age' would be a better predictor of the amount of time that immatures had the opportunity to observe their mothers, rather than the amount of time that immatures spent observing their mothers recorded in our footage; nevertheless, we took into consideration the object of immatures' observations in order to evaluate possible ontogenetic changes in the focus of their attention. We then asked whether mothers changed their behaviour to stimulate their offspring's learning process by providing learning opportunities, which could represent a form of functional teaching. Following Caro and Hauser (1992), functional teaching occurs when: (1) the demonstrator modifies its behaviour only in the presence of a naïve observer; (2) the demonstrator incurs some cost or at least does not obtain an immediate benefit for itself; and (3) as a result of the demonstrator's behaviour, the naïve individual acquires knowledge or learns a skill earlier in life or more rapidly or efficiently than in the absence of the demonstrator's behaviour. Expanding this definition, Hoppitt et al. (2008) stressed the active role that the demonstrator has in facilitating learning by naïve observers. In this study, we investigated the behaviour of the mothers to assess the first condition, and we discuss why the second condition is also satisfied in this context. Unfortunately, we could not address the key point represented by the third condition due to the low number of successful extractions achieved by immatures in our sample (N = 2), which prevented us from directly testing the factors influencing success rate among immatures.

Two main features of this technique qualify it as a particularly interesting case for investigating these topics. First, adult individuals in the study community use a highly complex honey extraction technique, consisting of structured sequences of exploratory and extractive actions, to reach an out-of-sight resource which is difficult to access. In particular, adults prefer to use the action transitions 'explore-pound-perforate-explore'. This order presumably allows the apes to locate the underground nest chamber by tracking down the entrance tube. Despite the occurrence of such recurrent transitions, action sequences are not rigidly fixed: on the contrary, they are highly flexible since they are adjusted depending on the specific environmental conditions found at each nest (Estienne, Stephens, & Boesch, 2017). The bee nests are deeply buried (located between 14 and 117 cm underground), their presence is inconspicuous and the precise location of the honey chamber is unknown (Estienne, Mundry, Kühl, & Boesch, 2017). These factors limit the success rates of skilled individuals, which require multiple attempts before accessing a nest (Estienne, Mundry et al., 2017). Moreover, each nest can be exploited only once, as the bees leave the nest after a successful extraction. Hence, immatures must acquire a specific sequence of actions in a context where they cannot gain information simply by being exposed to positive outcomes (i.e. consumption of honey) associated with the activity of an experienced individual, nor can they learn by multiple exposures to the technique associated with a specific nest, since the resource is hidden, available only once and rarely attained by adults. Moreover, although adults share the same technique in

terms of action sequencing, they differ in their preferences for the type of grip used to hold the tool when perforating nests. In particular, although there was a general preference for a grip involving the coordinated use of hands and feet together, individuals also differentially used other types of grip that employed the exclusive use of either hands or feet (Estienne, Stephens et al., 2017). Therefore, immatures are exposed to a variety of possibilities regarding how to perform a single action, with their mothers potentially having their own specific preference. This allowed us to analyse whether immatures imitate their mothers' preferences for the perforating grip type. With regard to the action sequences, one hypothesis (the latent solution hypothesis; Tennie & Hedwig, 2009) predicts that immatures acquire adult-like behaviour by mere social enhancement (that is, their attention is drawn to bee nests by the activity of their mothers at such sites; Heyes, 1994) and individual trial-and-error. In this case, we predicted that (1) immatures would direct their attention mostly or exclusively towards the bee nests, and (2) that as their extractive activity increases over time (assuming a general increase in frequency of actions with age; as seen for manipulative activity in capuchins, *Cebus apella*: Fragaszy & Adams-Curtis, 1997; nut cracking in chimpanzees: Inoue-Nakamura & Matsuzawa, 1997; larvae foraging in capuchins: Gunst, Boinski, & Fragaszy, 2010; object manipulation and nut cracking in capuchins: De Resende, Ottoni, & Fragaszy, 2008), all possible transitions between the species-typical actions in this context would initially increase in frequency, while with time the transitions 'explore-pound', 'pound-perforate' and 'perforate-explore' (that is, the transitions used most by adults) would become more common. Moreover, we would expect no difference between the sexes, as we did not expect any obvious sex difference in activity (as none was found in the studies listed above). Alternatively, we hypothesized that immatures acquire the adult action sequences through a combination of observing their mother's behaviour and individual practice. In particular, we predicted that (1) as immatures aged, they would change the focus of their attention (initially directed mostly towards the bee nests and later to the actions of their mothers), and (2) the relative frequency of certain (but not all) transitions would increase over time, specifically those transitions that resemble the adult technique. In addition, we predicted that females would produce adult-like transitions earlier than would males, as previous studies suggested that immature females tend to be more inclined to learn tool-aided techniques for food acquisition (e.g. Boesch & Boesch-Achermann, 2000; Gruber, Clay, & Zuberbühler, 2010; Lonsdorf, 2005). Similarly, we investigated how age and sex affected immatures' choice of grip type used when perforating. If immatures acquire their grip preference purely via individual trial-and-error we would predict that, with age, they would increase use of the grip type involving both hands and feet together (as this is the grip most commonly used by adults and requiring the greatest motor coordination), and that both sexes would use it with equal frequency. Alternatively, because mothers do differ in their frequencies of usage of different grip types, we hypothesized that immatures would imitate their own mother (that is, copy 'how' she performed an action) in the grip types used for perforating; thus, we predicted that, together with a general tendency to use the most common grip type more frequently, maternal preference for a specific grip would also affect the frequency of usage of that grip by her offspring. Moreover, we predicted that females would imitate their mothers both more than males and at an earlier age (Boesch & Boesch-Achermann, 2000; Lonsdorf, 2005).

Finally, this seems to represent an appropriate context for a form of teaching to have evolved, for two reasons: first, mothers would benefit from providing their offspring with skills to access a highly nutritious (although difficult to access) resource, and second, the opportunities that naïve individuals have to understand the link between the actions carried out by experienced individuals and the presence (and possible consumption) of the resource are limited (Thornton & Raihani, 2010). This link is, in fact, highly concealed as (1) the bee nest is not directly perceivable, (2) the actions of the active individual do not necessarily lead directly to getting the resource, and (3) successful extractions are relatively rare, and often only achieved after multiple visits to the same bee nest. Thus, mothers might be more motivated to invest in their offspring's learning opportunities than in other contexts where the resource is more directly perceivable and attainable. In particular, we hypothesized that mothers would support the acquisition of this technique in offspring by providing learning opportunities (Kline, 2015) in the form of spending 'inactive' time at bee nests, that is, time spent at those sites while not themselves performing any action aimed at digging out the nest (e.g. exploring the nest, manufacturing tools or performing extractive actions; Supplementary Material: Video S1). By doing so, mothers may provide opportunities for their offspring to familiarize themselves with the bee nests and artefacts accumulated there. In fact, repeated extractive attempts result in the accumulation of used artefacts at these sites, which could hint at the occurrence of previous extractive activity and thus promote immatures' exploratory and practising behaviour (Fragaszy et al., 2013). Based on previous observations (Boesch, 1991), we predicted that mothers would adjust their behaviour according to the age and sex of their offspring: in particular, they should provide more opportunities when their offspring are younger (and thus supposedly less skilled) and decrease this behaviour as offspring age, and they should provide more opportunities for male than female offspring (as females are known to be better learners and tool users than males; Lonsdorf, 2005). Additionally, mothers might spend more inactive time at a site if their offspring are highly interested in exploring the bee nests and the tools abandoned there by previous users, thus giving them more time to acquire information about these objects, whereas they might spend less time at a bee nest if their offspring are not interested in the nest site.

## METHODS

### Data Collection

Data were collected in Loango National Park, Gabon (2°04′S, 9°33′E), between April 2009 and August 2015. The area comprises mature, secondary, coastal and swamp forest and savannah. The rainy season lasts from October to April, interrupted by a short dry season (December—January), and the long dry season spans May to September. Further details about the ecology of this field site have been described elsewhere (Head, Boesch, Makaga, & Robbins, 2011; Head, Robbins, Mundry, Makaga, & Boesch, 2012). As the focal chimpanzee community (named Rekambo; Head et al., 2013) was not fully habituated to human observers during data collection, we used remote-sensor camera traps (Sony Handycam with Trailmaster 700V, Scoutguard 550 and Bushnell Trophy Cam) to record chimpanzees' extractive activity at 50 different underground bee nests. Cameras were placed at nest sites where researchers and field assistants opportunistically spotted evidence of previous activity by chimpanzees or other consumers of this resource, or noticed bees flying in and out of the entrance tube (see Estienne, Mundry et al., 2017 for further details about the bee nests). Sony cameras recorded continuously until no further movement was detected within a 2 min interval; the Scoutguard 550 and Bushnell Trophy Cam recorded 1 min clips and were reactivated as long as movement persisted. Interclip intervals varied between 1 s and a few minutes, owing to possible malfunctioning of the camera retrigger. Footage from cameras was collected every 2 weeks (further

details in Estienne, Mundry et al., 2017, Estienne, Stephens et al, 2017). We labelled as 'visits' all instances when one or more chimpanzees explored the entrance tube of an underground bee nest or tried to extract honey from it (with or without tools). Exploration and extraction included several actions, listed in Table 1. A visit began when the subject arrived at the entrance tube of a bee nest and ended when he/she departed from it; a visit could comprise one or more video clips separated by gaps of no more than 15 min. If the camera trap did not record an individual's arrival or departure (owing to a delayed trigger), the visit comprised all the time the subject was recorded at the nest site. For this study, we used footage from 16 individually identified immatures (six females and 10 males, from nine different mothers) for which we recorded a minimum of three visits each; our sample comprised 188 visits in total (Table 2). 'Immature' individuals comprise infants (aged 0–5 years), juveniles (5–10 years old) and adolescents (10–15 years old), distinguished by physical and behavioural characteristics following Boesch and Boesch-Achermann (2000). To attribute the age of immatures at the time of their visits, four experienced observers of chimpanzees independently estimated each immature's age at its first visit; the final estimated age was then the mean of the four values.

