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Maternal influence on the development of nut-cracking skills in the chimpanzees of the Taï forest, Côte d'Ivoire (*Pan troglodytes verus*)

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Abstract

Chimpanzees' (*Pan troglodytes*) nut-cracking behavior represents one of the most complex forms of tool-use known among nonhuman animals. Given the close phylogenetic relationship between these apes and humans, investigating how such complex behavior develops in immatures can reveal the evolutionary roots of the cognitive processes that enabled the evolution of outstanding technological skills in our lineage. In this study, we investigated whether maternal behavior directly enhanced nut-cracking skills in immature individuals. We analyzed the behavior of 11 immatures and their mothers ($N = 8$) during nut-cracking activity, spanning over three consecutive nut-cracking seasons in the Taï National Park, Côte d'Ivoire. We used generalized linear mixed models to (a) obtain values of maternal scaffolding (defined as provision of learning opportunities) and active nut-sharing behavior of each mother according to the age of their offspring, and their average nut-cracking efficiency; (b) to test whether these variables enhanced immatures' nut-cracking skills; and (c) to test whether immatures' features (age, sex, and begging behavior) influenced maternal behavior as observed in our videos. Although the predicted values of maternal scaffolding and active nut-sharing did not obviously affect immatures' skills, they were positively influenced by the average maternal efficiency and by sharing hammers with their mothers. In addition, our observations showed that mothers were more likely to share nuts with their sons than with their daughters, and the more their offspring begged. Concurrently, male immatures were also found to beg more often than females. Our results add evidence on the ontogenetic pathway leading to the full acquisition of nut-cracking in wild chimpanzees and on the effect that maternal behavior can have in promoting the acquisition of this complex tool-use behavior. Moreover, our study strengthens the importance of naturalistic observations to understand complex skill acquisition. Finally, we suggest future avenues for investigating the maternal influence on learning.

KEYWORDS

begging, efficiency, interindividual differences, learning, nut-sharing, ontogeny, opportunity provision, scaffolding, tool-sharing, tool-use

1 | INTRODUCTION

Signs of percussive actions on stone materials in the archeological record represent the earliest evidence of hominin's tool use behavior (Goren-Inbar, Sharon, Melamed, & Kislev, 2002). The appearance of stone tool usage in human behavior provides indirect evidence for the emergence of complex cognitive abilities, such as enhanced sensory-motor abilities; object-related action planning, evaluation and representation; coordination of flexible, hierarchically organized, and goal-directed sequences of actions (Stout & Chaminade, 2012; Stout, Toth, Schick, & Chaminade, 2008). Chimpanzees' nut-cracking behavior, first described in West African chimpanzees (*Pan troglodytes verus*; Boesch & Boesch, 1984a, 1984b), represents a percussive behavior employing stone tools. Nut-cracking requires the ability to dynamically relate three different objects and exploiting their mechanical properties To obtain a goal (Boesch & Boesch-Achermann, 2000; Matsuzawa, 2008) and it represents the most complex form of percussive technology known amongst nonhuman animals to date. Due to the similarities between this behavior and human stone flaking, and given the close phylogenetic relatedness between chimpanzees and humans, nut-cracking has received special attention by scholars interested in the origin and evolution of complex technological skills and associated cognitive abilities in our lineage (Bril, Parry, & Dietrich, 2015).

Cultural evolution theory proposed that the accurate transmission of information between individuals supported the evolution of increasingly more complex tool manufacturing and tool-using techniques in humans (Lewis & Laland, 2012). Although the ability of learning from the behavior of others (social learning; Heyes, 1994) is known to support the transmission of behaviors and technological skills in a wide range of nonhuman animals (Fragaszy & Perry, 2008), humans remain unmatched in the animal kingdom for the complexity and variety of their technological behaviors. High-fidelity transmission of information is believed to be mediated by two processes, supposedly unique to the human species: imitation (sensu Call, Carpenter, & Tomasello, 2004) and teaching (Dean, Vale, Laland, Flynn, & Kendal, 2014; Fogarty, Strimling, & Laland, 2011; Moore, 2013). Several lines of evidence suggest that nonhuman primates (hereafter, primates) are able to copy others' actions (Whiten & van de Waal, 2017). On the contrary, teaching has been strongly regarded as distinctively human (Csibra & Gergely, 2011; Tomasello, Kruger, & Ratner, 1993). Another approach, first proposed by Caro and Hauser (1992), defines teaching based on the observable functional aspects of this behavior. Based on this definition, evidence of functional teaching has been found thus far in meerkats (*Suricata suricatta*; Thornton & McAuliffe, 2006), pied babblers (*Turdoides bicolor*; Raihani & Ridley, 2008) and tandem-running ants (*Temnothorax albipennis*; Franks & Richardson, 2006). Early observations on wild West African chimpanzees from the Taï forest suggested that such a process could also occur in the context of acquisition of complex tool-using techniques (Boesch, 1991). More recently, a study focusing on tool transfer in wild Central African chimpanzees (*P. troglodytes*) provided additional evidence for functional teaching in this taxon (Musgrave, Morgan, Lonsdorf, Mundry, & Sanz, 2016).

In the specific case of nut-cracking, studies conducted on two species of primates that engage in this behavior, chimpanzees (Biro et al., 2003; Inoue-Nakamura & Matsuzawa, 1997) and capuchins (*Sapajus* spp.; Coelho et al., 2015; Eshchar, Izar, Visalberghi, Resende, & Fragaszy, 2016; Ottoni, Resende, & Izar, 2005), suggested that immature individuals acquire this behavior via different social learning processes, including local- and stimulus- enhancement, emulation, and social facilitation. A key condition for such learning to occur is a high level of tolerance that skilled individuals show towards unskilled individuals. This form of learning is known as "education by master and apprenticeship" (Matsuzawa et al., 2008), in which unskilled individuals acquire a skill via repeated observation of the actions performed by skilled individuals, mostly their mothers (Boesch, 1991; Lonsdorf, 2005), who are highly tolerant of the observers. Notably, observations from the field sites of Bossou and Gombe have stressed how mothers are rather uninterested in their offspring's nut-cracking behavior and do not intervene during their attempts (Inoue-Nakamura & Matsuzawa, 1997; Lonsdorf, 2006). These results suggest that teaching does not occur in chimpanzees and that inadvertent social learning processes (where the demonstrator passively provides information to the observer) supported by high role model tolerance and an extended association between mother-offspring pairs, would be sufficient to promote skill acquisition (Hoppitt et al., 2008). However, observations from wild chimpanzees inhabiting the Taï National Park, Côte d'Ivoire, suggested a more active role of mothers (Boesch, 1991; Boesch & Boesch-Achermann, 2000). Mothers could promote learning by providing opportunities for practicing nut-cracking (namely, by leaving nut-cracking materials such as intact nuts and tools available for their offspring to use), a process we refer to as "scaffolding" in this study. In addition, rare observations suggest that mothers could also actively manipulate the actions of their offspring, leading to a subsequent increase in her offspring's performance ("teaching" in Boesch, 1991; Boesch & Boesch-Achermann, 2000). Finally, food sharing has also been proposed as a potential mechanism supporting learning: by providing food rewards to their offspring, mothers would direct immatures' attention to the nut-cracking task, which in turn would enhance task acquisition (Boesch & Boesch-Achermann, 2000; Brown, Almond, & van Bergen, 2004). Here, we define food sharing as the transfer of cracked nuts from an individual who is in possession of a cracked nut to an individual who does not (Stevens & Gilby, 2004).

In this study, we investigated whether the above mentioned supportive maternal behaviors (scaffolding and nut-sharing) did positively impact the nut-cracking skills of immature individuals. These behaviors represent possible candidates for functional teaching in that they fulfill the first two requirements of the definition that we adopted. First, they occur only in the presence of juveniles: neither allowing access to tools or to intact nuts nor manipulating others actions have ever been observed occurring between adult chimpanzees at Taï (Boesch & Boesch-Achermann, 2000), and sharing cracked nuts between adults occurs very rarely (C. Boesch, *pers.comm.*). In addition, adults are known to transport

hammers between different nut-cracking sites or when going to collect nuts between bouts (Boesch & Boesch, 1984a, 1984b; H. Cohen, *pers.comm.*). Second, sharing food is a costly behavior for the donor (Boesch & Boesch-Achermann, 2000), as is the provisioning of tools (Musgrave et al., 2016).

