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When to choose which tool: multidimensional and conditional selection of nut-cracking hammers in wild chimpanzees

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Investigating cognitively complex behaviours in their natural ecological context provides essential insights into the adaptive value of animal cognition. In this study, we investigated the selection of hammers used for cracking *Coula* nuts by wild chimpanzees, *Pan troglodytes verus*, in the Taï National Park, Côte d'Ivoire, taking account of the availability of potential tools at the site and time of tool selection. Using GLMMs and focal follows of five adult females, we estimated the probability of an object being selected as a hammer according to its physical properties, transport distance and the location of the anvil on the ground or in trees. We found that chimpanzees took account of several variables at the same time (multidimensionality) when selecting nut-cracking tools and that their selection for hammer weight was adjusted to the state/value of other variables (conditionality). In particular, chimpanzees (1) preferred stones over wooden clubs and hard woods over soft woods; (2) selected heavy stones, but relatively lighter wooden hammers; (3) selected increasingly heavier hammers the closer they were to the anvil; and (4) selected lighter hammers when they were going to crack nuts on a tree. The latter two results represent instances of conditional tool selection based on the next steps in an operational sequence (transport and/or use of the tool in a stable or unstable location) and suggest that chimpanzees anticipated future events when they chose a tool. This large set of conditional rules suggests a high level of cognitive sophistication in a tool use task. Our results represent a compelling example of how powerful cognitive skills allow the optimization of an ecologically relevant foraging activity, supporting a food extraction hypothesis for the evolution of complex cognition in our closest relatives.

Documenting cognitively complex behaviours in a natural ecological context provides essential insights into the adaptive value of a species' cognitive skills (e.g. Boesch, 2013; Byrne & Bates, 2011; van Schaik, Damerius, & Isler, 2013). For example, if the emergence and fixation of complex cognitive abilities are driven by the fitness advantage they provide, we may expect cognitively demanding behaviours to emerge in foraging activities with large nutritional impacts. Optimal foraging theory predicts that individuals maximize the rate of energy gain from foraging. This can be achieved by increasing the rate of energy intake and/or decreasing the costs involved (Altmann, 1998; Stephens & Krebs, 1986). Tool use allows access to food resources that would otherwise be unexploitable (e.g. Tebbich, Taborsky, Fessl, & Dvorak, 2002; Visalberghi et al., 2008) or available only at a higher cost (e.g. Günther & Boesch, 1993; Möbius, Boesch, Koops, Matsuzawa, & Humle, 2008) resulting in a selective advantage for animals that are capable of such a behaviour.

Physical properties of the tool are among the main factors influencing the net benefit provided by tool use (e.g. Fragaszy et al., 2010). Selection of tools based on their physical properties is therefore an integral part of efficient tool use, and selectivity for tool features has been observed in most animals that habitually use tools in the wild (Sanz, Call, & Boesch, 2013). In particular, tool-using birds and primates have been found to select extractive tools by their diameter and/or length and pounding tools by their mass (e.g. Aumann, 1990; Byrne, Sanz, & Morgan, 2013; Chappell & Kacelnik, 2002; Gumert & Malaivijitnond, 2013) and capuchins, *Sapajus libidinosus*, and chimpanzees, *Pan troglodytes*, have also been reported to select from among different stone materials for nut-cracking tools (Carvalho, Cunha, Sousa, & Matsuzawa, 2008; Visalberghi et al., 2009). However, the efficiency of a tool depends on several variables at the same time (multidimensionality), some of them not intrinsic properties of the tool itself (e.g. the distance of the tool from the target resources). Therefore, an animal's preference