We used INTERACT 14 (Mangold, 2010) to code chimpanzees' actions, namely explorative actions, tool manufacturing actions and extractive actions including tool use (sensu Shumaker, Walkup, & Beck, 2011). In addition, we coded social interactions occurring between our subjects and other individuals that interacted with the bee nest. All operational definitions used are given in Table 1; all behaviours were coded as frequencies (starting when the action started) and for the following actions the duration was also coded: 'scratch', 'look at', 'pound', 'dig', 'eat', 'share–active', 'share––allowed', 'share–passive', 'hold–another individual', 'hold–active solicitation', 'hold–active manipulation' and 'hold–active restriction'. We also coded the grip type used by the subject as one of the following mutually exclusive types: 'hands only', when the subject exclusively used one or both hands; 'feet only', when the subject exclusively used one or both feet; and 'both', when the subject used hands (one or two) and feet (one or two) simultaneously. Chimpanzees' behaviour was coded by two observers: V.E. implemented the ethogram and coding scheme and then trained B.R., who coded the behaviour of the immatures for an internship. Interobserver reliability was assessed by comparing the observations coded by the two raters for 16 different video clips (one per individual immature chimpanzee). We tested reliability for the number of occurrences of the following actions: 'explore' (including looking at, manually inspecting, scratching or smelling the bee nest); 'look at an active individual'; 'dig' (manually); 'pound'; and 'perforate'. There was a high level of agreement for most actions ($r_S = 0.9, 0.9, 1$ and 1, for 'explore', 'look at an active individual', 'pound' and 'perforate', respectively) but agreement was low for manual digging ($r_S = 0.5$), suggesting that results regarding this action should be interpreted cautiously. Agreement was also high for the type of grip used during perforations (Cohen's kappa: $\kappa = 0.9$, $N = 26$, $P < 0.001$). Examples of the coding of immatures' behaviour, at

**Table 1**
Ethogram used for coding the behaviour of immature chimpanzees visiting underground bee nests in Loango National Park, Gabon

| Action | Operational definition |
| --- | --- |
| **Exploration** | |
| Scratch[a],[b] | Subject scratches the ground or the hole with hand/finger but no object (i.e. dirt, honey, leaves, residue of honeycomb left after the successful visit of a previous consumer) appears to be removed |
| Inspect[a] | Subject inserts a hand into the hole without removing any object (i.e. dirt, honey, leaves, residue of honeycomb left after the successful visit of a previous consumer) |
| Smell[a] | Subject brings an object (finger/stick/tool) to its nose |
| Look at[a] | Subject directs its head towards a target (e.g. behaviour of active individual, hole/tube, surroundings) |
| **Tool manufacture** | |
| Break[a] | Subject breaks a sapling or a branch attached to the substrate or tree, during the process of tool making |
| Cut off[a] | Subject cuts one of the ends of the tool in a sharp way, using hands, teeth and/or feet |
| Remove branches[a] | Subject removes leaves/side branches from the sapling |
| Strip bark[a] | Subject removes the bark from the sapling/tool |
| **Extraction** | |
| Pound[a],[a] | Subject strikes the tool against the ground repeatedly |
| Dig[a],[a] | Subject removes substrate/soil from the hole or from the area where the nest tunnel is located |
| Other[a] | Subject attempts to use a tool but the action is not identifiable based on any of the operational definitions |
| Perforate[a] | Subject inserts the tool into the ground and applies pressure to make the tool penetrate the ground |
| Rotate[a] | Subject keeps the tool inserted in the ground and moves it in circles or from side to side |
| Turn end[a] | Subject inverts the tool, switching the end of the tool that is closest to the ground |
| Extract (honey)[a] | Subject inserts a hand into the hole and extracts honey |
| Eat[a],[a] | Subject chews honeycomb/honey previously extracted from the nest |
| Lick[a] | Subject licks honey from hand/tool |
| **Social interactions** | |
| Share-active[b] | Subject directs an object (e.g. tool or food) towards another individual |
| Share-allowed[b] | Subject does not react when another individual accesses (e.g. holds or manipulates) an object that it possesses |
| Share-passive[b] | Subject changes posture or grip in a way that facilitates access to an object by another individual |
| Hold [a]- another individual[b] | Subject holds another individual without obviously affecting the latter's behaviour |
| Hold [a]-active solicitation[b] | Subject pulls an object held by another individual towards itself |
| Hold [a]-active manipulation[b] | Subject manipulates an object held by another individual |
| Hold [a]-active restriction[b] | Subject restricts the use of a limb or tool of another individual by holding it |
| Reach[a] | Subject extends a palm towards another individual that holds an object; the outcome (transfer of the object from one individual to another or not) and the type of object (e.g. honey, tools) were coded |
| Prevent[a] | Subject prevents another individual from accessing an object by one of the following behaviours: changing posture, changing grip, extending the arm such that the object is out of reach, or detaching the other's hand from the object |
| Threat | Subject displays an aggressive behaviour towards another individual |
| Displace[a] | Subject pushes another individual, which moves to a different place |

[a] Actions for which 'grip' was specified.
[b] Actions for which duration was coded; defined as starting when the action commenced and ending when the subject either stopped his/her activity for >2 s, dropped the tool or changed grip or body posture (Sousa, Biro, & Matsuzawa, 2009).

**Table 2**
Overview of the sample used in this study

| Immature ID | Sex | Mother ID | Age range (years) | No. of visits | No. of different nests/subject | Observation time (min) | Active time (min) |
|---|---|---|---|---|---|---|---|
| AR1 | M | ARO | 4.9–7.3 | 3 | 3 | 3.68 | 1.31 |
| AR2 | F | ARO | 0.7–1.2 | 3 | 2 | 3.32 | 0.74 |
| EM1 | F | EMM | 1.6–7 | 30 | 12 | 42.49 | 33.45 |
| ID2 | M | IDA | 0.5–1.9 | 5 | 4 | 6.17 | 2.34 |
| JOJ | F | IDA | 4.8–9.1 | 17 | 14 | 27.21 | 14.55 |
| KOU | F | IKO | 9–11.2 | 12 | 9 | 39.22 | 27.92 |
| IK2 | M | IKO | 0.6–1.3 | 5 | 4 | 2.83 | 0.30 |
| LO1 | M | LOL | 0.4–3.5 | 21 | 12 | 18.86 | 8.18 |
| ON1 | M | ONO | 4.5–7.9 | 12 | 8 | 7.47 | 4.82 |
| PAN | M | PEM | 8.3–13.2 | 19 | 13 | 42.00 | 30.89 |
| MOU | F | PEM | 3–9.2 | 15 | 11 | 12.88 | 6.98 |
| THE | M | SUZ | 7.1–11.1 | 22 | 16 | 31.21 | 23.67 |
| SU2 | M | SUZ | 1.4–1.7 | 5 | 4 | 7.01 | 3.71 |
| SU3 | M | SUZ | 0.9–3.9 | 8 | 5 | 9.62 | 2.73 |
| VE1 | M | VER | 6.8–9.2 | 5 | 4 | 5.43 | 3.46 |
| VE2 | F | VER | 1.4–2.9 | 6 | 5 | 7.01 | 2.65 |

For each immature subject, the table lists sex, maternal identity, range of estimated ages (in video footage), total number of visits, total number of different nests visited, total duration of recorded observation time and total duration of time that the subject was observed being active at a bee nest (that is, the total time that the individual was either manipulating tools, or interacting with the entrance tube of the bee nest or with another individual).

three different ages, are available in the Supplementary Material (Videos S2–S5).

*Ethical Note*

This noninvasive study was conducted in compliance with the regulations of the Centre National de la Recherche Scientifique et Technique of Gabon, within the framework of the Convention of Cooperation accepted by the Agence Nationale des Parcs Nationaux (N. 000359PR/SP and N. 000004/PR/ANPN/SE). Although monitoring bee nest sites with camera traps could potentially disturb colonies (owing to regular visits to these sites by researchers), we never observed clear signs of stress in bee behaviour as a consequence of our research activity (e.g. no nest was abandoned directly after camera placement). We consider it unlikely that our presence increased the likelihood that the bee nests were extracted, as previous results showed that the probability of successful extraction depends on the structural features of the bee nest (Estienne, Mundry et al., 2017).

*Data Analyses*

*Effect of age and sex on action sequences (Model 1)*

We analysed the effect of individual age and sex on the development of action sequences by examining the transitions between consecutive actions within a sequence. First, we defined a sequence of actions as any instance where at least two actions occurred during a subject's visit to a bee nest. Sequences comprised all actions that occurred within a visit; if gaps in the footage occurred during a visit (owing to impaired retrigger of camera traps; observed maximum gap duration = 14.2 s), the actions before and after these gaps were treated as separate sequences. Sequences performed by immatures could comprise any of the following behaviours: 'explore' (as defined above); 'look at an active individual'; 'tool manufacture' (including: 'break', 'cut off', 'strip bark' and 'remove side branches'); and all extractive actions, namely 'attempt', 'dig', 'pound', 'perforate' and 'rotate'. Different exploratory and tool-manufacturing actions were pooled into two distinct categories because the focus of our study was on the extractive technique. For this reason, we subsequently excluded the category 'tool manufacture' from our analysis. Likewise, we excluded from analysis the actions 'extract honey', 'eat' and 'lick', since they

necessarily occurred only when chimpanzees were successful. We also excluded all instances where actions were not clearly visible. From such sequences we created a data set comprising all transitions, each represented by an action and the immediately following action. One individual (IK2) was dropped from this data set because he was too young and never observed performing two relevant actions (that is, among those listed above) consecutively. We used generalized linear mixed models (GLMMs; Baayen, 2008) with binomial error structure and logit link function (McCullagh & Nelder, 1989; $N = 765$ transitions) to test whether age, sex and the type of immediately preceding action influenced the probability that perforating, exploring or looking at an active individual occurred within a sequence (models 1a, b and c, respectively). Since we hypothesized that the development of the sequence of actions differs depending on the types of action involved in a transition, we further included the interaction between age and type of previous action. The occurrence of digging and pounding could not be tested due to their rarity in the data. To avoid issues related to complete separation (Field, 2005) in the model testing the probability of looking at an active individual (model 1c), we used only the subset of actions 'explore' and 'look at an active individual' as levels for the predictor 'previous action' ($N$ for model 1c = 425). In all models, we controlled for transition number (accounting for the position within a sequence when a transition occurred) and included subject (15 levels for all models), nest site (42 levels for models 1a and b and 41 levels for model 1c) and visit identity nested within subject (accounting for the nonindependence of actions performed during the same visit by a subject; 109 levels for models 1a and b and 102 levels for model 1c) as random effects. As some mothers had more than one offspring we also included the random effect of mother identity (nine levels for all models). Finally, we included all necessary random slopes (Barr, Levy, Scheepers, & Tily, 2013; Schielzeth & Forstmeier, 2009), namely those of age, previous action, transition number and the interaction between age and previous action, within subject; age, previous action and transition number, within nest site; transition number within visit identity; age, previous action, transition number and the interaction between age and previous action, within mother.

*Effect of age on grip type (Model 2)*

The scarcity of perforations performed by immature females ($N = 85$) as compared to immature males ($N = 214$) led to model

stability issues (see subsection 'Model Implementation' for details about model stability). This prevented us from including in the model the interaction term to test our prediction about the influence of age and sex on the development of individual preferences in the usage of different grip types. As our major interest was testing the effect of maternal preference on the development of grip preference in immatures, we decided to limit our analysis to immature males. To test the effect of age, we used a GLMM with binomial error structure and logit link function where the response variable was whether a perforation was performed using the grip type 'both' (as compared to the grip types 'hands only' and 'feet only'; $N = 214$ perforations). The model controlled for soil hardness at the bee nest at the time of the visit (expressed as centimetres of penetration of a stick into the soil after a standardized strike; see Estienne, Mundry et al., 2017 for details about how this variable was derived). It also included the random effects of subject (seven levels; subjects that were never observed perforating were dropped from this data set), nest site (25 levels) and visit identity (nested within subject; 44 levels) as well as the random slope of age within subject.

*Effect of mother's preference on grip type (Model 2)*

In model 2 (see above), we also tested the effect of mothers' preferred grip types on their offspring's grip choice when perforating. Since we predicted that immature males are affected by their mothers' behaviour differentially depending on their age, we tested the interaction between maternal preference and immature age. Mother's preference was calculated as the proportion of times she used the grip type 'both'. We used only mothers for whom we had 15 or more perforations for calculating grip preference (range of number of perforations observed per mother 16–128).

*Learning opportunities provided by mothers (Model 3)*

We used a linear mixed model (LMM, $N = 67$ visits) to test how offspring sex, age and behaviour (defined as the proportion of time that they spent interacting with the bee nest, per visit) affected the proportion of time mothers spent being inactive at a nest site (per visit; Supplementary Material, Video S1). The interaction between immature age and sex was also included. The proportion of time an immature spent interacting with a nest was calculated as the summed duration of all exploratory and extractive actions performed during a visit, divided by the total visit time. We assumed that learning would develop nonlinearly over time, initially increasing until a plateau is reached and then decreasing again, and thus also included immature age as a squared term and its interaction with sex. The proportion of a mother's time inactive was calculated as the difference between the total duration of the mother's visit and the time spent on extractive actions, divided by the duration of her visit. If a mother had two offspring, we only considered the behaviour of the younger one, assuming that mothers would invest more time in the less experienced offspring. We also controlled for the number of social partners visible at the time of the visit, as a possible source of influence upon the mother's behaviour and included the random effects of mother's identity (nine levels) and nest site (28 levels). Visit identity was not included, as multiple mothers were never seen together within the same visit; offspring identity was not included since, in this analysis, we considered only the youngest offspring for each mother. We included the random slopes for immature's age, proportion of time immature interacted with nest and number of social partners, within mother. We weighted each data point by the duration of the mother's visit, such that longer visits had a greater impact on the model than shorter ones.