In addition, we considered maternal efficiency as a potential source of maternal influence on immatures' performance. Studies on capuchins (*Sapajus libidinosus*; Fragaszy et al., 2010) showed that nut-cracking efficiency is determined by several factors, including physical properties of the subject, of the nut, and of the tools used, but also behavioral factors (e.g., the elevation of hands holding the hammer above the nut; the body position in relation to the anvil; the ability to minimize nut displacement on the anvil). Moreover, recent findings showed interindividual differences in the grip used for handling tools in bonobos (nut-cracking; Neufuss, Humle, Cremaschi, & Kivell, 2016) and chimpanzees (underground honey extraction; Estienne, Stephens, & Boesch, 2017). The expected individual variation in tool-use behavior might thus affect mothers' nut-cracking performance. In addition, immature chimpanzees can acquire details about tool use behaviors by observing their mothers (Estienne, Robira, Mundry, Deschner, & Boesch, 2019; Lonsdorf, 2005). Taken together, this evidence supports our hypothesis that maternal individual-typical behavior can affect her efficiency and that this can be reflected in her offspring's behavior.

We hypothesized that immature's nut-cracking abilities were positively affected by maternal supportive behavior. We contrasted this hypothesis with the hypothesis that immature chimpanzees gained nut-cracking skills only by repeated observation of their mothers and individual practice (as postulated by the "education by master and apprenticeship" hypothesis). Immature chimpanzees are in constant association with their mothers until reaching 8 to 10 years of age and mothers represent their primary model for tool-aided food processing skills acquisition (Boesch & Boesch-Achermann, 2000; Lonsdorf, 2005, 2006). Also, our observations of mother-offspring interactions in the context of nut-cracking were considerably limited (as compared with the total amount of learning opportunities that immatures were actually exposed to; see Methods section for more details). Therefore, we used immatures' age as a proxy for the number of opportunities that immatures had to observe their mothers nut-cracking. If the "education by master and apprenticeship" hypothesis were true, we predicted (a) that "age" explains nut-cracking skill development and (b) that immatures' efficiency correlates with their mothers' efficiency. The latter prediction is expected as offspring of more efficient mothers would have more opportunities to learn or would be exposed to a better example than the offspring of less efficient mothers. Alternatively, if maternal behavior (together with exposure to mothers' behavior) supports the acquisition of immatures' nut-cracking skills, we predicted that maternal scaffolding and nut-sharing behavior would also have a positive effect on immature's nut-cracking skills, in addition to the effect of "age."

To understand whether mothers are sensitive to the development of their offspring's skills, we also tested whether they change their behavior according to their offspring's characteristics. Assuming that immatures' skills increase with age (due to individual practice) and that female offspring learn faster and more proficiently than males (Boesch & Boesch-Achermann, 2000; Gruber, Clay, & Zuberbühler, 2010; Lonsdorf, 2005), we predicted (a) that mothers decrease their supportive behavior as their offspring ages and (b) that they are less supportive towards females compared with males. The latter prediction originated by early observations of maternal nut-sharing behavior toward infants of different sexes reporting that sons receive a larger amount of nuts from their mothers than daughters do (Boesch & Boesch-Achermann, 2000). In the specific case of maternal sharing of nuts, we also tested the effect of immature's begging behavior, predicting that mothers are more likely to share with more persistent offspring. Finally, we investigated which factors influence the begging behavior of offspring, predicting that immature's frequency of begging changes with age following an inversed U-shape function (i.e., increases until the point when infants start becoming able to carry out the task, and decreases as they enhance their nut-cracking skills), and that sexes do not differ in this aspect.

2 | METHODS

2.1 | Data collection

Nut-cracking behavior of mothers and their offspring from two different chimpanzees communities (East and South) inhabiting the Taï National Park, Cote d'Ivoire (5°08'N to 6°07'N and 6°47'W to 7°25'W), was video recorded over three consecutive nut-cracking seasons (November–April; 2013–2014, 2014–2015, 2015–2016). Details about the habitat and nut-cracking behavior can be found in Boesch and Boesch-Achermann (2000). Taï chimpanzees crack the nuts of five tree species; these nuts have different physical properties and require different effort and skills to be cracked. In this study, we limited our investigation to *Coula edulis* nut cracking. The total sample included eight mothers (four from East community and four from South community), five immature females and six immature males (*N* total of immature subjects = 11). We use the term "immature" to refer to individuals that are still dependent on their mothers (infants and juveniles; following Boesch & Boesch-Achermann, 2000). For six immatures, information about the exact birthdate was available; for the others, this information was available to the monthly level. In the latter case, we used the 15th day of the month in which they were born as an estimated birthdate and calculated their ages accordingly, for each observation. Overall, our data included immatures aged between 2.4 and 8 years. Videos were recorded during daily all-day focal follows (Altmann, 1974). Overall, we obtained 69.7 hr of clear observation. Details about the exact duration of clear observation for each subject and season, sex and exact or estimated age range (in years, for immatures) are reported in Table 1 and summarized in Figure S1.

The Taï Chimpanzee Project has been running since 1979, and the two communities that were the focus of this study are

TABLE 1 Details of the sample used for this study

					Duration of visibility (hr)				Tot bouts	
			Age (years)		Season					
Subject ID	Group	Sex	Min	Max	2013–2014	2014–2015	2015–2016	Tot	*N*	Duration (hr)
Bamou	East				0.32			0.32	10	0.29
Beatrice	East	F	4.34	4.42	0.71			0.71	25	0.37
Elisa	East				1.66	1.46		3.12	64	2.64
Emma	East	F	2.38	3.35	1.44	1.90		3.35	48	0.74
Erasmus	East	M	7.03	7.98	0.97	1.26		2.24	84	1.98
Isha	South				1.31	4.09	2.76	8.16	209	7.47
Ithaca	South	M	6.54	6.58	2.31			2.31	67	1.87
Iniesta	South	M	1.96	2.98	0.63	3.05	2.20	5.88	127	0.71
Kinshasa	South				2.84	1.59		4.43	93	3.41
Kayo	South	F	2.78	3.84	2.66	1.59		4.24	39	0.62
Mbeli	South				0.57	1.31	1.02	2.90	116	2.57
Mohan	South	F	3.66	3.70	0.48	1.11	1.34	2.93	73	0.63
Pola	East				0.15	0.85	1.84	2.85	68	2.49
Pessoa	East	M	5.98	6.96	0.90	1.52		2.42	54	2.06
Placali	East	F	1.52	2.54	0.08	0.79	1.63	2.50	60	0.79
Sumatra	South				4.29	3.13	3.17	10.59	209	7.21
Solibra	South	M	2.43	4.44	2.90	2.90	2.96	8.76	175	2.77
Yeha	East				0.77			0.77	24	0.67
Yoyo	East	M	4.03	4.99	1.02	0.25		1.27	23	0.40
Tot					26.02	26.79	16.93	69.74	1568	39.68

Note: Mothers are indicated in bold; mothers and offspring are identified by having names starting with the same letter. "Sex" ("M" for males and "F" for females) and the range of "Age" (exact or estimated) are reported for offspring only. The duration of visibility, in hours for each season, refers to the total time each subject was clearly visible in the footage. The column "Tot bouts" shows the total number of nut cracking bouts ("*N*") and their total duration ("Duration (Hours)") for each subject.

well-habituated to human observers. This study is thus based on noninvasive observations and complies with the laws of Côte d'Ivoire, as well as with the American Society of Primatologists principles for the ethical treatment of primates. Moreover, all research protocols have been approved by the Ethics committee of the Max Planck Society on the August 4, 2014.

2.2 | Video coding

Chimpanzees' behavior was coded from video footage by two observers, H. C. and K. Corogenes, using the software INTERACT 14 (MANGOLD, 2015). All operational definitions used for coding are given in Table 2; all behaviors were coded as events (starting when the action started) and duration was coded for the time that each subject was visible in the video ("visibility"). A nut-cracking "bout" was defined as starting when the subject placed a nut on the anvil and ending when subjects changed tool or did not perform any nut-cracking related behavior for more than 2 s (Sousa, Biro, & Matsuzawa, 2009). For immatures, it could occur that they performed nut-cracking related actions (e.g., hitting on a substrate) while one or more of the three elements necessary for the successful accomplishment of the task (namely, nut, hammer, and anvil) were not available to them. In this case, a "bout" began when they started performing a nut-cracking related action and ended as described above. Hammer size and materials were coded as modifiers of behavior, when appropriate (see Table 2).

K. Corogenes trained H. C. in coding the footage until they reached good levels of interobserver agreement. Interobserver reliability was assessed on 2.6 hr of observation of two mother-offspring pairs by comparing the number of occurrences of maternal scaffolding (Spearman's rho = 0.88), maternal active sharing of cracked nuts (Spearman's rho = 0.93), immature's successful hits (Spearman's rho = 1), and immature's unsuccessful hits (Spearman's rho = 0.85).