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for some of the tool's properties may be adjusted to different contexts (conditionality). Efficient selection patterns should thus require, at the least, an ability to store and process a large amount of information and to flexibly compare physical properties of available potential tools taking account of contextual variables in each selection episode. To date, studies of animal tool selection have been based on either captive/field experiments or field observations. In the experiments the availability of raw materials was strictly controlled but animals usually faced a rather simplified set of conditions, in that (1) a small number of tools varying in one physical property at a time were presented (e.g. Schrauf, Call, Fuwa, & Hirata, 2012; Visalberghi et al., 2009) and/or (2) a fixed set of objects was provided in a fixed spatial arrangement (e.g. Carvalho, Biro, McGrew, & Matsuzawa, 2009). On the other hand, observations in the wild concerned animals facing more complex settings (e.g. every episode of tool selection takes place in the context of a unique set of raw materials with numerous potential tools varying in many physical properties and placed at different distances and orientations in space), but only the properties of tools used were recorded, without a detailed account of what was actually available at the place and time of tool selection (e.g. Luncz, Mundry, & Boesch, 2012; Spagnoletti, Visalberghi, Ottoni, Izar, & Fragaszy, 2011). The level of sophistication displayed by tool-using animals when selecting tools in their natural ecological context thus remains not fully explored.

The use of hammers and anvils for cracking open nuts is one of the most complex forms of animal tool use (Fragaszy, Visalberghi, & Fedigan, 2004; Matsuzawa, 2001). This behaviour has been observed in wild chimpanzees in western and central Africa (Boesch & Boesch, 1983; Morgan & Abwe, 2006; Sugiyama & Koman, 1979), in tufted capuchins in northeastern Brazil (Ottoni & Izar, 2008) and in a population of long-tailed macaques, *Macaca fascicularis*, in southern Thailand (Gumert & Malaivijitnond, 2013). Dependent upon the physical features of individuals (which in turn depend on sex, age and species), the benefit provided by a nut-cracking hammer will depend on, among others, its weight, hardness, size, density, distance to nuts and potential anvils (i.e. a stone, root or branch), the location of the anvil (on the ground versus on a tree) and on interactions among these variables. Therefore, efficient optimization of hammer selection for nut cracking implies that the animals are sensitive to the effect of several physical variables along the whole chain of actions involving the tool (search, transport, use) and that the evaluation of each variable is adjusted conditionally on the value or state of others. Chimpanzees, *P. t. verus*, in the Taï forest (Côte d'Ivoire) crack open five different species of nuts using wood and stone hammers on anvils on the ground (hard roots or stones) and on branches within a tree (Boesch & Boesch, 1983). For as much as 4 months per year, nuts of the genus *Coula* represent the most important source of energy in the Taï chimpanzees' diet, with adult individuals gaining up to 14 600 kJ per day from nut consumption (Boesch & Boesch-Achermann, 2000). Therefore, nut cracking by Taï chimpanzees (1) is a potentially complex behaviour from a cognitive perspective, (2) is deployed in a diversity of contexts and (3) has a strong nutritional significance, representing an ideal model to investigate the role of cognitive complexity in foraging optimization by tool selection in an ecologically relevant context.

In the present study, we investigated naturally occurring selection of nut-cracking tools by Taï chimpanzees in order to assess the extent to which this selection process follows a multidimensional, conditional optimization. We observed selection of hammers used to crack open *Coula* nuts by adult female chimpanzees, taking account of the availability of potential hammers at the site and time of each tool selection, and estimated the probability of a given object being selected as a hammer, given a set of variables (i.e. physical properties of hammers, transport distance, nut resistance, location of the anvil on the ground or in a tree).