*Model implementation*

All analyses were conducted in R (version 3.2.4; R Core Team, 2016). GLMMs and the LMM were fitted using the functions glmer or lmer, respectively, of the package lme4 (Bates, Maechler, Bolker, & Walker, 2015). For the LMM, we verified the assumptions of normally distributed and homogeneous residuals by visually inspecting a qqplot and the residuals plotted against fitted values. We ruled out collinearity among predictors by inspecting variance inflation factors (Field, 2005) using the function vif of the R package car (Fox & Sanford, 2011), based on standard linear models excluding the random effects and interactions (maximum VIF = 1.578). 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 we found no issues. In all cases, we first tested the significance of the test predictors as a whole by comparing the full model with a respective null model (Forstmeier & Schielzeth, 2011) comprising only control predictors and random effects, using a likelihood ratio test (R function anova with argument test set to 'Chisq'). When an interaction term had no significant effect, we fitted a reduced model including only the main effects. $P$ values for individual effects were based on likelihood ratio tests comparing the full model with a respective reduced model (R function drop1; Barr et al., 2013). All covariates were z-transformed to a mean of zero and a standard deviation of one (Schielzeth, 2010) before fitting the models.

## RESULTS

*Development of Action Sequence and Grip Repertoire*

Immatures started to observe the extractive behaviour of other individuals from as young as 0.4 years of age. In 77% of cases that an immature looked at an active individual this was its own mother, confirming that mothers represent the primary model observed by immatures ($N$ visits = 109; among these, the mother was the only other individual present at the site in 21 cases). The total time during which we observed immatures looking at the actions of another individual was 77.1 min (range 0–1 min per coded 'action'; $N = 576$); the total duration of looking at the bee nests was 2.6 min (range = 0–0.2 min per coded 'action'; $N = 53$), whereas the total duration of looking at surroundings while at the nest was 23.7 min (range 0–0.7 min per coded 'action'; $N = 372$; Supplementary Material: Video S6). As they aged, young chimpanzees started to interact with bee nests and the tools found there. The minimum age of manual inspection of a bee nest recorded was 1.5 years ($N = 111$), whereas olfactory inspection of tools was first observed at 2.8 years of age ($N = 161$). Immatures started to perform perforation and pounding at 2.8 years of age ($N = 337$ and 84, respectively), and around that time they also started to dig manually (3.2 years of age; $N = 39$). However, other extractive actions such as 'rotate' ($N = 29$) and 'turn end' ($N = 23$) appeared much later (at 3.3 and 6.0 years of age, respectively). Tool manufacture appeared last in the action repertoire ($N = 49$ instances of tool manufacture overall): immatures started to use the actions 'break' ($N = 14$) and 'remove side branches' ($N = 12$) when they were 4.8 years old, while other tool modifications appeared much later ('cut off' was first observed at 7.1 years of age and 'strip bark' at 8.4 years; $N = 17$ and 4, respectively). Overall, by age 6 years or more, immatures could perform all actions belonging to the adult behavioural repertoire. The first type of grip used by immatures in our sample was 'hands only' (observed in subjects as young as 2.9 years old; $N = 67$ from 10 different individuals), then the grip involving hands and feet appeared (first observed at 4.3 years of age; $N = 201$ from 10 different individuals),

and finally, the grip type 'feet only' was first observed in an individual 7.5 years old ($N = 36$ from two different individuals).

### Effect of Age and Sex on Action Sequences (Model 1)

The probability that 'perforate' occurred in the action sequences of immatures was significantly affected by age and type of action (model 1a, full versus null model: $X^2_{10} = 42.406$, $P < 0.001$; for results of the reduced model see Appendix Table A1) but not by their interaction (Appendix Table A1). As they aged, immatures became more likely to use perforation in their sequences (Fig. 1). Within a sequence, perforating was more likely to occur after pounding, while the transition 'look at an active individual–perforate' was particularly unlikely to occur (Fig. 2). The occurrence of transitions involving exploratory actions in the sequence was significantly affected by the age of subjects and the type of action preceding 'explore' (model 1b, full versus null model: $X^2_{10} = 21.071$, $P = 0.021$; for the interaction see Appendix Table A1). Specifically, as immatures aged, the transition 'look at an active individual–explore' became less likely to occur (Fig. 3b), while the transition 'dig–explore' occurred progressively more often (Fig. 3e). The occurrence of other types of transition did not change notably with age (Fig. 3). Finally, as immatures aged, the transition 'explore–look at an active individual' became less likely to occur (Fig. 4a), whereas the transition between two consecutive 'look at an active individual' (that is, the transition 'look at an active individual–look at an active individual') became more likely to occur, suggesting that immatures became more likely to observe others' actions, rather than being explorative (Fig. 4b; model 1c, full versus null model: $X^2_4 = 47.147$, $P < 0.001$; for the interaction see Appendix Table A1). Sex did not significantly affect the action sequencing of immatures, for any of the actions analysed (Appendix Table A1).
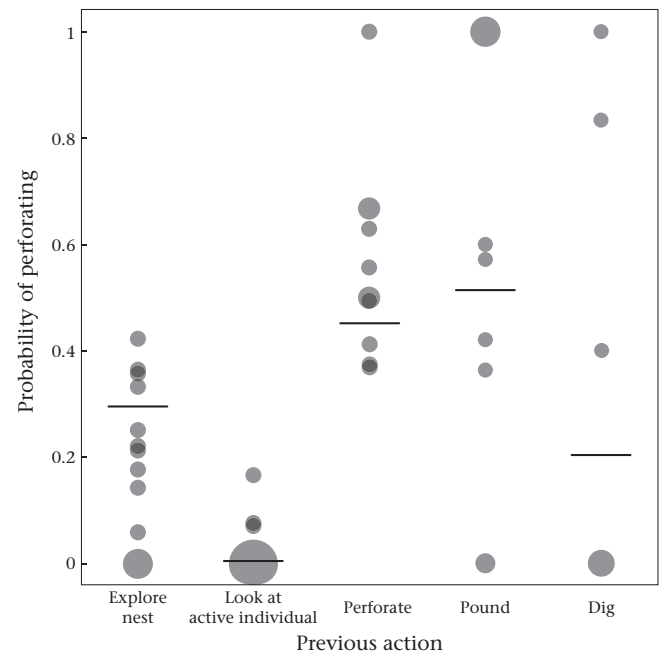


**Figure 2.** Effect of the type of action on the probability that perforating subsequently occurred in the sequences performed by immature chimpanzees in Loango National Park during visits to underground bee nests. The area of the points represents the frequency of occurrence of a specific action in the sequence per subject (total $N = 765$ actions), and horizontal lines show the fitted probabilities (model 1a).

### Effect of Age on Grip Type (Model 2)

The full model differed significantly from the null model ($X^2_3 = 8.407$, $P = 0.038$). Since the interaction between maternal preference and immature age had no significant effect on the response (Appendix Table A2), we removed the interaction and tested the effect of each variable separately. We found a significant positive effect of age on the probability of using the grip type 'both' in immature males (Appendix Table A2, Fig. 5).

### Effect of Mother's Preference on Grip Type (Model 2)

As reported above for model 2, the full and null model were significantly different, but maternal grip preference did not significantly affect immature males' choice of grip when perforating nests (Appendix Table A2). Nevertheless, it is notable that the grip type 'feet only' was mainly used by one immature, whose mother was the only adult individual that consistently used that grip in the Rekambo community (the mother–son pair 'PEM-PAN'; Table 3).

### Learning Opportunities Provided by Mothers (Model 3)

The sex and age of accompanying offspring significantly affected mothers' behaviour at bee nest sites (full versus null model: $X^2_6 = 18.688$, $P = 0.005$; for the interaction see Appendix Table A3). When accompanied by daughters, mothers progressively decreased the time they spent inactive at the bee nest as their daughters aged, until daughters reached approximately 6 years of age, at which point mothers seemed to increase inactive time again (Fig. 6a). When accompanied by sons, mothers showed a different pattern: they spent an increasing amount of time inactive at the bee nests as their sons aged, until this behaviour seemed to stabilize around the time when their sons were 5–6 years old (Fig. 6b). Offspring
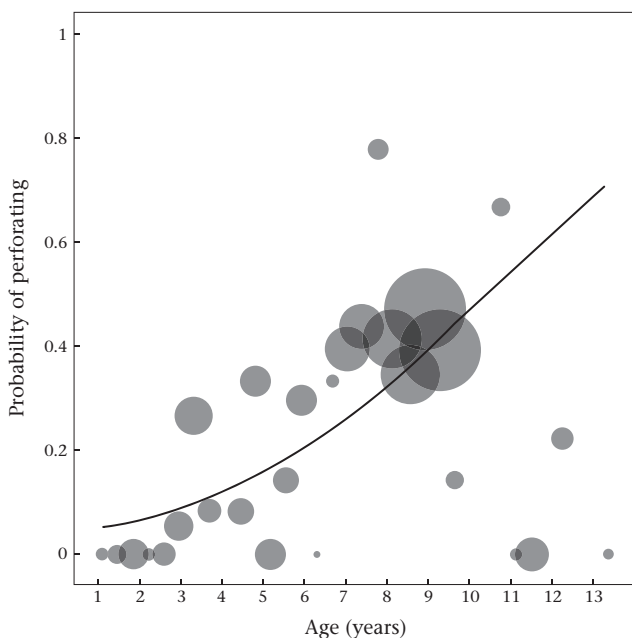