2.3 | Characterizing maternal behavior (models 1–3)

In our video coding, we scored maternal scaffolding every time that mothers provided opportunities for practicing nut-cracking to their offspring when departing from the anvil and leaving nut-cracking materials (intact nuts and/or hammer and/or anvil) available to their offspring (behaviors initiated by the mothers, see Table 2). As in our sample, we observed no instance of active manipulations of immatures' actions by their mothers, we omitted this aspect of maternal behavior from all following investigations. However, we did

TABLE 2 Ethogram used for coding the behavior of mother and immature chimpanzees recorded on footage for this study

Codes for Behaviors	Operational definitions
Visibility [a,b]	Time when the focal subject was visible in the video.
Proximity [c]	Distance between mother and immature.
	Modifier: Contact OR arm reach OR visible (but farther away than arms reach) OR unknown.
Nut placement [b]	Subject places a nut on an anvil cavity or on the ground; used as an indicator of starting a 'bout.'
Hit [b]	Subject moves the arm vertically against an object.
Success [b]	Successful hit that cracks a nut.
Change hammer [b]	Subject changes the hammer used for nut-cracking; used as an indicator of ending a 'bout.'
	Modifiers: Hammer material (stone OR wood); Hammer size (chest width OR bigger than chest width OR smaller than chest width).
Observed scaffolding	1 - Mother departs from the anvil and leaves nut-cracking material (intact nuts and/or hammer and/or anvil) available to her offspring; also used as indicator of ending a 'bout'. One behavior was logged regardless of how many nut-cracking objects were left behind by the mother.[d]
	Modifier: Immature present OR absent.
	2 - Mother hands out a hammer to her offspring, with no previous solicitation from their part.[d]
	Modifiers: Hammer material (stone OR wood); Hammer size (chest width OR bigger than chest width OR smaller than chest width).
	3 - Returning to the anvil, after having collected more nuts, mother does not push away the immature who took her spot; instead, she waits until the immature no longer performs any nut-cracking action before resuming nut-cracking, or she takes another position.[d]
	4 - Mother manipulates nuts in front of the immature.[d]
	5 - Immature uses mother's tools eliciting no reaction from their mother (hammer AND/ OR anvil) [c].
	Modifiers: Hammer material (stone OR wood); Hammer size (chest width OR bigger than chest width OR smaller than chest width).
	6 - Immature takes intact nut from mother's pile of nuts eliciting no reaction from their mother [c].
Beg [c]	1 - Immature outstretches hand towards mother's body (hand/ arm OR mouth).
	Modifier: Mother's activity (eating OR nut-cracking).
	2 - Immature outstretches hand towards mother's tool (anvil OR hammer).
	Modifier: Mother's activity (eating OR nut-cracking).
	3 - Immature touches mother's food.
	Modifier: Mother's activity (eating OR nut-cracking).
Active nut sharing [d]	1 - Mother hands out a nut (or parts of it) to the immature, with no previous solicitation ('Beg') from their part.
	2 - Mother facilitates access to cracked nuts (or parts of them) to the immature, after a begging gesture; access can be provided by the mother by directing her body towards the immature or by opening the hand that holds the nut.
Passive nut sharing [c]	1 - Immature takes nut from mother's mouth/hand.
	2 - Immature takes cracked nut (or parts of it) from mother's anvil.
Refusal [d]	1 - After a begging gesture (see 'Beg') from the immature, the mother prevents the immature from accessing a cracked nut (or part of it) by performing one of the following behaviors: mother moves herself AND/ OR the cracked nut away from the immature; mother pushes the immature away, mother takes back from the immature the nut (or parts of it) that s/he previously took from her.
	2 - Mother ignores immature's begging gesture (see 'Beg').

[a]Code for which duration was recorded.
[b]Coded for both mothers and immatures.
[c]Coded for immatures only.
[d]Coded for mothers only.

observe one instance in which a mother positioned a nut in front of her infant, replacing the nut that he previously placed (video S1); we counted this observation among the scaffolding events. Finally, we also counted as scaffolding all instances where immatures took nut-cracking material previously used by their mothers (i.e., intact nuts or tools; behaviors initiated by the immatures, see Table 2), their mother being present and eliciting no reaction from her. We pooled together these behaviors because we considered them as two ways in which mothers could facilitate practicing opportunities to her offspring: on the one hand, they can allow access to nut-cracking

materials when departing from the nut-cracking site and leave tools and intact nuts behind, a behavior that usually does not occur in adult chimpanzees (Boesch, 1991); on the other hand, they could also allow access to tools and intact nuts by suspending their own nut-cracking activity for some time, during which their offspring can use nut-cracking materials.

With regard to nut-sharing, our coding scheme differentiated between "active" and "passive" maternal nut-sharing: "active" nut-sharing referred to instances when mothers either handed cracked nuts to their offspring with no obvious previous solicitation (begging gesture) from their parts, or instances when mothers facilitated the transfer of cracked nuts to their offspring, after a begging gesture; "passive" nut-sharing referred to instances when immatures took possession of cracked nuts that were either on their mother's hand or on the anvil that she used for cracking, and this did not elicit any immediate reaction of their mothers (i.e., mothers allowed the infant to take cracked nuts). Because we considered that active sharing better reflects the behavior of the mother (as opposed to "passive" sharing, which was initiated by the immature), we characterized maternal behavior only based on active nut-sharing and used this variable in the following analyses.

Based on these observations, we needed to quantitatively characterize maternal scaffolding and nut-sharing behavior to be used as test predictors of immatures' nut-cracking skills. Despite the fact that our data were collected over three seasons and comprised a relatively large number of subjects, our observations are limited in two important aspects: first, they represent only a limited fragment of the nut-cracking experience of our study subjects, both in each specific season included in this study and in comparison with the entire lifespan of each individual; and second, they were also greatly scattered over time (see Figure S1). These two factors made it impossible to know the exact amount of scaffolding or nut-sharing received by an immature before our observation, or between two of our observations. For example, the immature male "Erasmus" was sampled only between 7 and 8 years of age (Figure S1b): at that age we expected that his mother would not support his learning of nut-cracking, as his skills allow him to be already independent in this task (Boesch & Boesch-Achermann, 2000); thus, the number of scaffolding behaviors performed by his mother that we recorded would likely drastically underestimate the real number he had experienced. Therefore it is obviously inappropriate to use the observed number of scaffolding/nut-sharing behaviors, observed in our videos where both mothers and their offspring were recorded together, as a predictor of immatures' performance. In addition, as we did not have a complete picture of the maternal behavior until the time of our observation, it was impossible for us to calculate the cumulative number of scaffolding (or sharing) behaviors that occurred before a certain age, for each mother-immature pair. To overcome such limitations, we used generalized linear mixed models (GLMMs; Baayen, 2008) to extract predicted values of maternal scaffolding and nut-sharing behavior according to the identity of the mother and the age of her offspring (Figures S2 and S3 for details). We accounted for immature age as we expected that it affects the extent to which mothers provide practicing opportunities and share nuts with their offspring (Boesch, 1991; Boesch & Boesch-Achermann, 2000); when a mother had more than one offspring, the immature's characteristics referred to the immature in closest spatial proximity to her. We used these variables as test predictors in the following models (see methods used for fitting models 4–6).

To obtain such values we fitted two models, having as response variables (a) the frequency of observed scaffolding behaviors, per video (Model 1, with negative binomial error distribution; *N* videos = 479); and (b) the probability that mothers actively shared a cracked nut with their infant, per video, expressed as the number of times that active share was observed versus the number of times that mothers were observed to successfully crack a nut but did not share it with their offspring (Model 2, with binomial error distribution; *N* videos = 425). Both models included the fixed effects of immature's age and sex (two levels), with immature's age included as linear, as well as squared term, as we expected an inversed U-shaped relationship between infants age and maternal supportive behavior (see Figures S2 and S3). All models included the random intercept of maternal identity ("mother ID," eight levels); moreover, Model 1 included an offset term accounting for the duration of visibility of each mother in a video. These models allowed extracting an expected value of maternal scaffolding or nut-sharing, respectively, across all mothers and immatures' ages. The predicted values consist of the sum of the effects of the random slope of immature's age within "mother ID" (both linear and nonlinear) plus the random intercept of "mother ID" (best linear unbiased predictors, "BLUPs" sensu Baayen, 2008). The values expressed by the random intercept (one for each individual mother) represent the deviation in the average response of each individual mother from the average of the fitted model, across all immatures' ages. The values of the random slopes, in turn, represent the variance in the effect of immatures' age on the response among individual mothers. Their sum thus represents the age-corrected deviation of maternal behavior (for each mother) from the fitted model (see captions of Figures S2 and S3 in the Supporting Information for further details on this).