We hypothesized that chimpanzees' selectivity for nut-cracking hammers aims at maximizing the rate of net energy gain, as predicted by optimal foraging theory. In this study we did not directly measure the efficiency of nut cracking, but we rather relied on theoretical predictions about how the physical properties of hammers affect the energetic balance of a nut-cracking session (Figs 1 and 2). More specifically, in this paper we argue that an energetically efficient hammer is a tool that provides both power and control, by (1) storing kinetic energy when it is in motion; (2) conserving its shape when it hits the nut (which avoids energy dissipation); (3) allowing the user to precisely transfer kinetic energy to the nut's shell (energy is wasted if the nut is not hit precisely, or, if the nut is smashed, extra work will be required to collect the fragments of the kernel and part of the kernel can be completely lost). Accordingly, chimpanzees are expected to select those physical properties of the hammers that are most likely to influence power and control (i.e. weight, size, density and hardness). In natural objects such as stones and wooden clubs used by chimpanzees, weight and size are strongly correlated, while density corresponds to the ratio weight/volume (volume being a component of size). In turn, hardness correlates with density (stones are both harder and denser than wooden clubs, and harder woods also tend to be denser than softer woods). Fig. 1 illustrates how each physical property is expected to affect nut-cracking efficiency and the corresponding testable predictions about chimpanzees' choice from among natural potential hammers. While most physical properties have a linear effect on the expected efficiency, the effect of weight is expected to be nonlinear, as the optimal weight of a hammer depends on a trade-off between power and control (Fig. 1). Theoretical arguments (see Fig. 2) show that optimal hammer weight depends on (1) other physical properties of the same hammer and (2) contextual variables such as the distance to the anvil, the location of the anvil (ground or tree) and the expected nut resistance (which depends on ripeness and, hence, decreases along the season, Luncz et al., 2012). Therefore, optimal foraging theory predicts that chimpanzees will show a conditional selection for hammer weight (Fig. 2).

The focus of this study was not to describe the cognitive processes underlying tool selection (i.e. association versus 'high' cognition, see Heyes, 2012) but rather to look at measurable aspects of behavioural and cognitive complexity. Therefore, we adopted a quantitative perspective on cognitive complexity, based on a measure of the minimum number of operational 'rules' needed to describe an observed information-processing behaviour. We propose that such 'rules' may correspond to the terms of a statistical model. The number of rules will thus depend on (1) how many variables have a measurable effect on the behaviour (dimensionality: one 'rule' per variable), whether these effects are linear or nonlinear (each nonlinear effect implies two 'rules'), and (2) whether the effects of multiple variables are additive or conditional (conditionality: one additional 'rule' for each combination of variables that must be accounted for).

METHODS

Study Site and Data Collection

We collected behavioural data on chimpanzees from the North Community of the Taï National Park, Côte d'Ivoire (see Boesch & Boesch-Achermann, 2000 for more details on the habitat and nut-cracking behaviour) during individual daily focal sampling conducted by G.S. 6 days per week during two consecutive *Coula*

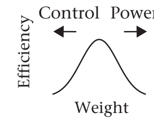
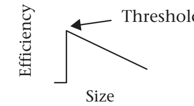
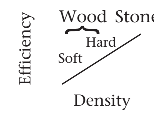
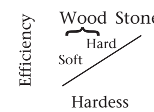
Property	Theoretical argument	Testable prediction	
Weight	Heavy hammers may produce more powerful hits (higher kinetic energy), but lighter hammers are easier to control. Hammer weight determines a trade-off between power and control	1.1 Nonmonotonic preference for hammer weight	
Size	Chimpanzees need hammers above a minimum size, so as to be able to crack the nuts without hurting their fingers. Above this limit, size negatively affects hammer control and precision of striking	1.2 Monotonic preference for small sizes (above a minimum threshold size)	
Density	Since, weight being equal, small hammers are easier to handle and control precisely (see above), a dense hammer provides the power of a heavy hammer with a smaller size	1.3 Stones preferred over wooden hammers and hard woods over soft woods	
Hardness	The harder a hammer, the smaller its deformations when it hits the nut, and the less of its kinetic energy is dissipated		

Figure 1. Physical properties of the hammer influencing nut-cracking efficiency. For each property, the rationale for such expectations is also reported (theoretical argument), as well as the corresponding prediction about chimpanzees' selection on natural potential hammers (testable prediction).

nut-cracking seasons (November 2011–March 2012 and November 2012–February 2013). We decided to restrict our data collection to (1) adult individuals, as previous studies show them to have become fully proficient at nut cracking (Boesch & Boesch-Achermann, 2000), and (2) females, since sex differences in the frequency and efficiency of nut cracking have been reported for Taï chimpanzees (Boesch & Boesch, 1984a), and only one adult male was present in the North Community at the time of data collection.