**Figure 1.** Effect of age on the probability that perforating occurred in the action sequences performed by immature chimpanzees in Loango National Park during visits to underground bee nests. The area of the points represents the frequency of occurrence of perforations per binned age and subject, and the line shows the fitted probability (model 1a; $N = 765$ actions).
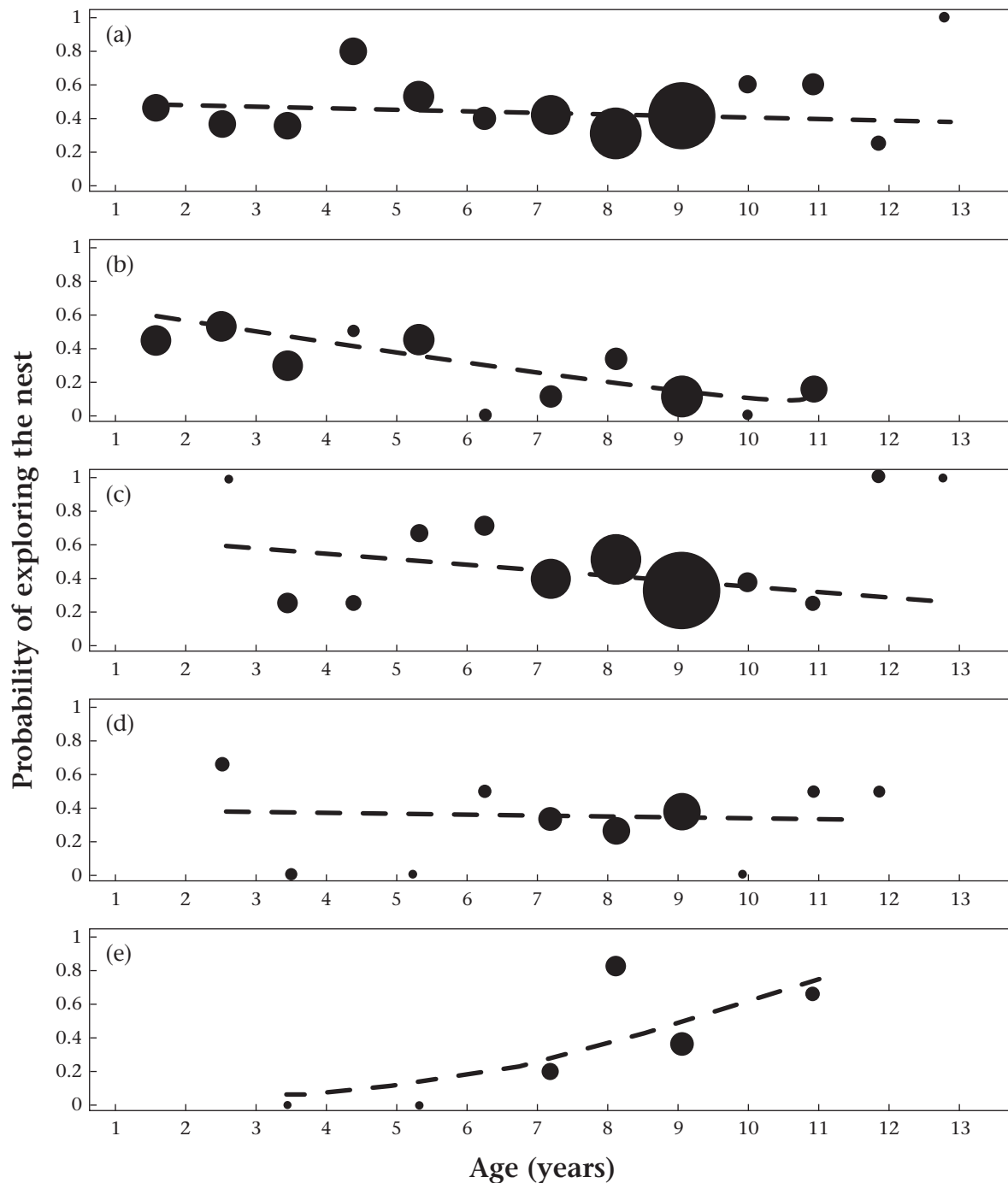
**Figure 3.** Effect of the interaction between age and type of preceding action on the probability that exploration of the nest occurred in the sequences of actions performed by immature chimpanzees in Loango National Park during visits to underground bee nests. Actions are (a) 'explore the nest', (b) 'look at active individual', (c) 'perforate', (d) 'pound' and (e) 'dig'. The area of the points represents the frequency of occurrence of a specific action at a given age (total $N = 765$ actions), and dashed lines show the fitted probabilities (model 1b).

behaviour did not obviously affect their mother's behaviour (Appendix Table A3).

Owing to the scarcity of visits by adult females without offspring ($N = 6$), we could not statistically test whether the presence of immatures had an effect on adult females' behaviour. Nevertheless, we observed that the time that adult females without offspring spent inactive at bee nests was less than 1 min (mean = 0.2 min; range 0–0.7 min; $N = 6$ visits) whereas mothers

spent on average 1.2 min inactive at bee nests (range 0–10 min; $N = 67$ visits).

We never observed mothers actively manipulating their offspring's actions; on the contrary, on one occasion an infant manipulated a tool held by her mother. Immatures often tried to reach the tool used by another individual ($N = 30$, in 25 of which it was their mother) and even actively solicited their mothers to access the latter's tools ($N = 44$ observations). In the majority of these
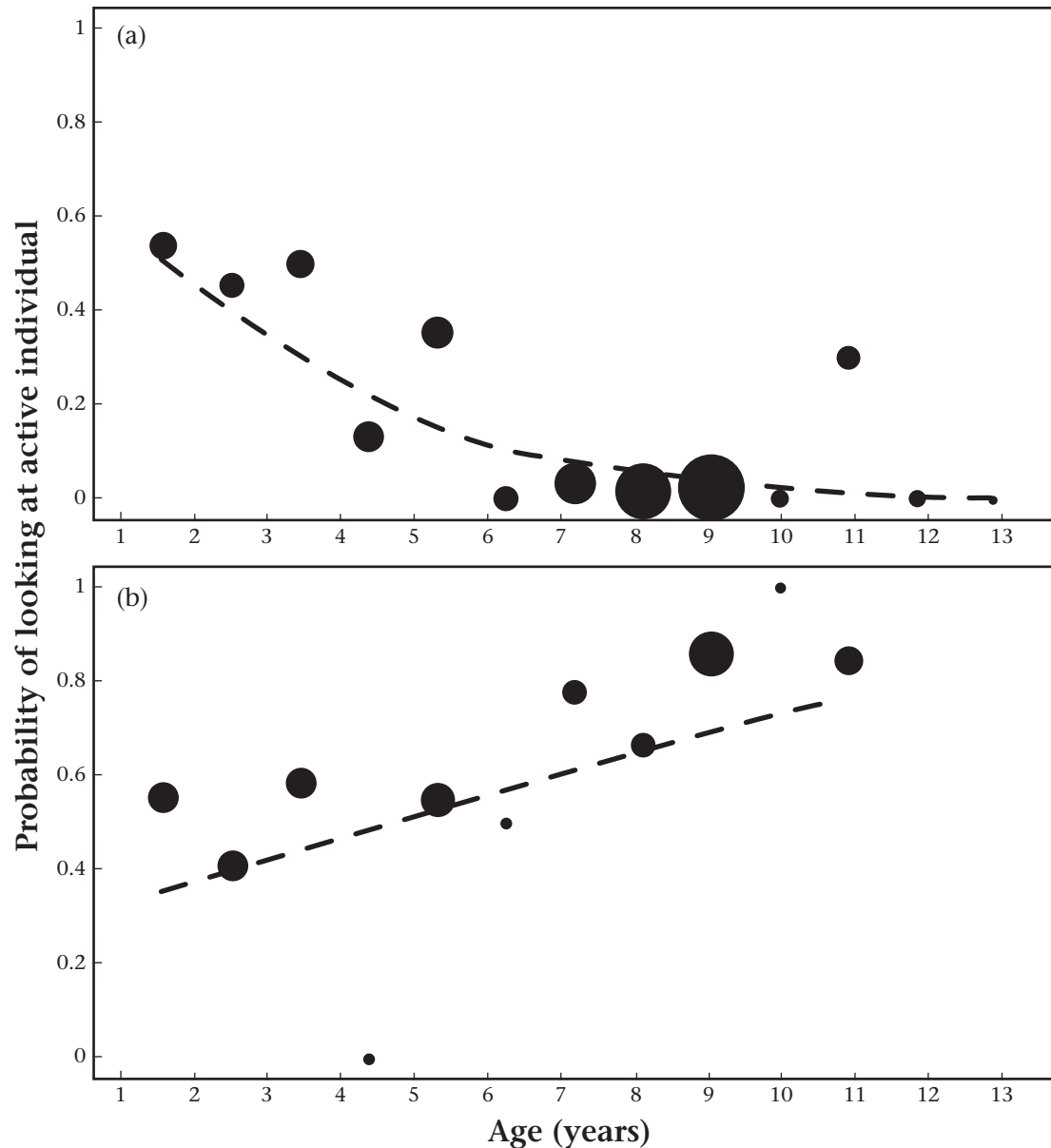
**Figure 4.** Effect of the interaction between age and type of preceding action on the probability that looking at an active individual occurred in the sequences performed by immature chimpanzees in Loango National Park during visits to underground bee nests. Actions are (a) 'explore the nest' and (b) 'look at active individual'. The area of the points represents the frequency of occurrence of a specific preceding action at a given age (total $N = 425$ actions), and dashed lines show the fitted probabilities (model 1c).

cases ($N = 42$ of 44) mothers allowed tool sharing. Interestingly, in some cases mothers prevented their offspring from manipulating the tools that they were using ($N = 22$, although 18 observations derive from a single mother–offspring pair; Supplementary Material, Video S2), and in four cases we observed that one mother actively restricted her daughter's attempts to use a tool while she (the mother) was attempting to dig out a nest. We never observed instances of active (that is, initiated by the owner of the object) or passive (whereby the owner of the object facilitates the exchange of an object by changing posture or grip) sharing of tools or food. Nevertheless, when a nest was successfully extracted ($N = 6$), all individuals present were allowed to access the hole and extract food, even if they had not actively participated in the extraction and were not obviously related to the individual that dug. In only two cases did adult females threaten immature individuals that were not their offspring, and only once did an immature threaten another youngster.

## DISCUSSION

In this study, we described the acquisition of a complex extractive technique for accessing underground bee nests by immature chimpanzees and investigated the effect of individual attributes and maternal factors on the development of immatures' behaviour in two specific aspects of this technique: sequence of actions and grip choice when perforating nests. Although it is conceivable that our opportunistic sampling method could have biased the estimation of the earliest age of occurrence of specific actions and grips, we are confident that these data reflect a realistic scenario as the number of recorded visits was relatively homogeneously distributed across all ages (Appendix Fig. A1).

Age explained the shift in immatures' attention and their acquisition of adult action sequences, as well as the development of their preference for grip type used when perforating, at least for males. We found no sex bias for acquisition of the adult sequence of
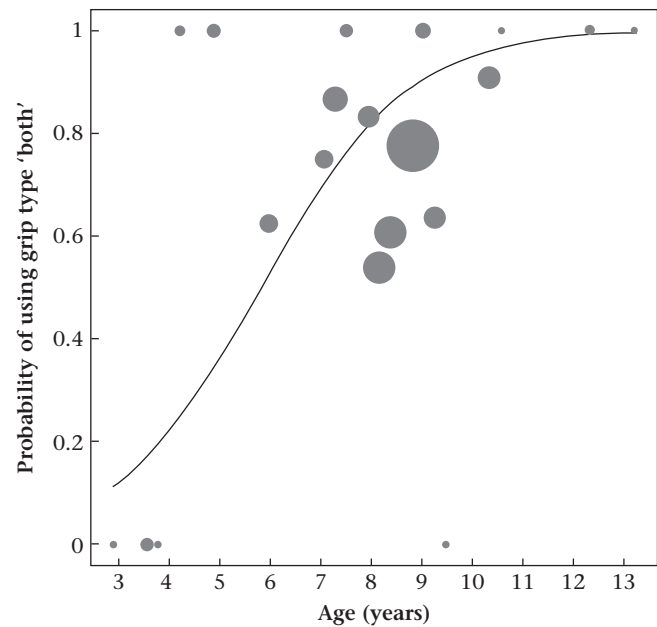
**Figure 5.** Effect of age on the probability that immature male chimpanzees in Loango National Park used the grip type 'both' when perforating the ground around bee nests. The area of the points represents the frequency of using the grip 'both' per binned age and subject, and the line shows the fitted probability (model 2; $N = 214$ perforations).
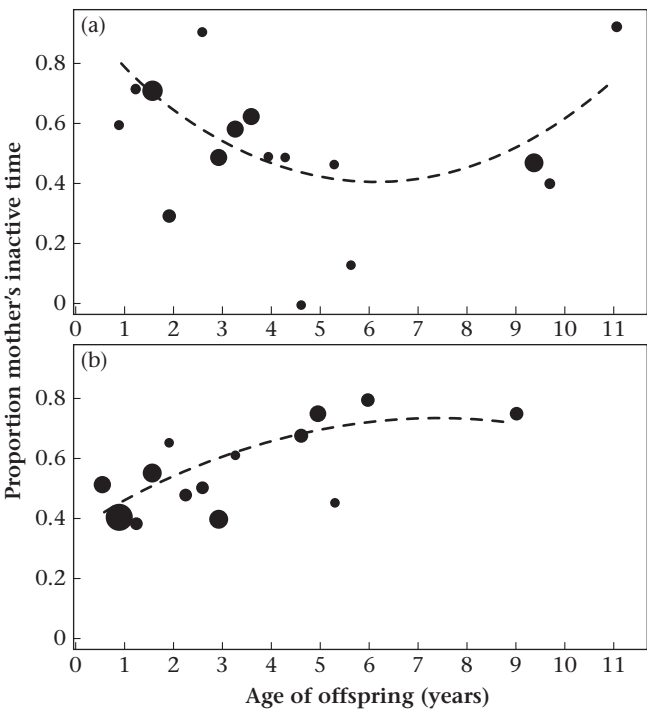