Finally, we also characterized mothers with regard to their nut-cracking efficiency. Nut-cracking efficiency was calculated as the number of successfully cracked nuts per minute of nut-cracking time. As we did not expect that offspring age would affect maternal efficiency, we obtained average, individual-specific indices of maternal nut-cracking efficiency (Model 3). To obtain average nut-cracking efficiency values for each individual mother, we used a GLMM having as response variable the number of successes per bout (modeled with Poisson error structure and log link function; *N* bouts = 793). This model controlled for how many days passed between the date in which the video was recorded and the beginning of the nut-cracking season ("days in season"), as nuts become progressively easier to crack throughout the season (Luncz, Mundry, & Boesch, 2012). We determined the beginning of the nut-cracking season based on direct observations of chimpanzees' feeding behavior in Taï, so that the start date of each season was set to the first day in which a chimpanzee was seen consuming *Coula* nuts (namely, Nov 2, 2013 for season 1, Nov 3, 2014 for season 2, and

Nov 2, 2015 for season 3); the model included the random intercept of maternal identity ("mother ID," eight levels) and an offset term accounting for the duration of each nut-cracking bout. From this model, we obtained the intercepts of the random effect "mother ID" (BLUPs): this value expresses the individual variation in efficiency. Intercepts varied between −0.057 and 0.130. Complete formulas for each model listed above are reported in Table S1.

2.4 | Factors affecting immatures' nut-cracking skills development (models 4–6)

Next we tested the effects of the variables extracted above on the development of immatures' nut cracking skills. Immatures' nut-cracking skills were quantified as three different response variables. In Model 4, we considered as an indication that the immatures reached a general understanding of the task whether, for each time that they started a nut-cracking bout (model having a binomial error structure and logit link function; $N = 775$), all three elements needed for this task were present (namely, nuts, hammer, and anvil) or not. This model included the fixed effects of "predicted maternal scaffolding" (represented by one value for each age at which an immature was observed in the videos; this variable includes the age-corrected and individual-specific deviations of maternal behavior from the fitted model, obtained from Model 1), "predicted maternal active nut-sharing" (represented by one value for each age at which an immature was observed; same as above, obtained from Model 2), immature's age, immature's sex (two levels), and community ID (two levels), the random effects of video ID (328 levels), date when the video was recorded nested in immature ID ("date-immature," 146 levels), immature ID (11 levels), mother ID (eight levels), and the random slopes of immature's age, "predicted maternal scaffolding," and "predicted maternal active nut-sharing" within immature ID and within mother ID.

Model 5 considered immatures' efficacy, indicated by the number of successes versus number of failures, per nut-cracking bout (model with binomial error structure and logit link function; $N = 603$); this was expressed as the number of successful hits (resulting in a cracked nut) versus the number of unsuccessful hits per nut-cracking bout. This model included, in addition to all fixed effects listed for the previous model, the following fixed effects: whether immatures, during a bout, used the anvil just previously used by their mother ("use mother's anvil (yes/no)," 2 levels), whether immatures, during a bout, used the hammer just previously used by their mother ("use mother's hammer (yes/no)," 2 levels), hammer material (2 levels, wood or stone), hammer size (3 levels, chest width, bigger than chest width, smaller than chest width), and number of days passed between the observation and the beginning of the nut season ("days in season"). The predictors "use mother's anvil (yes/no)" and "use mother's hammer (yes/no)" were included to control for when immatures used the tools used by their mothers at the level of each bout, and it was scored regardless of the presence of the mother. On the other hand, the variable "predicted maternal scaffolding" reflected maternal behavior. The possible correlation between the two variables was ruled out by inspecting variance inflation factors (VIF; see Section 2.6). The predictors "hammer material" and "hammer size" controlled for hammers' physical properties, which we expected to affect nut-cracking performance. The random intercepts of this model included bout ID (603 levels), video ID (277 levels), date nested in immature ID ("date-immature," 128 levels), immature ID (11 levels), mother ID (8 levels), anvil ID (324 levels), and hammer ID (293 levels). Random slopes included those of "use mother's anvil," "use mother's hammer," "hammer material," "hammer size," "immature's age," "days in season," "predicted maternal scaffolding," and "predicted maternal active nut-sharing" within immature ID and mother ID.

Finally, Model 6 considered immatures' efficiency, calculated as the number of nuts opened per minute of nut-cracking activity (modeled with Poisson error structure and log link function; N bouts = 603). This model included all fixed effects listed for Model 5, plus a fixed effect indicating average maternal efficiency (one value for each mother). The random effects structure was identical to that of Model 5. This model also included an offset term accounting for bout duration.

To pinpoint the effect of maternal behavior on immatures' skill development, for all models described in this section, we specifically tested the effect of these variables on the development of immatures' nut-cracking skills. This was done by comparing the full model with a null model lacking exclusively the effects of maternal behaviors, namely, "predicted maternal scaffolding" and "predicted active nut-sharing" for models 4 and 5, and "predicted maternal scaffolding," "predicted active nut-sharing" and "average maternal efficiency" for Model 6. Immature's age was always considered as a control variable, as we expected it to have an effect on the development of immatures' skills. All models also included immature's sex as a control variable, as females are known to perform better than males in this task (Boesch & Boesch, 1984a, 1984b), and daughters become independent from their mothers in obtaining nuts earlier than sons (Boesch & Boesch-Achermann, 2000).

2.5 | Drivers of maternal supportive behavior (models 7–09)

To understand whether mothers changed their supportive behavior (scaffolding and active nut-sharing) according to the age of their offspring, we fitted two models. In Model 7, we tested the effects of immatures' attributes (age and sex) on the frequency of observed scaffolding behaviors that occurred in our videos (modeled with Poisson error structure and log link function; N videos = 488); we included immature's age as a linear as well as a squared term, as we expected that mothers' scaffolding peaked at an intermediate infant age (Figure S2). This model controlled for community ID (2 levels), and it included an offset term accounting for the duration of mother's visibility. We included the random intercepts of immature ID (11 levels), mother ID (8 levels), and date nested within mother ID ("date-mother," 148 levels); as random slopes, we included immature's age (linear and squared) within immature ID and mother ID.

In Model 8, we tested the effect of immatures' attributes (age and sex) and begging persistence on the probability that mothers refused sharing of a cracked nut, after a begging gesture. This model included 1,381 begging gestures and had a binomial error structure and logit link function. As above, age was included as a linear and squared term (Figure S3); immature's begging persistence was included in the model as a covariate consisting of the order of each begging gesture in the sequence of gestures performed by immatures ("begging order"). We controlled for: mother's age, used as a proxy for mother's rank as mothers of higher rank were observed to share more with their offspring (Boesch & Boesch-Achermann, 2000); mothers' age was estimated based on the long-term data set available for the Taï Chimpanzees Project. Additional control variables were community ID (two levels); and nut-cracking season ID (three levels), to control for potential differences in nut-production (hence, availability) in different years, as during more productive years mothers could afford sharing more nuts with their offspring. Random intercepts were immature ID (10 levels), mother ID (eight levels), video ID (253 levels), and date nested within mother ID ("date-mother," 105 levels).

Finally, we also tested how age and sex affected the begging persistence of immatures, computed as the number of begging gestures produced by an immature during one nut-cracking bout of the mother (model 9, with Poisson error structure and log link function; *N* bouts = 672). Immature's age was included again as a linear and a squared term, as we hypothesized that immatures would progressively increase their begging effort as they age while they are not yet successful in nut-cracking and then would subsequently decrease it as they acquire proficiency in nut-cracking. This model controlled for the effects of community ID (two levels) and for maternal efficiency (as this variable could drive offspring's begging behavior). We included random intercepts of immature ID (11 levels), mother ID (eight levels), date nested within immature ID ("date-immature," 145 levels), video ID (408 levels), and maternal nut-cracking bout ID ("mother bout ID," 659 levels) as multiple begging gestures could occur during the same bout. Random slopes included the immature age within immature ID and mother ID. Finally, the model accounted for the duration of each mother's bout, included as an offset term.