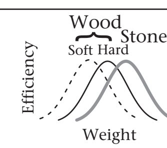
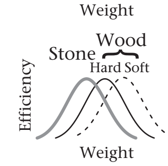
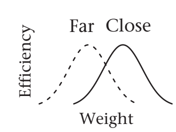
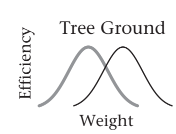
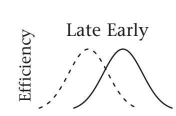
	Interacting variable	Theoretical argument	Testable prediction	
Physical properties	Density of hammer	Weight being equal, denser hammers are smaller. When selecting a denser hammer, a chimpanzee can choose a heavier weight (high power) with a smaller reduction of control (see Fig. 1: Size)	2.1a Heavier weights preferred for denser hammers than for less dense hammers	
	Hardness of hammer	If chimpanzees aim at hitting the nut with a given kinetic energy (the nut needs to be opened but not smashed), a harder hammer can provide the same effective hitting energy with less kinetic energy than a softer hammer (which is more prone to deformation)	2.1b Lighter weights preferred for harder hammers than for softer hammers	
Contextual variables	Distance to anvil	Cost of hammer transport increases with both weight and distance	2.2 Heavier weights preferred when hammer is close to the anvil than when it is further away	
	Position of anvil (ground/tree)	To crack nuts on a tree, chimpanzees must transport a hammer while climbing, increasing the negative effect of weight. Poor control of striking while on a tree branch may easily lead to losing the entire nut. Control is more decisive than when on the ground	2.3 Heavier weights preferred when anvil is on the ground than when it is on a tree branch	
	Nut resistance (season)	When nuts are more resistant (early in season) they require more energy to be opened. When nuts are less resistant (late in season) they are more easily smashed. Power is more important early in the season, and control is more decisive late in the season	2.4 Heavier weights preferred when nuts are more resistant (early in season) than when they are less resistant (late in season)	

Figure 2. Conditional selection for hammer weight. List of physical properties of hammer and contextual variables that are expected to influence chimpanzees' preference for hammer weight (interacting variables). The rationale for such expectations is also reported (theoretical argument), as well as the corresponding prediction about chimpanzees' selection on natural potential hammers (testable prediction).

Therefore, data were collected on five adult females. The study is based on noninvasive observations and complies with the laws of Côte d'Ivoire and the ASAB/ABS Guidelines for the treatment of animals in behavioural research and teaching.

To look at chimpanzees' hammer selection, we compared chosen hammers with all available potential hammers at the spot and the moment of each observed selection. A hammer selection episode was scored every time an individual was observed to pick up a stone or a wooden club and use it to hit at least one nut (independently of the success in cracking the nuts open). We excluded from our data set all hammer selection episodes when an individual switched hammer (i.e. while cracking with a hammer A an individual dropped it and took hammer B, while A was still available). This exclusion was intended to avoid the analysis of nonindependent hammer selection episodes (i.e. the second choice could be conditional on the first).

A potential hammer was defined as a wooden club or a stone within a given range for a set of physical properties based on existing data on hammers actually used by chimpanzees in the Taï forest (Boesch & Boesch, 1983, 1984b; Steiner, 1992). We therefore considered as potential hammers those wooden clubs and stones with a minimum weight of 0.2 kg, a maximum length of 250 cm and a circumference between 10 cm and 50 cm.