**Figure 6.** Effect of the interaction between the sex and age of offspring on the proportion of time that their mothers spent inactive during a visit to a bee nest. (a) Female and (b) male offspring. The area of the points represents number of observations per age (total $N = 67$ visits), and dashed lines show the fitted probabilities (model 3).

actions, but we could not test its effect on the development of grip preference. As immatures grew older, they shifted the focus of their attention. In particular, they progressed from switching their attention between the social model's action and the bee nest, to focusing more exclusively on the model's behaviour, as indicated by the finding that the transition 'explore–look at an active individual' (as well as the reverse 'look at an active individual–explore') became less common over time, while the repeated occurrence of the action 'look at an active individual' became more common. A

similar developmental trend was found in another study showing that chimpanzees became less explorative as they aged (Massen, Antonides, Arnold, Bionda, & Koski, 2013). The observed shift in immatures' focus of attention could suggest that, initially, they were mostly interested in the connection between the bee nest and the behaviour of the active individual, as indicated by the high

**Table 3**
Descriptive statistics for use of each grip type by mothers and immatures, as observed in footage of chimpanzees visiting underground bee nests in Loango National Park, Gabon

| Mother ID | Immature ID | Grip type | | | | | | | | | $N_p$ |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Both | | | Feet only | | | Hands only | | | |
| | | Median | 25% | 75% | Median | 25% | 75% | Median | 25% | 75% | |
| ARO | | 4.0 | 3.0 | 4.5 | 0.0 | 0.0 | 0.5 | 1.0 | 0.5 | 1.5 | 15 |
| | AR1 | 1.0 | 1.0 | 1.0 | 0.0 | 0.0 | 0.0 | 1.0 | 1.0 | 1.0 | 2 |
| EMM | | 2.0 | 1.0 | 3.0 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 2.3 | 103 |
| | EM1 | 0.0 | 0.0 | 1.0 | 0.0 | 0.0 | 0.0 | 1.5 | 0.8 | 2.3 | 23 |
| IDA | | 1.5 | 1.0 | 6.5 | 0.0 | 0.0 | 0.0 | 1.0 | 0.8 | 2.5 | 56 |
| | JOJ | 2.0 | 1.0 | 2.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 28 |
| IKO | | 2.5 | 1.3 | 7.3 | 0.0 | 0.0 | 0.0 | 2.5 | 0.0 | 5.5 | 125 |
| | KOU | 15.0 | 7.5 | 22.5 | 0.0 | 0.0 | 0.0 | 10.5 | 5.8 | 15.3 | 51 |
| LOL | | 2.0 | 2.0 | 3.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 1.0 | 43 |
| | LO1 | 1.0 | 0.5 | 1.5 | 0.0 | 0.0 | 0.0 | 0.5 | 0.3 | 0.8 | 3 |
| ONO | | 0.5 | 0.0 | 1.8 | 0.0 | 0.0 | 0.0 | 0.5 | 0.0 | 1.3 | 8 |
| | ON1 | 1.0 | 0.5 | 1.5 | 0.5 | 0.3 | 0.8 | 0.5 | 0.3 | 0.8 | 4 |
| PEM | | 3.0 | 1.5 | 10.5 | 2.0 | 1.0 | 5.0 | 3.0 | 1.5 | 4.0 | 39 |
| | PAN | 3.5 | 1.8 | 6.0 | 1.5 | 0.0 | 4.0 | 0.0 | 0.0 | 1.0 | 106 |
| | MOU | 3.0 | 2.5 | 3.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.3 | 12 |
| SUZ | | 1.0 | 0.5 | 4.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.0 | 1.5 | 35 |
| | THE | 1.5 | 1.0 | 4.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 61 |
| | SU3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 2.5 | 1.8 | 3.3 | 5 |
| VER | | 0.5 | 0.0 | 2.3 | 0.0 | 0.0 | 0.0 | 2.5 | 1.5 | 3.3 | 16 |
| | VE1 | 4.5 | 3.3 | 5.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 9 |

The table shows the median, second and third quartiles of the number of times each grip type was used per visit by each individual, as well as the total number of perforations observed ('$N_p$').

occurrence of the transitions 'explore—look at an active individual' and 'look at an active individual—explore' when immatures were very young; whereas, as they aged, they directed their attention to the actions of the model individual and practised their own actions, as revealed by the concurrent increase in occurrence of the transitions 'look at an active individual—look at an active individual' and 'dig—explore' at around 5—7 years old. With regard to extractive activity, immatures were more likely to perforate after pounding, as were adults, and they gradually used the transition 'dig—explore' more frequently as they aged. Although the progressive increase in the transition 'dig—explore' over time is consistent with the hypothesis that immatures learn how to sequence these actions via individual practice, note that the probability of the transition 'pound—perforate' did not change with age, and that immatures included progressively more perforations within their sequences as they grew older. These results suggest that 'perforating', when performed, was included in the sequence of actions in the same way as adults do. The increase in occurrence of this action is consistent with the findings of other studies showing a progressive increase in immatures' activity over time (De Resende et al., 2008; Fragaszy & Adams-Curtis, 1997; Gunst et al., 2010; Inoue-Nakamura & Matsuzawa, 1997), and suggests that the action became more consistently used as immatures acquired body strength and motor coordination. Moreover, observational data suggested that immatures spent more time observing the actions of other individuals than either the bee nests or the surroundings, and that the action 'perforate' appeared in the immature repertoire around the same time as they began 'digging'. Overall, our results suggest that immatures presumably acquire the adult sequence of actions via diverse processes. Their mother's activity first directs their attention towards bee nests (consistent with the hypothesis that they learn about this resource by social enhancement); however, immatures direct their attention not only to the bee nests per se but also primarily to the activity of their model (consistent with the hypothesis that they learn by observational learning). Finally, individual practice and physical growth probably also play a role, as perforations are likely to be easier as individuals gain strength. Our study cannot disentangle the relative importance of different learning processes in the development of this technique. Nevertheless, three considerations suggest our results do not support the hypothesis that immatures acquire adult action sequences purely by social enhancement and individual trial-and-error (as predicted by the latent solution hypothesis). First, immatures observed the actions of other individuals, and did not merely explore the bee nests. Second, we found that one of the typical transitions between extractive actions used by adults ('pound—perforate') did not emerge with time in the behaviour of the immatures. Third, immatures produced this adult-like transition between actions before being physically able to perform it in an effective way, and probably before being able to carry out a successful extraction by themselves (Supplementary Material, Video S7). Ideally, the most effective transitions would become fixed in an individual's repertoire once it achieved a successful extraction, as its behaviour would be reinforced by gaining a reward. Unfortunately, we do not have a record of a successful extraction by an immature subject in our study; we observed immatures accessing the honey only twice (aged 8.5 and 11.4 years) and that happened only after their mother or other adults, respectively, dug the bee nests extensively beforehand. Although more comprehensive observations are needed to determine at what age chimpanzees are capable of successfully extracting underground bee nests, it seems likely that this only occurs long after they are able to sequence their actions in the way adults consistently do. These considerations make the latent solution hypothesis unlikely in our context. It seems more likely that chimpanzees acquire this tool use technique via a diverse set of

social processes, among them the observation of skilled individuals in their group (as found in other studies of primates: Biro, Sousa, & Matsuzawa, 2006; van de Waal, Bshary, & Whiten, 2014). To disentangle the relative effects of different processes in learning this technique more detailed studies are required, for example manipulating the environment where chimpanzees use this technique or presenting the task to another population in which this technique is not commonly used. Contrary to our predictions, we found no obvious difference between the sexes in how action sequences developed. These findings differ from studies of other tool use techniques, which have shown that females are faster and better than males in learning adult-like behaviour (e.g. nut cracking: Boesch & Boesch-Achermann, 2000; termite fishing: Lonsdorf, 2005) and that behaviour of female offspring resembles their mother's technique more closely than that of males does (Lonsdorf, 2005; Perry, 2009). One possible explanation for the apparent lack of a sex difference is that the high level of complexity of underground honey extraction, coupled with the unpredictability of the challenges presented by the highly variable structure of underground bee nests, leaves little room for a sex bias to occur (Estienne, Stephens et al., 2017).

With regard to the development of grip preference, our analysis did not support the prediction that maternal grip preference significantly influences immatures' choice of a particular grip, at least when considering males. This result contrasts with extensive evidence for the importance of maternal example in the development of immatures' techniques in several other contexts (e.g. in chimpanzees: termite fishing, Lonsdorf, 2005; high-arm grooming style, Wrangham et al., 2016; moss sponging, Lamon, Neumann, Gruber, & Zuberbühler, 2017; processing of *Luehea candida* in white-faced capuchins, *Cebus capucinus*: Perry, 2009; grape handling in vervet monkeys: van de Waal et al., 2014). Nevertheless, grip preferences changed significantly with age. This could be because different grips require different motor skills, which individuals acquire as they age. Indeed, our descriptive results hinted at the progressive appearance of different grip types, requiring different degrees of motor coordination, as immatures aged. Other studies have revealed that immatures gradually changed their grip preference over time until they eventually settled for the one used by their mothers (Lonsdorf, 2005; Perry, 2009), supporting the hypothesis that individual practice, together with maternal example, shaped the development of their technique. Although we did not find statistical evidence for immatures copying their mothers' grip preferences, our descriptive results showed that one immature male (PAN) used the grip type 'feet only' more often than any other immature, and he used it with a frequency comparable to that of his mother (PEM), who in turn was the only adult female in our sample to frequently use this grip type (Table 3; Supplementary Material: Video S5). This observation suggests that, once physically able to perform this specific grip type, he frequently used it as his mother did. The alternative explanation would be that grip preference is genetically determined. However, this can be excluded as this immature male performed more than one grip type, yet nevertheless matched his mother's preference (as in Perry, 2009). Interestingly, another immature (ON1) was observed to use the grip type 'feet only', although his mother was never observed to do so. This raises the interesting question of how this grip could become included in an individual's behavioural repertoire, and therefore how variants of this technique spread within the group. This could be addressed by using network-based diffusion analysis of behavioural variants (Hobaiter et al., 2014). We could not use this analysis here, however, as camera traps were used for data collection. Thus, our observations of each individual are scattered over time (we recorded 188 visits over more than 4 years of monitoring; Appendix Fig. A1), as recorded visits to the monitored bee nests were highly

stochastic. Our sampling method means that we probably missed the majority of cases of immatures having the opportunity to observe their mothers or other individuals; thus, our picture of social networks among individuals would be highly biased. Observational data suggested that immatures could perform actions the way their mothers do, which would be compatible with the definition of imitation (Call et al., 2005), but a more complete sample is needed to thoroughly test this hypothesis. The specific circumstances of this task probably exclude the possibility that immatures copy their mothers to achieve a specific desired result (that is, copying by goal imitation), or that they learn an action as a result of the interaction they have with the food acquired by scrounging from other individuals (Boesch & Boesch-Achermann, 2000; Caldwell & Whiten, 2003), as successful extractions are relatively rare and achieved only after multiple visits to a bee nest, and perforations do not lead to any visible result or reward (i.e. food). Therefore, although immatures may be repeatedly exposed to the behaviour of skilled individuals, they are only rarely exposed to its outcome. Owing to the limitations of our sample, we could not formally test whether males and females differed in how closely they resembled their mothers' grip type preferences, as done in other studies (Lonsdorf, 2005; Perry, 2009).