2.6 | Model implementation

All analyses were conducted in R (version 3.4.2; R Core Team, 2017). We fitted GLMMs using the functions glmer (for Poisson and binomial models) or glmer.nb (for negative binomial models) of the package lme4 (Bates, Maechler, Bolker, & Walker, 2015). We ruled out collinearity among predictors by inspecting VIFs (Field, 2005) using the function VIF of the R-package car (Fox & Weisberg, 2011), based on standard linear models excluding the random effects and squared terms (max. VIF = 2.2). We did not detect overdispersion in any of the Poisson models (models 3, 6, 7, and 9: dispersion parameters = 0.93, 0.89, 0.94, 0.41 respectively). A negative binomial model (Model 1) was used instead of Poisson models when overdispersion appeared to represent an issue (overdispersion parameter = 2.1); using a negative binomial model led to an over-dispersion parameter of 1.6. We assessed model stability 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. For models 4 to 9, we 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, random effects and the offset term (if present), using a likelihood ratio test (R-function anova with argument test set to "Chisq"). When a squared term had no significant effect, we fitted a reduced model including only the main effect of the same variable (models 7 and 8). *p* values for individual predictors were based on likelihood ratio tests comparing the full with a respective reduced model (R-function drop1; Barr, Levy, Scheepers, & Tily, 2013). Before fitting the models, all covariates were *z*-transformed to a mean of zero and a standard deviation of one (Schielzeth, 2010) and all offset terms were log-transformed.

3 | RESULTS

3.1 | Factors affecting immatures' nut-cracking skills development (models 4–6)

Observed maternal scaffolding behavior occurred in 86.7% of the cases in the presence of offspring (*N* = 370 over a total number of 427 scaffolding behaviors coded). However, neither "predicted maternal scaffolding" nor "predicted maternal active nut-sharing" significantly affected the achievement of task understanding by immatures (Model 4, full vs. null model: $X^2 = 1.375$, $df = 2$, $p = .503$). Immature's age was the only variable that had a significant positive effect on the probability that immatures used all three elements when attempting nut-cracking (Table S2). Immatures reached a consistent use of all three elements needed for functional nut-cracking between 3 and 4 years of age (Figure 1a). However, in our sample immatures began to produce nut-cracking related actions (i.e., hits) as young as 1.5 years of age, and the first success was recorded at 2.4 years of age.

Likewise, predicted maternal behavior did not obviously affect immatures' efficacy (Model 5, full vs. null model: $X^2 = 2.965$, $df = 2$, $p = .227$), and immature's age had a strong positive effect on immature's efficacy (Figure 1b; Table S3). Regarding immatures' efficiency, average maternal efficiency (but not "predicted maternal scaffolding" or "predicted maternal active maternal nut-sharing") appeared to strongly influence this variable (Model 6, full vs. null model: $X^2 = 17.883$, $df = 3$, $p < .001$). As above, age had a positive effect on immatures' efficiency (Figure 1c; Table 3). However, we also found that average maternal efficiency had a strong significant positive effect on the response (Figure 2; Table 3).

Other factors that significantly affected immatures' skills were hammer material and hammer size. Wooden hammers significantly decreased immatures' efficacy, and hammers bigger than chest width improved efficacy (Table S3; Figure S4); similarly, wooden hammers

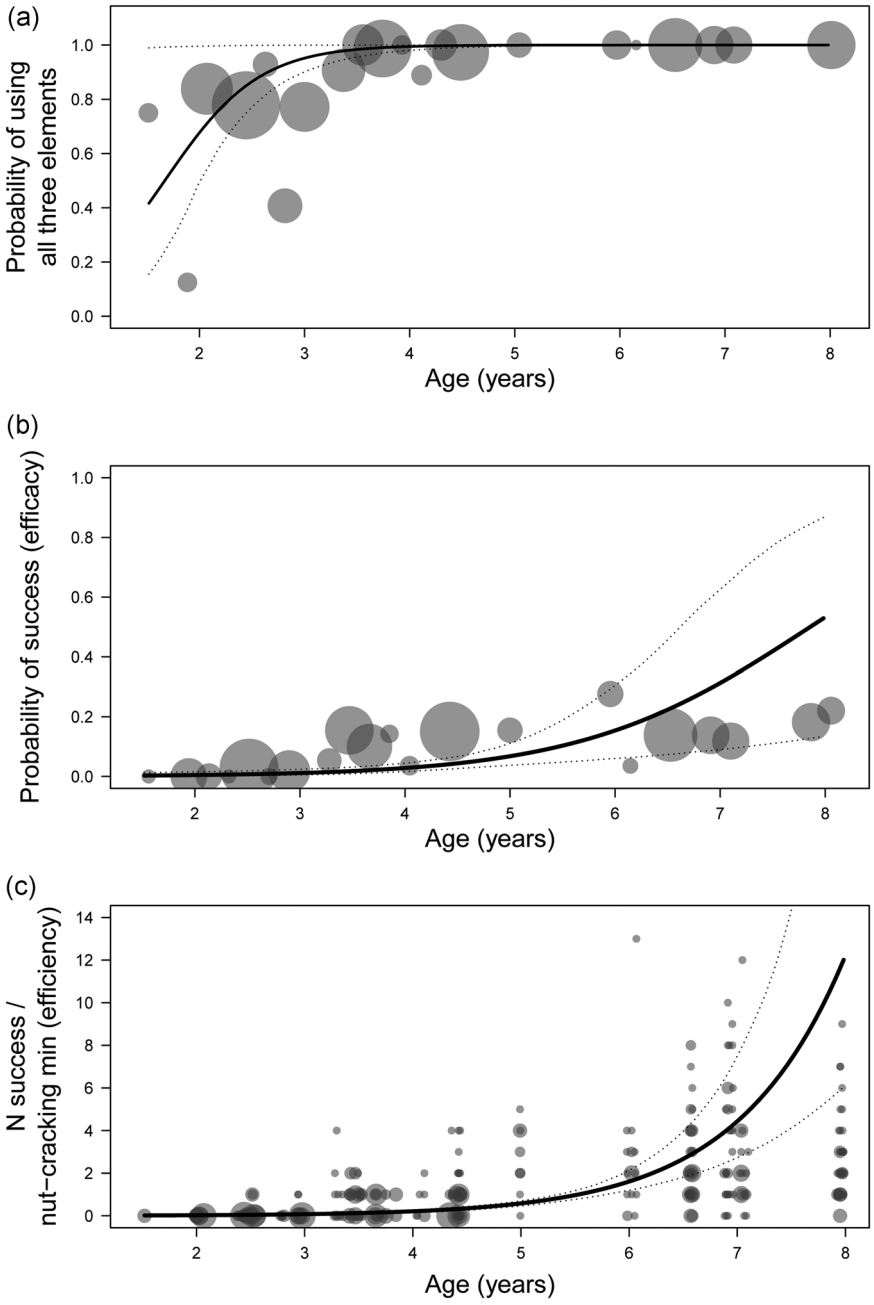

FIGURE 1 Effect of age on the development of the three variables used to indicate immatures' nut-cracking skills in this study. (a) Effect of immatures' age on the probability that immatures used all three elements needed for successfully achieving the task (nut, hammer, and anvil) when attempting nut-cracking (Model 4, $N = 775$ bouts); data have been binned across age of immatures' and the area of the circles is proportional to the number of bouts for binned age. (b) Effect of immatures' age on the proportion of successful hits over the total number of hits used for each nut-cracking bout (efficacy; Model 5, $N = 603$ bouts); the area of the dots represents the frequency of occurrence of binned value of "number of cracked nuts" per each value of "maternal efficiency." (c) Effect of immatures' age on the number of nuts successfully cracked by an immature individual, per minute of nut-cracking activity (efficiency; Model 6, $N = 603$ bouts); the area of the circles is proportional to the number of observations for each combination of "N success" and immatures' age. In all plots, solid lines show the fitted values and dotted lines indicate confidence intervals

significantly reduced immatures' efficiency, but hammer size did not obviously influence this variable (Table 3; Figure S5). We also found that using mother's hammer had a weak positive effect on immature's efficacy (Table S3; Figure 3a), and a similar but stronger effect on their efficiency (Table 3; Figure 3b). Finally, the number of days passed since the beginning of the season also significantly affected immatures' efficiency (Table 3).

3.2 | Drivers of maternal supportive behavior (models 7–9)

Immatures' sex and age did not obviously affect the frequency of occurrence of observed scaffolding behaviors by their mothers (Model 7, full vs. null model comparison: $X^2 = 5.551$, $df = 3$, $p = .136$; Table S4).