To operationally determine the set of potential hammers that should be considered available for each hammer selection episode, we delimited hammer availability transects as follows (Fig. 3). After observing a hammer selection episode, G.S. marked the point where the hammer was picked up (selection point) with red-white plastic tape, recorded the geographical coordinates with a GPS device (Garmin 62), and noted (using a compass) the direction of the chimpanzee's approach to the selection point. At the end of the nut-cracking session (when the focal animal dropped the hammer and left the site), G.S. stayed at the site until the group moved on in order to check that the original set of potential hammers encountered by the focal animal had not been modified by other chimpanzees (e.g. importing/removing hammers). On the next day, G.S. or a field assistant came back to the selection point in order to describe the nut-cracking site. Using two tape measures, we marked two perpendicular axes originating in the selection point and oriented such that one axis (y axis) was parallel to the chimpanzee's direction of approach to the selection point. With the selection point having coordinates ($x = 0$, $y = 0$), the hammer availability transect was the rectangle defined by $y > -3$ m, $y < 12$ m, $x > -3$ m, $x < 3$ m (Fig. 3), and potential hammers within it were considered available hammers. The rationale for this definition was to consider as available hammers all potential hammers that lay within the clear visual range of the focal chimpanzee when she picked up the chosen hammer, or immediately before that. Based on a preliminary survey, we estimated that an object lying on the forest floor was always clearly visible within a range of 3 m from a human observer whose eyes were ca. 80 cm above the ground (approximating the height of the eyes of a knuckle-walking chimpanzee). Therefore, the available hammers were assumed to include all potential hammers that were clearly visible to the chimpanzee when she was at the selection point and during the last 12 m of her approach route (with 12 m being an arbitrary limit).

Two or more hammer selection episodes could define partially overlapping transects, containing partially overlapping sets of available hammers. Two transects were assigned to the same location (GPS point) if their selection points were less than 20 m apart.

The position (x, y) of all available hammers within each transect was recorded, along with the following physical properties: (1) weight, measured with a spring balance (for hammers up to 10 kg we used a Pesola WPe 40010 spring scale, with a capacity of 10 kg

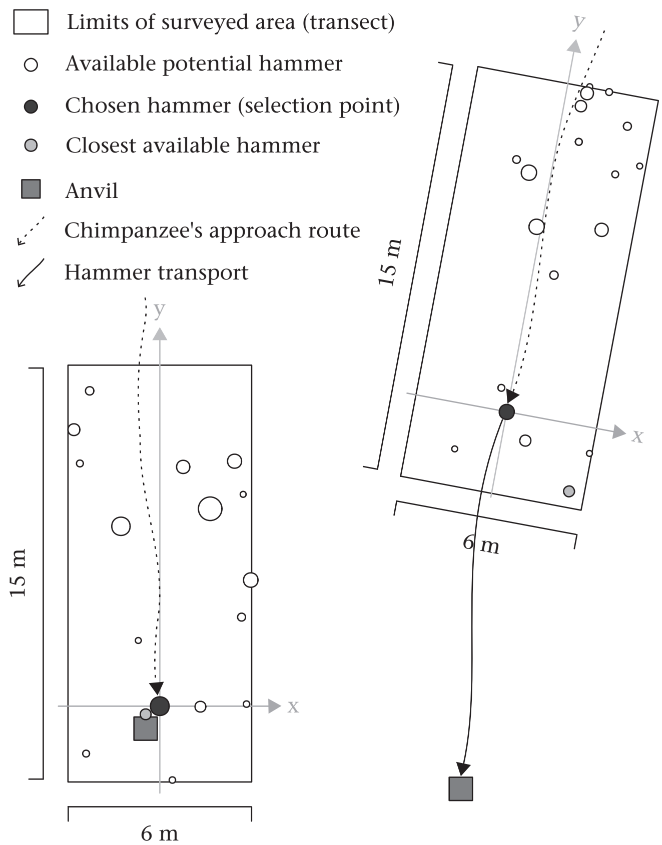


Figure 3. Survey of available hammers. The observer noted the approach route of the focal chimpanzee (dashed line) to the point where the animal picked up the chosen hammer (selection point: dark circle). A rectangular area of 15 m × 6 m (hammer availability transect) around the selection point was defined using two tape measures (x and y axes). Position and physical properties of available hammers and of the chosen hammer were recorded. The position (grey circle) of the available hammer closest to the anvil (grey square) was used for the standardization of distances (see 'Standardization of variables' for details). Two examples are presented: on the left the anvil lies inside the transect, on the right it lies outside the transect.