Mothers not only affected the development of their offspring's technique by serving as models for the acquisition of action sequencing, but also seemed to change their own behaviour to promote the learning process. We found that they changed the time spent being inactive at bee nests depending upon their offspring's age and sex. This behaviour could provide learning opportunities for immatures, as they can explore the bee nests and the tools accumulated there. By doing so, immatures may be stimulated into acquiring information about the nest site and the tools associated with it (Fragaszy et al., 2013), as previously proposed in the context of nut cracking (Boesch & Boesch-Achermann, 2000). Spending time at a bee nest without attempting to dig it out is probably a costly behaviour for mothers, since by doing so they necessarily miss foraging opportunities, potentially directly negatively affecting their daily food intake and indirectly their offspring's nourishment, as has been demonstrated for Hadza hunter-gatherers (Hawkes, O'Connell, & Blurton Jones, 1997). In fact, lactating female chimpanzees are known to visit fewer feeding sites per day, travel less and consume more fruit than sexually receptive females, and were suggested to optimize their feeding efficiency to face the energetic costs associated with lactation (Bates & Byrne, 2009; Murray, Lonsdorf, Eberly, & Pusey, 2009). Thus, one would not expect mothers of young offspring to spend time at a site where they do not feed. Moreover, mothers were never observed feeding on resources other than bee products at these sites, nor engaging in affiliative behaviours. The stimulation hypothesis is further supported by two additional observations: first, females without offspring spent hardly any inactive time at bee nests, and second, as predicted, mothers stabilized this behaviour once their offspring reached approximately 5–6 years of age. In particular, mothers' inactive time at the nest reached a plateau, possibly reflecting a change in maternal behaviour corresponding to a specific level of knowledge. Notably, the complete repertoire of extractive actions was reached by an offspring age of approximately 6 years. More puzzling are the opposite trajectories of maternal behaviour for female and male offspring. Although one possible explanation is that this result is an artefact of our sample, we are confident in regarding this as unlikely because the results for model stability did not indicate that the model was strongly influenced by certain data points (if the model suffered from small sample size, that would be revealed by an unstable model). Alternatively, the difference could be explained by immature females observing their mothers using tools for longer and learning faster than their male counterparts

(Lonsdorf, 2005) and females generally being better tool-users than males (Gruber et al., 2010). Thus, it is possible that mothers concentrate their effort with daughters when the latter are very young and can decrease investment quickly over time, because their daughters are generally more interested in observing them, while they may invest more in their possibly less attentive sons. Unfortunately, we were unable to directly assess the absolute amount of time for which immatures looked at their mothers, due to the limitations imposed by camera trapping (as mentioned above). Although the evidence reported here is inconclusive, we think it represents an example of the types of behaviour and contexts that could be investigated in wild apes to identify forms of functional teaching by stimulation. Indeed, teaching has been proposed to occur in a range of forms in both animal (Hoppitt et al., 2008) and human populations (Kline, 2015; Lancy, 2010; Stout, 2002), depending on the trade-off between costs and benefits for the demonstrator. One important piece of evidence still lacking is whether the number of opportunities provided by mothers directly affects their offspring's efficiency in this skill. However, this was impossible to test with our sample due to the lack of successful extractions by immatures. We did not find any evidence for mothers enhancing offspring learning in a more active way, for instance by sharing tools (Musgrave et al., 2016). Indeed, mothers never initiated tool transfer and sometimes avoided it if initiated by their offspring. Moreover, in a few cases mothers also restricted their offspring's actions by holding their limbs, thus preventing them from manipulating or using tools (Supplementary Material, Video S2). These discordant observations could be linked to substantial differences between termite fishing (Musgrave et al., 2016) and honey extraction in terms of accessibility of the resource and complexity of the task. In fact, termite mounds allow multiple access points to the resource and the technique that chimpanzees need to master to be successful is relatively simple. In contrast, an underground honey chamber needs to be tracked down by following the nest's entrance tube, creating a unique point of access, and the technique used to reach the chamber is highly complex. Such differences might determine the differing behaviour of mothers in the two contexts: in one case, independent resource acquisition is possible, and mothers can gain by enhancing their offspring's access to the resource, whereas when direct competition over access to a resource exists, mothers may be more motivated to dig out the resource by themselves. The specific challenges involved in honey extraction could also explain why mothers should be particularly disposed to enhance learning by their offspring in this context. The amount of inactive time spent by mothers at the bee nests is likely to be linked to their own motivation rather than their offspring's interest in the nests. To test this hypothesis, more detailed data would be needed than camera trap footage: in fact, the motivations for mothers to visit a feeding site or to leave it are dictated by a multitude of factors (e.g. social context, individual's energetic status, nutritional value of the resource as compared to others available, environmental conditions, etc.). Although in our analysis we attempted to control for social factors, more comprehensive, precise and informative data can be achieved only by daily follows of chimpanzees. Nevertheless, in the majority of the visits in our sample, mothers were the first to arrive at bee nest sites and the first to leave them, indicating that they directed the movement. Moreover, it seems unlikely that mothers would spend inactive time at bee nests to guard their offspring as mothers often left the site while their offspring was still actively interested in the bee nest. We also recorded 16 visits in which immatures were possibly alone (that is, mothers were not visible in the detection area of the camera trap).

In conclusion, our findings reinforce the idea that different processes may be at play in the acquisition of tool-using behaviour

by chimpanzees (Heyes, 1994; Whiten et al., 2004; 2009). Moreover, we have presented results suggesting that mothers adjust their behaviour at bee nest sites to provide their offspring with learning opportunities. Although the current study is limited by the type of data employed (camera trap footage) and more comprehensive data are needed to elucidate the exact nature of the learning processes mediating acquisition of this complex extractive technique, it nevertheless provides some intriguing results to be considered in the debate on the processes involved in acquisition of complex techniques by chimpanzees, in particular those regarded as supporting higher copying fidelity, namely the abilities to imitate and teach. Since these abilities are generally considered among the main features distinguishing humans from other animals (Gruber, 2016), examining the behaviour of our closest living relatives can provide insights into the evolutionary origins of these traits. Finally, our study highlights the importance of considering the specific ecological characteristics of the task and the implications for both learners and demonstrators when investigating the learning process for a certain trait, as well as the importance of investigating the behaviour of animals under natural conditions to be able to appreciate its true complexity.

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## Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.anbehav.2018.11.002.

## References

Baayen, R. H. (2008). *Analyzing linguistic data: a practical introduction to statistics using R.* Cambridge, U.K.: Cambridge University Press.

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language, 68*(3), 255–278. https://doi.org/10.1016/j.jml.2012.11.001.

Bates, L. A., & Byrne, R. W. (2009). Sex differences in the movement patterns of free-ranging chimpanzees (*Pan troglodytes schweinfurthii*): Foraging and border checking. *Behavioral Ecology and Sociobiology, 64*(2), 247–255. https://doi.org/10.1007/s00265-009-0841-3.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software, 67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01.

Biro, D., Sousa, C., & Matsuzawa, T. (2006). Ontogeny and cultural propagation of tool use by wild chimpanzees at Bossou, Guinea: Case studies in nut cracking and leaf folding. In T. Matsuzawa, M. Tomonaga, & M. Tanaka (Eds.), *Cognitive development in chimpanzees* (pp. 476–508). Tokyo, Japan: Springer. https://doi.org/10.1007/4-431-30248-4_28.

Boesch, C. (1991). Teaching among wild chimpanzees. *Animal Behaviour, 41*(3), 530–532. https://doi.org/10.1016/S0003-3472(05)80857-7.

Boesch, C. (2013). Ecology and cognition of tool use in chimpanzees. In C. Sanz, J. Call, & C. Boesch (Eds.), *Tool use in animals: Cognition and ecology* (pp. 21–47). Cambridge, U.K.: Cambridge University Press.

Boesch, C., & Boesch-Achermann, H. (2000). *The chimpanzees of the Taï Forest: behavioural ecology and evolution.* New York, NY: Oxford University Press.

Byrne, R. W. (2002). Imitation of novel complex actions: What does the evidence from animals mean? *Advances in the Study of Behavior, 31*, 77–105. https://doi.org/10.1016/S0065-3454(02)80006-7.

Byrne, R. W. (2003). Imitation as behaviour parsing. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 358*(1431), 529–536. https://doi.org/10.1098/rstb.2002.1219.

Byrne, R. W., Hobaiter, C., & Klailova, M. (2011). Local traditions in gorilla manual skill: Evidence for observational learning of behavioral organization. *Animal Cognition, 14*(5), 683–693. https://doi.org/10.1007/s10071-011-0403-8.

Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *Behavioral and Brain Sciences, 21*(5), 667–684.

Caldwell, C. A., & Whiten, A. (2003). Scrounging facilitates social learning in common marmosets, *Callithrix jacchus. Animal Behaviour, 65*(6), 1085–1092. https://doi.org/10.1006/anbe.2003.2145.

Call, J., Carpenter, M., & Tomasello, M. (2005). Copying results and copying actions in the process of social learning: Chimpanzees (*Pan troglodytes*) and human children (*Homo sapiens*). *Animal Cognition, 8*(3), 151–163. https://doi.org/10.1007/s10071-004-0237-8.

Caro, T. M., & Hauser, M. D. (1992). Is there teaching in nonhuman animals? *The Quarterly Review of Biology, 67*(2), 151–174. http://www.jstor.org/stable/2831436.

Crockford, C., Wittig, R. M., Mundry, R., & Zuberbühler, K. (2012). Wild chimpanzees inform ignorant group members of danger. *Current Biology, 22*(2), 142–146. http://doi.org/10.1016/j.cub.2011.11.053.

De Resende, B. D., Ottoni, E. B., & Fragaszy, D. M. (2008). Ontogeny of manipulative behavior and nut-cracking in young tufted capuchin monkeys (*Cebus apella*): A perception–action perspective. *Developmental Science, 11*(6), 828–840. https://doi.org/10.1111/j.1467-7687.2008.00731.x.

Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: A comparative perspective. *Biological Reviews, 89*(2), 284–301. https://doi.org/10.1111/brv.12053.

Estienne, V., Mundry, R., Kühl, H. S., & Boesch, C. (2017). Exploitation of underground bee nests by three sympatric consumers in Loango National Park, Gabon. *Biotropica, 49*(1), 101–109. https://doi.org/10.1111/btp.12354.

Estienne, V., Stephens, C., & Boesch, C. (2017). Extraction of honey from underground bee nests by central African chimpanzees (*Pan troglodytes troglodytes*) in Loango National Park, Gabon: Techniques and individual differences. *American Journal of Primatology, 79*(8), e22672. http://DOI.org/10.1002/ajp.22672.

Field, A. P. (2005). *Discovering statistics using SPSS.* London: Sage Publications Ltd.

Forstmeier, W., & Schielzeth, H. (2011). Cryptic multiple hypotheses testing in linear models: Overestimated effect sizes and the winner's curse. *Behavioral Ecology and Sociobiology, 65*(1), 47–55. https://doi.org/10.1007/s00265-010-1038-5.

Fox, J., & Sanford, W. (2011). *An R companion to applied regression.* Thousand Oaks, CA: Sage.

Fragaszy, D. M., & Adams-Curtis, L. E. (1997). Developmental changes in manipulation in tufted capuchins (*Cebus apella*) from birth through 2 years and their relation to foraging and weaning. *Journal of Comparative Psychology, 111*(2), 201–211. https://doi.org/10.1037/0735-7036.111.2.201.

Fragaszy, D. M., Biro, D., Eshchar, Y., Humle, T., Izar, P., Resende, B., et al. (2013). The fourth dimension of tool use: Temporally enduring artefacts aid primates learning to use tools. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 368*(1630). https://doi.org/10.1098/rstb.2012.0410, 20120410.

Fragaszy, D. M., & Perry, S. (2008). *The biology of traditions: Models and evidence.* Cambridge, U.K.: Cambridge University Press.