We observed 1,381 cases of immatures begging to their mothers for nuts: in 13% of the cases mothers actively shared nuts with their offspring ($N = 180$) and in 22.2% of the cases they allowed immatures to take nuts ($N = 307$); in 894 cases (64.8%) mothers actively refused nut sharing after a begging gesture. Our model showed that immatures' characteristics and behavior did significantly change the probability that their mothers were observed to refuse sharing nuts with them (Model 8, full vs. null model comparison: $X^2 = 11.345$, $df = 4$, $p = .023$). As age squared was not significant, we ran a reduced model; all results are reported in Table 4. Mothers were less likely to refuse sharing with a son than with a daughter (Figure 4a) and were less likely to refuse sharing the longer the immature begged

TABLE 3 Results of model investigating immatures' efficiency (Model 6)

	Estimate	*SE*	CI 2.5%	CI 97.5%	χ^2	*df*	*p*
Intercept	−4.640	0.392	[a]	[a]	[a]	[a]	[a]
Predicted maternal scaffolding [b]	0.112	0.181	−0.270	0.594	0.146	1	.702
Predicted maternal active nut-sharing [c]	0.204	0.547	−0.971	1.397	0.077	1	.781
Use mother's hammer (yes)	0.678	0.272	0.185	1.176	4.718	1	.030
Immature's age [d]	1.899	0.288	1.383	2.560	18.121	1	<.001
Average maternal efficiency [e]	0.862	0.183	0.530	1.284	14.094	1	<.001
Immature's sex (male)	−0.515	0.448	−1.432	0.385	0.790	1	.374
Community ID (south)	0.715	0.359	−0.013	1.506	2.896	1	.089
Use mother's anvil (yes)	−0.036	0.215	−0.469	0.349	0.028	1	.867
Hammer material (wood)	−0.485	0.199	−0.812	-0.104	5.677	1	.017
Hammer size (chest width)	−0.124	0.133	−0.387	0.130	2.516	2	.284
Hammer size (smaller than chest width)	−0.539	0.352	−1.254	0.180			
Days in season [f]	0.288	0.074	0.148	0.425	8.935	1	.003

Note: For categorical predictors, the values of the estimate and *SE* refer to the difference in the response between the reported level of the predictor (indicated in parenthesis, next to each predictor) and the reference category. References categories are: "female" for the predictor "Immature's sex"; "east" for the predictor "Community ID"; "no" for the predictors "Use mother's hammer" and "Use mother's anvil"; "stone" for the predictor "Hammer material"; and "bigger than chest width" for the predictor "Hammer size".

Abbreviations: CI, confidence interval; *SE*, standard error.

[a]Not shown due to having a very limited interpretation.

[b]Predicted value of maternal scaffolding from Model 1, *z*-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were 0.559 and 0.238, respectively.

[c]Predicted value of maternal active nut-sharing from Model 2, *z*-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were 0.029 and 0.046, respectively.

[d]*z*-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were 4.522 and 1.911 years, respectively.

[e]Maternal intercepts from Model 3, *z*-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were −0.005 and 0.102, respectively.

[f]*z*-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were 61.794 and 17.505 days, respectively.

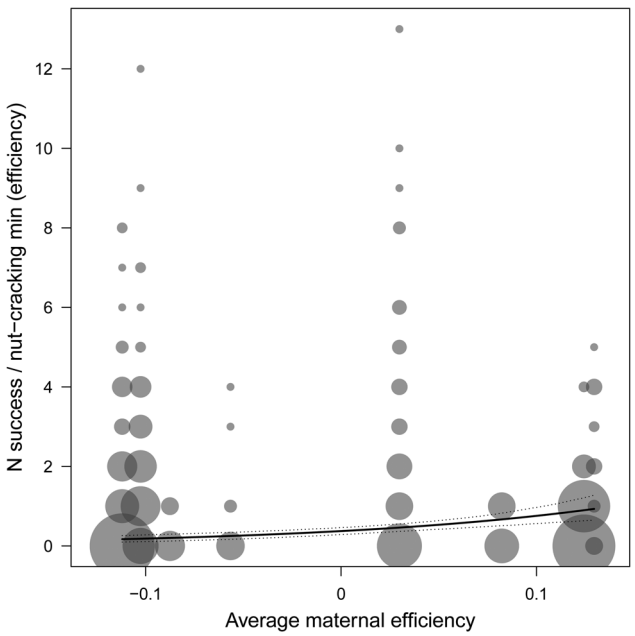

FIGURE 2 Effect of average maternal efficiency on immatures' efficiency. The area of the circles represents the number of observations per each combination of value of the predictor and response; the solid line shows the fitted values and dotted lines indicate confidence intervals (Model 6; *N* = 603 bouts)

(Figure 4b). Immature's age did not have a significant effect on observed mother's sharing behavior, but community membership did, with mothers from the 'south' community being more likely to share with their offspring as compared with mothers from the 'east' community.

Immatures' begging behavior was explained by their age and sex (Model 9, full vs. null model comparison: $X^2 = 14.670$, $df = 3$, $p = .002$; Table 5): begging frequency increased until immatures reached 3 to 4 years of age, and decreased thereafter (Figure 5a), and males begged more often than females (Figure 5b). Immatures belonging to different communities did not obviously differ in their begging behavior.

4 | DISCUSSION

In this study, we used detailed observations of both mothers and offspring in the context of nut-cracking to test whether maternal behavior enhanced offspring's learning of this task. Against our predictions, we found that neither the general tendency of producing different forms of practicing opportunities provided by mothers ("predicted maternal scaffolding") nor nut-sharing ("predicted maternal active nut-sharing") promoted immatures' skills, measured

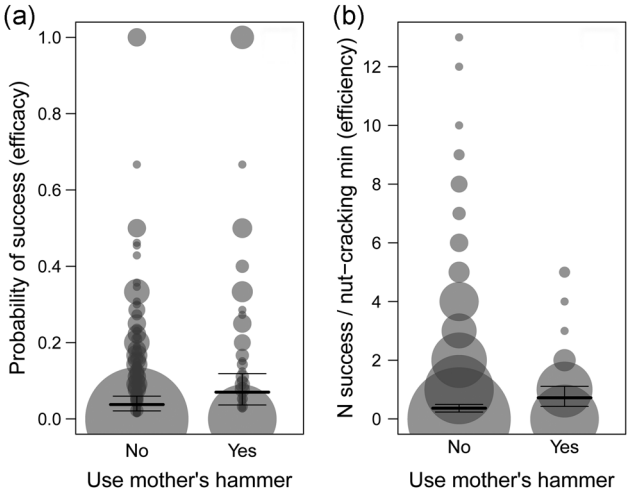

FIGURE 3 Effect of using a hammer just previously used by the mother on immature's nut-cracking efficacy (a) and efficiency (b; Models 5 and 6, $N = 603$ bouts in both cases). The area of circles is proportional to the number of observations per each combination of the value of the predictor and response. In both plots, the thicker, solid line shows the fitted values, and thinner solid lines indicate confidence intervals

as achievement of task understanding, probability that they successfully cracked a nut (efficacy), and number of nuts cracked per minute of nut-cracking (efficiency). However, using hammers that were just previously used by their mothers had a strong positive effect on immatures' efficiency and, seemingly, efficacy. In addition, immatures' efficiency positively correlated with maternal efficiency. In accordance with the "education by master and apprenticeship" hypothesis, age had the greatest impact in the development of immatures' nut-cracking skills in all measures that we considered (a general understanding of the task, efficacy, and efficiency). Other factors that significantly affected immature's nut-cracking performance were linked to hammer properties. Wooden hammers significantly limited efficacy and efficiency (as compared with stone hammers), as did hammers smaller than chest width or as big as chest width (as compared with hammers being bigger than chest width) on efficacy. We also tested whether observed maternal scaffolding and nut-sharing behavior changed depending on the offspring's characteristics. We found that maternal scaffolding did not significantly change depending on immatures' age or sex. However, immature's sex and begging behavior (but not age) strongly affected the probability that mothers shared cracked nuts with them: mothers

TABLE 4 Results of model investigating maternal nut-sharing behavior, as observed in our video footage (Model 8)

Full model	Estimate	*SE*	CI 2.5%	CI 97.5%	χ^2	*df*	*p*
Intercept	0.616	0.204	[a]	[a]	[a]	[a]	[a]
Immature's age [b]	0.007	0.067	[a]	[a]	[a]	[a]	[a]
Immature's age [2] [b]	0.044	0.038	−0.022	0.155	1.478	1	.224
Immature's sex (male)	-0.824	0.290	−1.431	-0.235	6.492	1	.011
Mother's age [c]	0.072	0.113	−0.148	0.321	0.408	1	.523
Begging order [d]	-0.117	0.060	−0.238	0.010	3.829	1	.050
Community ID (south)	0.585	0.205	0.190	1.021	7.774	1	.005
Season ID (2)	0.106	0.142	−0.175	0.401	0.775	2	.679
Season ID (3)	0.141	0.178	−0.190	0.488			
Reduced model							
Intercept	0.600	0.203	[a]	[a]	[a]	[a]	[a]
Immature's age [b]	0.031	0.063	−0.089	0.159	0.239	1	.625
Immature's sex (male)	-0.694	0.267	−1.257	-0.181	5.393	1	.020
Mother's age [c]	0.029	0.107	−0.184	0.243	0.072	1	.788
Begging order [d]	-0.130	0.058	−0.257	−0.013	4.635	1	.031
Community ID (south)	0.543	0.201	0.150	0.951	6.889	1	.009
Season ID (2)	0.114	0.141	−0.175	0.394	0.653	2	.721
Season ID (3)	0.123	0.177	−0.235	0.491			

Note: For categorical predictors, the values of the estimate and *SE* refer to the difference in the response between the reported level of the predictor (indicated in parenthesis, next to each predictor) and the reference category. References categories are "female" for the predictor "Immature's sex"; "east" for the predictor "Community ID"; and "1" for the predictor "Season ID."