and divisions every 0.1 kg; for heavier hammers we used a Pesola WPe 40020 spring scale with a capacity of 20 kg and divisions every 0.2 kg); (2) length and (3) circumference, both measured with a tape measure to the nearest centimetre; (4) material (wood or stone); (5) hardness of wooden clubs (varies according to the tree species they belong to, and to how rotten they are). To quantify hardness in the field, we modified the protocol proposed by Falquet (1990) who estimated hardness from the resistance of wood to penetration of a nail. In detail, a 10 cm nail was placed 1 cm deep into the wood and a 2 kg weight was dropped on it three times through a plastic tube (to ensure a vertical drop) from a height of 70 cm. The length of the portion of the nail still emerging from the wood (measured with 1 mm precision) provides an estimate of the wood's hardness (h), with a highest possible value of $h = 9$ cm (no penetration of the nail in the wood). Unfortunately, h could not be determined when the wood was too soft or thin, so that the whole length of the nail penetrated the wood before the third hit (46% of measured wooden hammers). For this reason, we also assigned a 'subjective' hardness value to each wooden hammer on an ordinal scale (h_S) ranging from 1 (soft wood) to 3 (hard wood), based on visual cues, sound produced and vibrations transmitted to the hand when it was hit against a hard root. The 'subjective' h_S and the 'objective' h were found to be clearly correlated across the 953 hammers for which h was determined (Spearman $r_S = 0.47$, $P < 0.001$; note that this correlation is actually an underestimate, as it does not consider hammers with undetermined *h*, 48% of which were assigned $h_S = 1$).

The position (*x*, *y*) of the first anvil used to crack nuts with the chosen hammer (hereafter simply 'the anvil') was recorded directly whenever the anvil was within 20 m from the selection point. When the anvil was further away, its position relative to the transect's coordinates was estimated from GPS data, since it was obviously unpractical to unroll a tape measure along very long distances on the forest litter. The Euclidean distance of each available hammer to the anvil was then calculated from the hammer and anvil coordinates. Last, for each hammer selection episode, the location of the anvil (a root on the ground versus a branch of a tree) was also recorded, as well as the date when the episode was observed.

Statistical Analyses

Tested predictors

Figs 1 and 2 list our set of testable predictions about chimpanzee selection of natural hammers based on the effects of physical or contextual variables on nut-cracking efficiency. Arguments concerning hammer density and hardness result in identical (Fig. 1, prediction 1.3) or opposite (Fig. 2, predictions 2.1a, 2.1b) predictions about hammer material (stones versus wood) and woods of different hardness. This is because hardness and density are strongly correlated properties of different natural materials. In particular, stones are both harder and denser than any wood, and harder woods are expected to be denser than softer woods. Therefore, we created a combined predictor of hardness/material by assigning a 'hardness' value $h_S = 4$ to all stones. By doing so, we were able to test prediction 1.3 ('chimpanzees prefer stones over wooden hammers and hard woods over soft woods', see Fig. 1) and the two opposite predictions about chimpanzees' conditional preference for weight according to hardness and density of the hammer (Fig. 2, predictions 2.1a, 2.1b). Length and circumference of hammers were both strongly correlated with weight (both Pearson $r > 0.6$). Therefore, we chose not to consider a measure of hammer size as an independent predictor of chimpanzee hammer selection. Our final predictors thus included weight, hardness/material, distance to anvil, location of the anvil (ground/tree) and seasonal variation in nut resistance (the day in the season, i.e. number of days elapsed since the onset of the respective *Coula* nut-cracking season, was used as a proxy for nut resistance, since *Coula* nuts are known to be more resistant early in the season, Boesch & Boesch, 1984a; Luncz et al., 2012).