Franks, N. R., & Richardson, T. (2006). Teaching in tandem-running ants. *Nature, 439*. https://doi.org/10.1038/439153a, 153–153.

Galef, B. G., & Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: Causal mechanisms and adaptive functions. *Animal Behaviour, 61*(1), 3–15. https://doi.org/10.1006/anbe.2000.1557.

Galef, B. G., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *BioScience, 55*(6), 489–499. https://doi.org/10.1641/0006-3568(2005)055[0489:SLIAES]2.0.CO;2.

Goodall, J. (1968). *The behaviour of free-living chimpanzees in the Gombe Stream Reserve.* London, U.K.: Baillière, Tindall & Cassell.

Gruber, T. (2016). Great apes do not learn novel tool use easily: Conservatism, functional fixedness, or cultural influence? *International Journal of Primatology, 37*(2), 296–316. https://doi.org/10.1007/s10764-016-9902-4.

Gruber, T., Clay, Z., & Zuberbühler, K. (2010). A comparison of bonobo and chimpanzee tool use: Evidence for a female bias in the *Pan* lineage. *Animal Behaviour, 80*(6), 1023–1033. https://doi.org/10.1016/j.anbehav.2010.09.005.

Gunst, N., Boinski, S., & Fragaszy, D. M. (2008). Acquisition of foraging competence in wild brown capuchins (*Cebus apella*), with special reference to conspecifics' foraging artefacts as an indirect social influence. *Behaviour, 145*(2), 195–229. https://doi.org/10.1163/156853907783244701.

Gunst, N., Boinski, S., & Fragaszy, D. M. (2010). Development of skilled detection and extraction of embedded prey by wild brown capuchin monkeys (*Cebus apella apella*). *Journal of Comparative Psychology, 124*(2), 194–204. https://doi.org/10.1037/a0017723.

Hawkes, K., O'Connell, J. F., & Blurton Jones, N. G. (1997). Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. *Current Anthropology, 38*(4), 551–577. https://doi.org/10.1086/204646.

Head, J. S., Boesch, C., Makaga, L., & Robbins, M. M. (2011). Sympatric chimpanzees (*Pan troglodytes troglodytes*) and gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: Dietary composition, seasonality, and intersite comparisons. *International Journal of Primatology, 32*(3), 755–775. https://doi.org/10.1007/s10764-011-9499-6.

Head, J. S., Boesch, C., Robbins, M. M., Rabanal, L. I., Makaga, L., & Kühl, H. S. (2013). Effective sociodemographic population assessment of elusive species in ecology and conservation management. *Ecology and Evolution, 3*(9), 2903–2916. https://doi.org/10.1002/ece3.670.

Head, J. S., Robbins, M. M., Mundry, R., Makaga, L., & Boesch, C. (2012). Remote video-camera traps measure habitat use and competitive exclusion among sympatric chimpanzee, gorilla and elephant in Loango National Park, Gabon. *Journal of Tropical Ecology, 28*(6), 571–583. https://doi.org/10.1017/S0266467412000612.

Heyes, C. M. (1994). Social learning in animals: Categories and mechanisms. *Biological Reviews, 69*(2), 207–231. https://doi.org/10.1111/j.1469-185X.1994.tb01506.x.

Heyes, C. M., & Dawson, G. R. (1990). A demonstration of observational learning in rats using a bidirectional control. *Quarterly Journal of Experimental Psychology, 42*(1), 59–71. https://doi.org/10.1080/14640749008401871.

Hobaiter, C., Poisot, T., Zuberbühler, K., Hoppitt, W., & Gruber, T. (2014). Social network analysis shows direct evidence for social transmission of tool use in wild chimpanzees. *PLoS Biology, 12*(9). https://doi.org/10.1371/journal.pbio.1001960. e1001960.

Hoppitt, W. J. E., Brown, G. R., Kendal, R., Rendell, L., Thornton, A., Webster, M. M., et al. (2008). Lessons from animal teaching. *Trends in Ecology & Evolution, 23*(9), 486–493. https://doi.org/10.1016/j.tree.2008.05.008.

Hoppitt, W., & Laland, K. N. (2008). Social processes influencing learning in animals: A review of the evidence. *Advances in the Study of Behavior, 38*, 105–165.

Inoue-Nakamura, N., & Matsuzawa, T. (1997). Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 111*(2), 159–173. https://doi.org/10.1037/0735-7036.111.2.159.

Jaeggi, A. V., Dunkel, L. P., van Noordwijk, M. A., Wich, S. A., Sura, A. A. L., & van Schaik, C. P. (2010). Social learning of diet and foraging skills by wild immature Bornean orangutans: Implications for culture. *American Journal of Primatology, 72*(1), 62–71. https://doi.org/10.1002/ajp.20752.

Kaminski, J., Call, J., & Tomasello, M. (2008). Chimpanzees know what others know, but not what they believe. *Cognition, 109*(2), 224–234. http://doi.org/10.1016/j.cognition.2008.08.010.

Kline, M. A. (2015). How to learn about teaching: An evolutionary framework for the study of teaching behavior in humans and other animals. *Behavioral and Brain Sciences, 38*, e31. https://doi.org/10.1017/S0140525X14000090.

Lamon, N., Neumann, C., Gruber, T., & Zuberbühler, K. (2017). Kin-based cultural transmission of tool use in wild chimpanzees. *Science Advances, 3*(4), e1602750. https://doi.org/10.1126/sciadv.1602750.

Lancy, D. F. (2010). Learning 'from nobody': The limited role of teaching in folk models of children's development. *Childhood in the Past, 3*(1), 79–106. https://doi.org/10.1179/cip.2010.3.1.79.

Lonsdorf, E. V. (2005). Sex differences in the development of termite-fishing skills in the wild chimpanzees, *Pan troglodytes schweinfurthii*, of Gombe National Park, Tanzania. *Animal Behaviour, 70*(3), 673–683. https://doi.org/10.1016/j.anbehav.2004.12.014.

Mangold (Ed.). (2010). *INTERACT User Guide. Mangold International GmbH.* www.mangold-international.com.

Massen, J. J. M., Antonides, A., Arnold, A.-M. K., Bionda, T., & Koski, S. E. (2013). A behavioral view on chimpanzee personality: Exploration tendency, persistence, boldness, and tool-orientation measured with group experiments. *American Journal of Primatology, 75*(9), 947–958. https://doi.org/10.1002/ajp.22159.

McCullagh, P., & Nelder, J. A. (1989). *Generalized linear models.* London, U.K.: Chapman and Hall.

Murray, C. M., Lonsdorf, E. V., Eberly, L. E., & Pusey, A. E. (2009). Reproductive energetics in free-living female chimpanzees (*Pan troglodytes schweinfurthii*). *Behavioral Ecology, 20*(6), 1211–1216. https://doi.org/10.1093/beheco/arp114.

Musgrave, S., Morgan, D., Lonsdorf, E., Mundry, R., & Sanz, C. (2016). Tool transfers are a form of teaching among chimpanzees. *Scientific Reports, 6*, 34783. https://doi.org/10.1038/srep34783.

Perry, S. (2009). Conformism in the food processing techniques of white-faced capuchin monkeys (*Cebus capucinus*). *Animal Cognition, 12*(5), 705–716. https://doi.org/10.1007/s10071-009-0230-3.

Price, E. E., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2009). A potent effect of observational learning on chimpanzee tool construction. *Proceedings of the Royal Society of London Series B, Biological Sciences, 276*(1671), 3377–3383. https://doi.org/10.1098/rspb.2009.0640.

R Core Team. (2016). *R: A language and environment for statistical computing.* Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/.

Raihani, N. J., & Ridley, A. R. (2008). Experimental evidence for teaching in wild pied babblers. *Animal Behaviour, 75*(1), 3–11. https://doi.org/10.1016/j.anbehav.2007.07.024.

Rendell, L., Fogarty, L., Hoppitt, W. J. E., Morgan, T. J. H., Webster, M. M., & Laland, K. N. (2011). Cognitive culture: Theoretical and empirical insights into social learning strategies. *Trends in Cognitive Sciences, 15*(2), 68–76. https://doi.org/10.1016/j.tics.2010.12.002.

Schielzeth, H. (2010). Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution, 1*(2), 103–113. https://doi.org/10.1111/j.2041-210X.2010.00012.x.

Schielzeth, H., & Forstmeier, W. (2009). Conclusions beyond support: Overconfident estimates in mixed models. *Behavioral Ecology, 20*(2), 416–420. https://doi.org/10.1093/beheco/arn145.

Schuppli, C., Meulman, E. J. M., Forss, S. I. F., Aprilinayati, F., van Noordwijk, M. A., & van Schaik, C. P. (2016). Observational social learning and socially induced practice of routine skills in immature wild orang-utans. *Animal Behaviour, 119*, 87–98. https://doi.org/10.1016/j.anbehav.2016.06.014.

Shumaker, R. W., Walkup, K. R., & Beck, B. B. (2011). *Animal tool behavior: the use and manufacture of tools by animals.* Baltimore, MD: The Johns Hopkins University Press.

Sousa, C., Biro, D., & Matsuzawa, T. (2009). Leaf-tool use for drinking water by wild chimpanzees (*Pan troglodytes*): Acquisition patterns and handedness. *Animal Cognition, 12*(1), 115–125. https://doi.org/10.1007/s10071-009-0278-0.

Stout, D. (2002). Skill and cognition in stone tool production: An ethnographic case study from Irian Jaya. *Current Anthropology, 43*(5), 693–722. https://doi.org/10.1086/342638.

Tennie, C., Call, J., & Tomasello, M. (2006). Push or pull: Imitation vs. emulation in great apes and human children. *Ethology, 112*(12), 1159–1169. https://doi.org/10.1111/j.1439-0310.2006.01269.x.

Tennie, C., Call, J., & Tomasello, M. (2009). Ratcheting up the ratchet: On the evolution of cumulative culture. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 364*(1528), 2405–2415. https://doi.org/10.1098/rstb.2009.0052.

Tennie, C., & Hedwig, D. (2009). How latent solution experiments can help to study differences between human culture and primate traditions. In E. Potocki, & J. Krasinski (Eds.), *Primatology: Theories, methods, and research* (pp. 95–112). Hauppauge, NY: Nova Science.

Thornton, A., & McAuliffe, K. (2006). Teaching in wild meerkats. *Science, 313*(5784), 227–229. https://doi.org/10.1126/science.1128727.

Thornton, A., & Raihani, N. J. (2010). Identifying teaching in wild animals. *Learning & Behavior, 38*(3), 297–309. https://doi.org/10.3758/LB.38.3.297.

Tomasello, M., & Call, J. (1997). *Primate cognition.* New York, NY: Oxford University Press.

Tomasello, M., Call, J., & Hare, B. (2003). Chimpanzees understand psychological states–the question is which ones and to what extent. *Trends in Cognitive Sciences, 7*(4), 153–156. http://doi.org/10.1016/S1364-6613(03)00035-4.

Tomasello, M., Kruger, A. C., & Ratner, H. H. (1993). Cultural learning. *Behavioral and Brain Sciences, 16*(3), 495–511. https://doi.org/10.1017/S0140525X0003123X.

Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour, 60*(2), 195–202. https://doi.org/10.1006/anbe.2000.1457.

van de Waal, E., Bshary, R., & Whiten, A. (2014). Wild vervet monkey infants acquire the food-processing variants of their mothers. *Animal Behaviour, 90*, 41–45. https://doi.org/10.1016/j.anbehav.2014.01.015.

van de Waal, E., & Whiten, A. (2012). Spontaneous emergence, imitation and spread of alternative foraging techniques among groups of vervet monkeys. *PLoS One, 7*(10), e47008. https://doi.org/10.1371/journal.pone.0047008.

Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology, 112*(3), 270–281.

Whiten, A., Horner, V., & de Waal, F. B. M. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature, 437*, 737–740. https://doi.org/10.1038/nature04047.