Abbreviations: CI, confidence interval; *SE*, standard error.

[a]Not shown due to having a very limited interpretation.

[b]z-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were 2.890 and 0.672 years, respectively.

[c]z-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were 40.655 and 10.506 years, respectively.

[d]z-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were 6.104 and 6.087 (order position in a sequence).

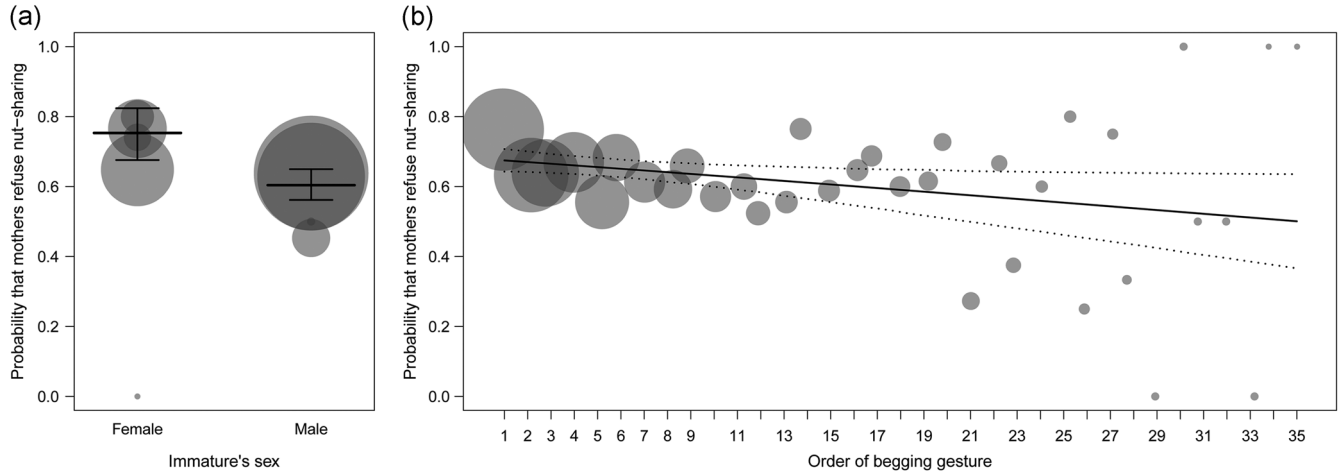

FIGURE 4 Effect of immature's sex (a) and of the order of occurrence of a begging gesture (b) on the probability that mothers refused nut-sharing after a begging gesture (Model 8; N = 1,381 begging gestures). In (a), the area of the circles represents the frequency of occurrence of refusing sharing for each combination of mother ID and immature sex; in (b), it represents the frequency of occurrence of refusing sharing for per binned "order of begging." In both plots, the thicker, solid line shows the fitted values; confidence intervals are indicated by thinner solid lines (a) and dotted lines (b)

were more likely to share with male offspring and after more begging gestures occurred. Our results also showed that immatures' begging behavior significantly changed according to immatures' age and sex: begging frequency followed an inversed U-shaped curve over time (as predicted), and male immatures did beg more often than females.

Our results strengthen the evidence in support of the hypothesis that mastery of this task is reached after a long period of apprenticeship (Matsuzawa et al., 2008). Despite the overarching effect of age, our analyses revealed that also social factors had a significant impact on immature's nut-cracking performance in three different aspects. First, confirming earlier observations, the full acquisition of nut-cracking understanding was reached around 3–4 years of age (Boesch & Boesch-Achermann, 2000; Inoue-Nakamura & Matsuzawa, 1997), and nut-cracking performance (measured as efficacy and efficiency) started to rise around 5 - 6 years of age (Figure 1b and c). Nevertheless, immatures attempted nut-cracking much earlier in life: we observed infants hitting nuts with a hammer as young as 1.5 years old, that is, a year before the first success was recorded. These observations contrast with findings from studies on the ontogeny of this behavior in captivity (Hirata, Morimura, & Houki, 2009), where young individuals included hitting actions in their repertoire only shortly before first succeeding in nut-cracking. This suggests that the social environment in which immature individuals develop under natural conditions is likely to play a crucial role in the learning process of complex tool-use behaviors. It holds however true that immatures did attempt nut-cracking while lacking one or more of the three elements necessary to correctly manage the task, and the consistent use of all three elements was only reached after long practice.

Second, the transfer of hammers from mother to offspring significantly enhanced nut-cracking performance in immatures.

TABLE 5 Results of model investigating immatures' begging behavior, as observed in our video footage (Model 9)

	Esti-mate	*SE*	CI 2.5%	CI 97.5%	χ^2	*df*	*p*
Intercept	−5.322	0.433	[a]	[a]	[a]	[a]	[a]
Immature's sex (male)	1.484	0.589	0.295	2.700	5.094	1	.024
Immature's age [b]	0.275	0.130	[a]	[a]	[a]	[a]	[a]
Immature's age [2] [b]	−0.376	0.077	−0.644	−0.246	11.949	1	.001
Maternal efficiency [c]	0.111	0.286	−0.520	0.721	0.152	1	.697
Community ID (south)	−0.038	0.545	−1.209	1.013	0.005	1	.944

Note: For categorical predictors, the values of the estimate and *SE* refer to the difference in the response between the reported level of the predictor (indicated in parenthesis, next to each predictor) and the reference category. References categories are "female" for the predictor "Immature's sex"; and "east" for the predictor "Community ID."

Abbreviations: CI, confidence interval; *SE*, standard error.

[a]Not shown due to having a very limited interpretation.

[b]z-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were 2.918 and 1.060 years, respectively.

[c]Maternal intercepts from Model 3, z-transformed to a mean of zero and a standard deviation of one; mean and *SD* of the untransformed variable were 0.001 and 0.103, respectively.

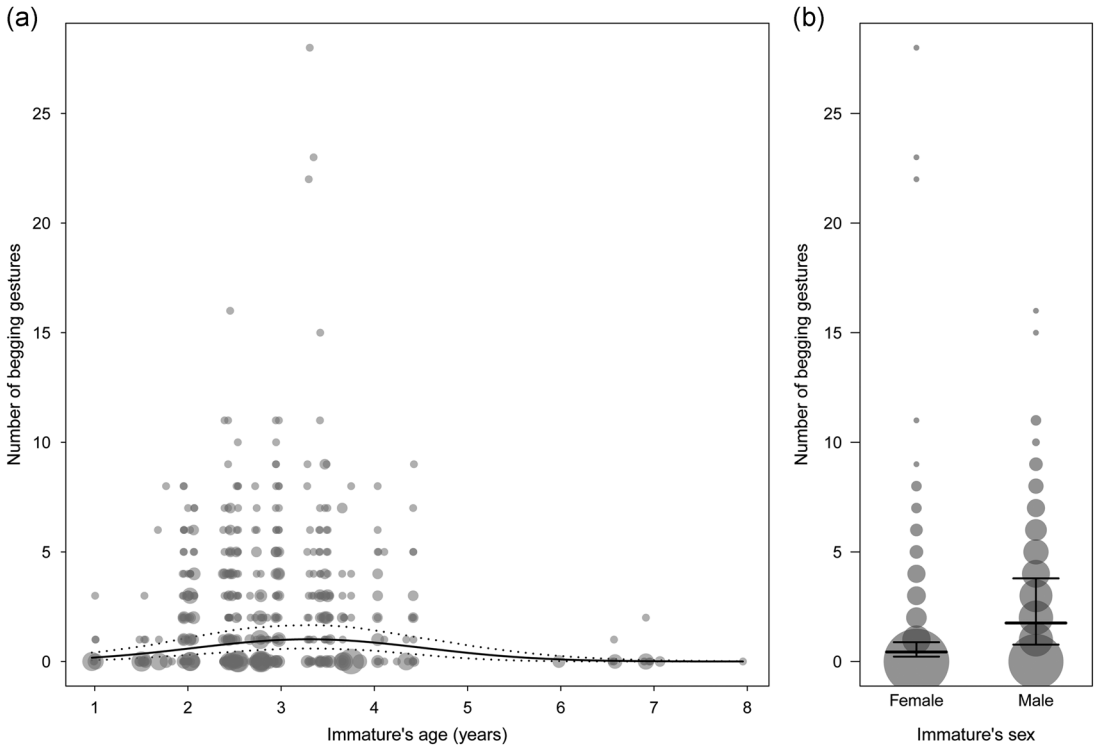

FIGURE 5 Effect of age (a) and sex (b) on the number of begging gestures produced by an immature chimpanzee, per minute of maternal nut-cracking activity (Model 9; $N = 672$ bouts). In (a), the area of the circles represents the number of observations per combination of the number of begging gestures and binned age of the immature; in (b), the area of the circles represents the number of observations per each combination of sex and number of begging gestures. In both plots, the thicker, solid line shows the fitted values; confidence intervals are indicated by dotted lines (a) and thinner solid lines (b)