Standardization of variables

Chimpanzees performed each of their hammer selections from among a unique set of available hammers (number, position and physical properties of available hammers were different for each hammer selection episode). This means that the relative optimality of each hammer depended upon other hammers available at the time of selection. For example, a hammer lying 5 m away from the anvil would be the optimal one (all the rest being equal) if it was the closest within its transect, but it would not be optimal in another transect, where other hammers were closer to the anvil. Therefore, to make comparisons across different hammer selection episodes, we had to standardize each variable across the different hammer selection episodes. We calculated a standardized 'Relative Distance' of each hammer to the anvil used, i.e. how much further away a given hammer was from the anvil than the closest hammer at the respective site. Obviously, a standardized distance value alone would not allow for the detection of the expected conditional preference for weight according to the distance to the anvil. Furthermore, we expected the effect of Relative Distance to decrease with increasing distance of the closest available hammer. For example, two hammers that differ in their distance from the anvil by 4 m would represent very different alternatives when both of them are very close to the anvil (e.g. 0 and 4 m from the anvil) but would be rather similar when both are far away from the anvil (e.g. 40 and 44 m). Therefore, along with the Relative Distance, we also included as a predictor the 'Distance of the Closest Hammer' in the transect (a variable having the same value for all hammers in a given transect). By doing so, (1) we kept the information about the absolute distance of each hammer to the anvil (as the sum of Relative Distance and Distance of the Closest Hammer) and (2) we were able to detect both a preference for weight that was conditional on transport distance and the decreasing effect of Relative Distance with increasing Distance of the Closest Hammer (by including the three-way interaction between the two distance variables and weight squared; see below). Similarly, for hardness/material, we considered two predictors: the 'Relative Hardness' (i.e. the difference in hardness between a given hammer and the hardest hammer in the transect) and the 'Hardness of the Hardest Hammer' in each transect. This parameterization of hardness/material and distance to the anvil was possible because we hypothesized that both variables had a linear effect on chimpanzee preference (with the hardest and closest hammer being 'optimal'). For weight, we used the original values, because weight was expected to have a nonlinear effect on chimpanzees' choices (see Fig. 1), so that it was not possible to determine a priori which hammer was optimal with regard to weight in any given transect.

To ensure that this parameterization of distance from the anvil, hammer hardness and weight allowed us to detect the effects we hypothesized, we simulated chimpanzees choosing hammers according to our hypotheses and analysed the simulated data with submodel 1 (see below). The simulated data were identical to the original data with regard to the particular combination of available hammers at the given sites. We created 1000 simulated data sets. These results showed that the parameterization and model allowed us to detect the patterns of choices we hypothesized.

Generalized linear mixed models

To investigate whether hammer weight, hammer hardness/material, distance to anvil, location of anvil (ground/tree), seasonal variation in nut resistance (day in the season) and their relevant interactions (see Figs 1 and 2) had an effect on the probability of a certain hammer being chosen, we used generalized linear mixed models (GLMM, Baayen, 2008) with binomial error structure (binary response variable: 'chosen', yes/no) and logit link function. A full model testing all our predictors simultaneously would have been too complex for the data at hand (particularly given the limited number of choices), considering the many terms, random effects and random slopes (Barr, Levy, Scheepers, & Tily, 2013, see below) that had to be accounted for. To cope with the extreme complexity of the full model, we fitted three separate submodels, each testing a specific set of predictions. In all submodels we included both a linear and a squared term for hammer weight (accounting for nonlinearity), so that all submodels tested our prediction that chimpanzees would prefer intermediate weights (see Fig. 1). In addition to weight, each submodel included one or more of the remaining predictors, and their interactions with hammer weight, in order to test for the effect of each variable (Fig. 1) and for the conditional selection of hammer weight (Fig. 2). Consequently, each submodel tested for a given set of the operational 'rules' listed in Table 1.