Whiten, A., Horner, V., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape? *Animal Learning & Behavior, 32*(1), 36–52. https://doi.org/10.3758/BF03196005.

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences, 364*(1528), 2417–2428. https://doi.org/10.1098/rstb.2009.0069.

Wrangham, R. W., Koops, K., Machanda, Z. P., Worthington, S., Bernard, A. B., Brazeau, N. F., et al. (2016). Distribution of a chimpanzee social custom is explained by matrilineal relationship rather than conformity. *Current Biology, 26*(22), 3033–3037. https://doi.org/10.1016/j.cub.2016.09.005.

# Appendix

**Table A1**
Results of models investigating the development of action sequencing

| Response variable [Model] | Estimate | SE | $\chi^2$ | df | P |
|---|---|---|---|---|---|
| **Perforating (yes/no) [Model 1a]: full model** | | | | | |
| (Intercept) | −1.085 | 0.311 | a | a | a |
| Previous action (look at active individual) [b] | −7.221 | 3.156 | a | a | a |
| Previous action (perforate) [b] | 0.748 | 0.233 | a | a | a |
| Previous action (pound) [b] | 1.047 | 0.34 | a | a | a |
| Previous action (dig) [b] | −0.46 | 1.946 | a | a | a |
| Age (years) [c] | 0.867 | 0.254 | a | a | a |
| Sex (male) [d] | 0.243 | 0.337 | 0.443 | 1 | 0.506 |
| Transition number [e] | −0.086 | 0.125 | 0.339 | 1 | 0.56 |
| Previous action (look at active individual) * Age (years) | 0.741 | 0.962 | 3.976 | 4 | 0.409 |
| Previous action (perforate) * Age (years) | −0.408 | 0.302 | | | |
| Previous action (pound) * Age (years) | −0.796 | 0.465 | | | |
| Previous action (dig) * Age (years) | −0.251 | 1.505 | | | |
| **Perforating (yes/no) [Model 1a]: reduced model** | | | | | |
| (Intercept) | −1.049 | 0.318 | a | a | a |
| Previous action (look at active individual) [b] | −4.549 | 1.286 | 27.606 | 4 | <0.001 |
| Previous action (perforate) [b] | 0.673 | 0.248 | | | |
| Previous action (pound) [b] | 0.927 | 0.371 | | | |
| Previous action (dig) [b] | −0.497 | 1.925 | | | |
| Age (years) [c] | 0.765 | 0.232 | 9.853 | 1 | 0.002 |
| Sex (male) [d] | 0.254 | 0.348 | 0.472 | 1 | 0.492 |
| Transition number [e] | −0.084 | 0.125 | 0.309 | 1 | 0.578 |
| **Exploring (yes/no) [Model 1b]: full model** | | | | | |
| (Intercept) | −0.462 | 0.228 | a | a | a |
| Previous action (look at active individual) [b] | −0.958 | 0.285 | a | a | a |
| Previous action (perforate) [b] | 0.029 | 0.233 | a | a | a |
| Previous action (pound) [b] | −0.283 | 0.308 | a | a | a |
| Previous action (dig) [b] | −0.391 | 0.880 | a | a | a |
| Age (years) [c] | −0.106 | 0.152 | a | a | a |
| Sex (male) [d] | 0.180 | 0.250 | 0.530 | 1 | 0.467 |
| Transition number [e] | 0.121 | 0.111 | 0.785 | 1 | 0.376 |
| Previous action (look at active individual) * Age (years) | −0.585 | 0.208 | 10.888 | 4 | 0.028 |
| Previous action (perforate) * Age (years) | −0.208 | 0.282 | | | |
| Previous action (pound) * Age (years) | 0.051 | 0.364 | | | |
| Previous action (dig) * Age (years) | 1.431 | 1.115 | | | |
| **Looking at another active individual (yes/no) [Model 1c]: full model** | | | | | |
| (Intercept) | −2.264 | 0.425 | a | a | a |
| Previous action (look at active individual) [b] | 2.889 | 0.357 | a | a | a |
| Sex (male) [d] | −0.292 | 0.388 | 0.472 | 1 | 0.492 |
| Age (years) [f] | −1.287 | 0.265 | a | a | a |
| Transition number [g] | −0.674 | 0.283 | 5.068 | 1 | 0.024 |
| Previous action (look at active individual) * Age (years) | 1.817 | 0.312 | 20.882 | 1 | <0.001 |

All models tested the effects of the interaction between the type of immediately preceding action and immature age (in years), and the effect of sex on the probability that perforating, exploring or looking at an active individual, respectively, occurs next in the sequence (models 1a, 1b or 1c, respectively, GLMM; N = 765 transitions for models 1a and 1b, N = 425 for model 1c).

[a] Not shown as having a very limited interpretation. P values for intercepts would refer to the proportion of 'yes' over 'no', when all covariates are at zero (here, equal to their average value, as all covariates were z-transformed) and all factorial predictors are at their reference category. For the main effects of predictors involved in an interaction term, P values would refer exclusively to the effect of that predictor with the interacting covariate at zero, or the interacting factor at its reference category. Therefore, we consider P values of main effects to be meaningful only when the predictors are not involved in an interaction.

[b] Estimate and SE refer to the difference in response between the reported level of the predictor and the reference category (explore).

[c] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 7.6 and 2.5 years, respectively.

[d] Estimate and SE refer to the difference in response between the reported level of the predictor and the reference category (female).

[e] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 41.73 and 52.31 transitions, respectively.

[f] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 7.0 and 2.8 years, respectively.

[g] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 33.91 and 48.54 transitions, respectively.

**Table A2**
Results of model investigating factors influencing the frequency of the grip type 'both' used when perforating nests, by immature male chimpanzees in Loango National Park

| | Estimate | SE | $\chi^2$ | df | P |
|---|---|---|---|---|---|
| **Full model** | | | | | |
| (Intercept) | 1.705 | 0.617 | a | a | a |
| Mother's preference [b] | −0.068 | 0.486 | a | a | a |
| Age (years)[c] | 1.056 | 0.299 | a | a | a |
| Soil hardness [d] | 0.441 | 0.317 | 1.837 | 1 | 0.175 |
| Mother's preference * Age (years) | −0.138 | 0.296 | 0.193 | 1 | 0.660 |
| **Reduced model** | | | | | |
| (Intercept) | 1.692 | 0.582 | a | a | a |
| Mother's preference [b] | 0.058 | 0.427 | 0.013 | 1 | 0.909 |
| Age (years)[c] | 1.012 | 0.280 | 8.177 | 1 | 0.004 |
| Soil hardness [d] | 0.504 | 0.293 | 3.002 | 1 | 0.083 |

This model tested the effect of the interaction between mother's grip preference and immature's age on the probability of immature males using the grip type 'both' when perforating nests (model 2, GLMM; N = 214; each data point corresponds to one perforation).
[a] Not shown as having a very limited interpretation; see footnotes to Table A1 for details.
[b] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 0.581 and 0.071, respectively.
[c] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 8.27 and 1.46 years, respectively.
[d] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 16.5 and 0.2 cm, respectively.

**Table A3**
Results of model investigating the factors affecting the proportion of time that mothers spent inactive when they visited underground bee nests

| | Estimate | SE | $\chi^2$ | df | P |
|---|---|---|---|---|---|
| (Intercept) | 0.508 | 0.042 | a | a | a |
| Interaction with the nest by immature (proportion of time) [b] | −0.006 | 0.035 | 15.523 | 1 | 0.883 |
| Immature age$^2$ | 0.109 | 0.03 | a | a | a |
| Immature age (years) [c] | −0.215 | 0.057 | a | a | a |
| Sex of immature (male) [d] | 0.119 | 0.056 | a | a | a |
| Number of social partners [e] | 0.043 | 0.035 | 16.384 | 1 | 0.347 |
| Sex of immature (male) * Immature age$^2$ | −0.159 | 0.044 | 22.500 | 1 | 0.008 |
| Sex of immature (male) * Immature age | 0.361 | 0.065 | a | a | a |

This model tested how offspring attributes (sex and age) and behaviour (proportion of time spent interacting with the bee nest, per visit) affected the proportion of time mothers spent being inactive at a bee nest site (model 3, GLMM; N = 67; each data point corresponds to one visit).
[a] Not shown as having a very limited interpretation; see footnotes to Table A1 for details.
[b] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 0.12 and 0.21, respectively.
[c] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 3.4 and 2.7 years, respectively.
[d] Estimate and SE refer to the difference in response between the reported level of the predictor and the reference category (female).
[e] z-transformed to a mean of zero and SD of one; mean and SD of the untransformed variable were 1.42 and 2.15, respectively.
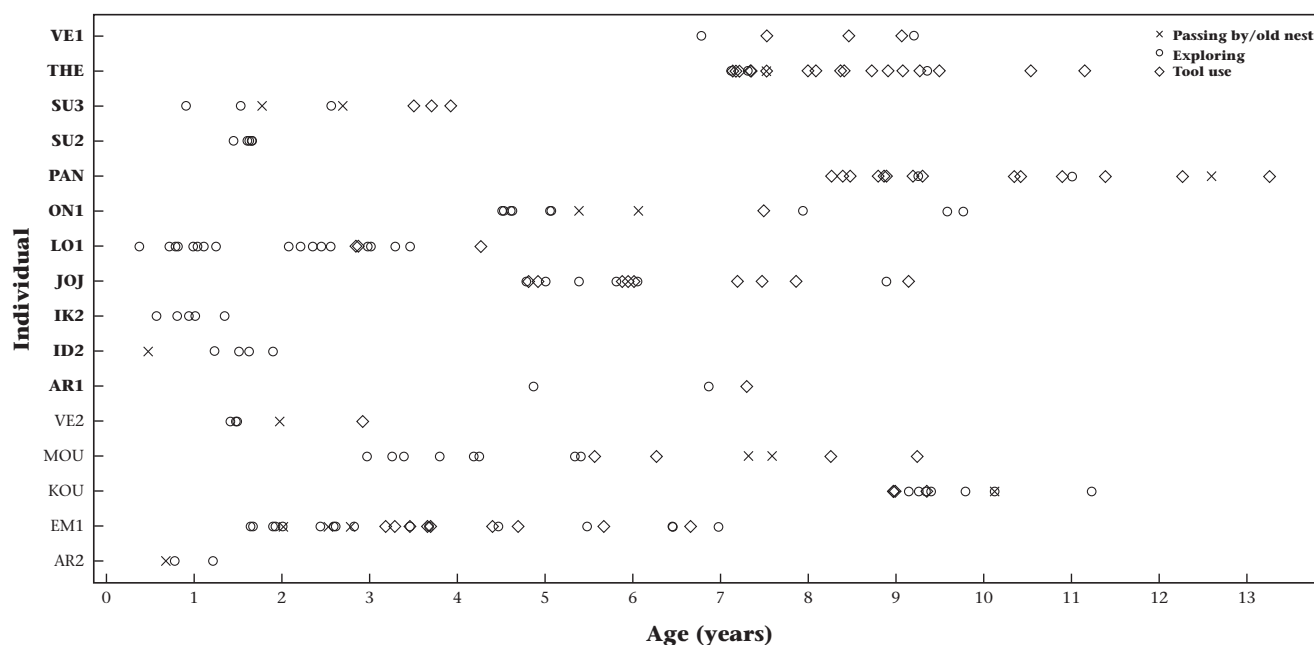


**Figure A1.** Overview of the ages covered by our video footage for each of the immature individuals in the study. Symbols represent different types of nest visit, depending on the behaviour of the subject: crosses represent videos where the immature merely passed by a nest or visited a nest previously accessed and consumed; circles represent visits during which they performed only exploratory actions; and diamonds represent visits in which they also used tools. Although the number of visits is limited for a few subjects, all ages are fairly evenly represented overall.