This result matched the findings from a study on termite fishing in central African chimpanzees, where the transfer of fishing probes from mothers to offspring provided significant advantages for the latter (Musgrave et al., 2016). Noticeably, in the above-mentioned study tool transfer was always initiated by the recipient. On the contrary, in our sample, immatures produced a begging gesture directed to the hammer held by their mothers in only 28 cases over a total number of 1,383 begging gestures observed, and in only two cases this resulted in tool transfer (with a maximum time lag between begging gesture and tool transfer of 3 seconds). Thus, the majority of tool transfers in our data happened either when mothers departed from the anvil leaving hammers available for their offspring ($N = 339$) or when immatures used the hammer previously used by their mothers, eliciting no reaction from the mothers ($N = 199$). In either case, although mothers did not actively give their hammers to their offspring, immatures did not obviously solicit the tool transfer either. Thus, in this context, mothers allow tool transfer by leaving the tool available for their offspring. Noticeably, adult females would rarely leave their hammers unattended unless their infants were present, or no other adults were around (Boesch, 1991). Mothers are expected to optimize their hammer choice depending on their functional features (Sirianni, Mundry, & Boesch, 2015). Our results showed that using mothers' hammers (a hammer, thus, that has been selected by an experienced individual according to its physical properties) does positively impact immatures' performance. Therefore, by directly experiencing the effect of hammers selected by skilled individuals, unskilled individuals can gain information about the physical properties of hammers and about their effect on their own performance. Thus, ultimately, they acquire information about what an efficient hammer looks like and how to proficiently carry out this task. While confirming the proposition that nut-cracking learning in chimpanzees is mediated by high levels of tolerance by mothers toward their offspring (Matsuzawa et al., 2008), our results added quantitative evidence on the effect that tolerance for sharing functional hammers has on the acquisition of this task by unskilled individuals. Our study thus adds to findings showing how maternal behavior, although potentially unintentional, can positively influence the acquisition of tool-use skills in chimpanzees (Boesch & Boesch-Achermann, 2000; Musgrave et al., 2016).

Third, immatures seemed to benefit from having more efficient mothers. The variable used in our analysis represented the average individual-specific efficiency of each mother, therefore, this result was not likely related to the particular circumstances of each nut-cracking bout, but rather reflected a general trait of each mother. Maternal efficiency might be directly related to each individual's nut-cracking technique (e.g., individual differences in dexterity) and be transmitted to their offspring. Recent studies showed that nut placement preferences can affect nut-cracking performance in capuchins (*Sapajus libidinosus*; Falótico, Luncz, Svensson, & Haslam, 2016) and also that fine differences in movement can be transmitted from mothers to

offspring (Fuhrmann, Ravignani, Marshall-Pescini, & Whiten, 2014). In this study we did not directly investigate which factors (environmental or behavioral) contributed to interindividual differences in nut-cracking efficiency, however, our results suggested that these differences influenced offspring's performance. Evidence suggesting that consistent interindividual differences in behavior can potentially affect individual fitness begins to accumulate (Dingemanse & Réale, 2005; Smith & Blumstein, 2008). Under this perspective, future studies could focus on understanding the drivers of maternal efficiency and their effect on immatures' learning of this task.

The general tendency of maternal active nut-sharing (for each mother, at a given age of her offspring) had no obvious effect on any of the behaviors that we used to indicate immatures' nut-cracking skills. Observed maternal nut-sharing was driven by immatures' sex and begging behavior. As previously reported (Boesch & Boesch-Achermann, 2000), mothers were more likely to share nuts with male offspring and the more their offspring begged. Concurrently, male immatures also begged more than females. Our results suggest thus, that maternal nut-sharing correlates with immatures' begging behavior. Infants' intrusive behavior has been suggested as the major driver for food transfer among primates (Thornton & Raihani, 2008). However, recent evidence clearly argues against the hypothesis that harassment mediates food sharing among chimpanzees in Taï, suggesting instead, that the social bond between individuals supports this behavior (Samuni et al., 2018). Therefore, in the context of nut-cracking learning, the delayed food reward resulting from mothers refusing nut sharing could lead, as a byproduct, to keeping immatures' attention focused on mothers' actions. Ultimately, this could function to enhance social learning and thus promoting immatures' learning of this task. Our analyses showed that mothers are more likely to refuse nut-sharing with daughters than with sons (see also Figure S6). This could explain previous observations showing that females acquired nut-cracking skills earlier than males and that they perform better than males (Boesch & Boesch, 1984a, 1984b; Boesch & Boesch-Achermann, 2000). Therefore, besides functioning to transmit information about food sources and give nutritional benefits to the offspring (Boesch & Boesch-Achermann, 2000; Galef & Giraldeau, 2001; Jaeggi, van Noordwijk, & van Schaik, 2008), delayed nut-sharing could also support social learning of this task.

Under the scenario described above, the lack of a significant positive effect of the variable "predicted maternal active nut-sharing" on immatures' performance is puzzling. However, such inconsistency could be due to the fact that "predicted maternal active nut-sharing" was calculated based on cases of active nut-sharing exclusively: while this assured to capture maternal behavior, it might have failed to capture the effect that passive nut-sharing could have on learning. This would further support the hypothesis that nut-cracking learning is mediated by the high level of maternal tolerance, which allows the transfer of nuts initiated by immatures.

Our model highlighted strong intergroup differences in the probability that mothers shared nuts with their offspring: mothers from the South community were more likely to share nuts with their offspring as compared with mothers from the East community. Previous studies on the same communities showed that cultural differences occurred in tool selection for nut-cracking (Luncz et al., 2012), and that the South community reached overall greater nut-cracking efficiency as compared with the East and North communities (Luncz, Sirianni, Mundry, & Boesch, 2018). Thus, mothers in the South community are likely to achieve a higher nut-intake as compared with mothers from other communities. This might, in turn, lead to a greater propensity to share (as food intake might be less limited). This could explain the community-specific difference in nut-sharing found in our study.

Finally, ecological factors also had a crucial effect on immatures' nut-cracking performance. Hammer selection is a sophisticated process in both chimpanzees (Sirianni et al., 2015) and capuchins (*Sapajus libidinosus*; Luncz et al., 2016). This result further elucidates tool preference and selection in Taï chimpanzees: previous findings showed that adult individuals prefer stone hammers over wooden hammers and that they also account for the weight (Sirianni et al., 2015). Our results thus showed that immature chimpanzees already experience the effects that hammers with different properties impose on their performance, and this likely leads to the high competence in tool choice observed in adults.

Overall, our study revealed two indirect ways in which maternal behavior enhanced nut-cracking performance in immature wild chimpanzees and added evidence on the social and ecological variables that affect the development of complex tool related processes. Our results showed that, although potentially unintentional, maternal behavior did have an effect on the development of immatures' nut-cracking skills. Future studies, based on extensive naturalistic observations, could highlight other forms of maternal behaviors that could mediate and support learning in this taxon. For example, Moore (2013) suggested to specifically focus on subtle forms of attention-soliciting behaviors, which could support learning (what he named "minimal pedagogy"). One example could be the inactive time spent by mothers at underground bee nests, which could mediate learning about this resource (Estienne et al., 2019). Noticeably, ecological (e.g., resource availability) and social variables should be directly accounted for when considering maternal behavior. In addition, this study also contributed to identify the drivers of maternal nut-sharing. Future studies should focus on which factors (ecological, social and behavioral) affect mothers' nut-cracking performance and test (controlling for tool availability and properties) whether individual differences in this technique are transmitted from mothers to offspring. As a concluding remark we would like to stress the importance that naturalistic observations have for gaining realistic knowledge about skill acquisition and other complex behaviors, and in primates in particular given their distinctive life-history features.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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