In detail, our submodels were as follows.

(1) Submodel 1 includes the three-way interaction among weight squared and the two terms for distance: Relative Distance

Table 1
Minimum set of operational 'rules' describing chimpanzees' tool selection

Rule	Description	Tested by[a]
1. Linear preference for weight	'Select the heaviest hammer (all the rest being equal)' OR 'Select the lightest hammer (all the rest being equal)'	Interaction of weight as a linear term with other variables Submodels **1**†,2[nt], **3*****
2. Quadratic preference for weight	'Select an intermediate weight'	Interaction of weight squared with other variables Submodels 1,**2***,3
3. Stones preferred over wooden hammers and hard woods preferred over soft wood	'Select the hardest and densest available hammer'	Interaction of weight with hardness/material Submodel **2***
4. Conditional preference for weight according to material (stone, wood) and hardness of woods	'Select heavier weights when choosing harder/more dense hammers' (see Fig. 2, 2.1a) OR 'Select lighter weights when choosing harder/more dense hammers' (see Fig. 2, 2.1b)	Interaction of weight with hardness/material Submodel **2***
5. Linear preference for distance	'Select the closest hammer (all the rest being equal)'	Interaction of weight with distance Submodel **1**†
6. Conditional preference for weight according to distance	'Select lighter weights when choosing from among more distant hammers'	Interaction of weight with distance Submodel **1**†
7. Account for anvil location (ground/tree)	'Account for anvil location (ground/tree)'	Interaction of weight with anvil location Submodel **3*****
8. Modify preference for weight according to anvil location (ground/tree)	'Select lighter weights when about to crack on a tree than when on the ground'	Interaction of weight with anvil location Submodel **3*****
9. Account for nut resistance (season)	'Account for nut resistance (season)'	Interaction of weight with day in season. Submodel 3
10. Modify preference for weight according to nut resistance (season)	'Select lighter weights later in the season (when nuts are less resistant)'	Interaction of weight with day in season. Submodel 3

†$P = 0.07$; *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$; [nt] not testable in model 2 which includes the "weight squared" term in its final version.
[a] Terms of tested GLMM corresponding to the described rule. The tested submodels for which the term was present are indicated by their numbers. Numbers in bold indicate submodels for which the term was statistically significant or showed a clear statistical trend.

and Distance of the Closest Hammer (see 'Standardization of variables'). Predictions: 1.1 (Fig. 1), 2.2 (Fig. 2). 'Rules': 1,2,5,6 (Table 1).

(2) Submodel 2 includes the three-way interaction among hammer weight squared and the two terms for hammer hardness/material: Relative Hardness and Hardness of the Hardest Hammer (see 'Standardization of variables'). Predictions: 1.1, 1.3 (Fig. 1), 2.1a, 2.1b (Fig. 2). 'Rules': 1,2,3,4 (Table 1).

(3) Submodel 3 includes the two-way interaction between weight squared and day in the season (proxy of nut resistance) and the two-way interaction between weight squared and location of the anvil (we chose to analyse day in season and anvil location in a single model, in order to allow interpretations of their effects while controlling for the effect of the other, because we observed a highly significant, although moderate, correlation between them: Spearman $r_S = 0.37$, $P < 0.001$). Predictions: 1.1 (Fig. 1), 2.3, 2.4 (Fig. 2). 'Rules': 1,2,7,8,9,10 (Table 1).

In each submodel, we included the following random effects: individual, location (GPS) and hammer selection episode. Moreover, we included the log-transformed inverse of the number of available hammers per selection episode (representing the random probability of a hammer being selected) as an offset term. We accounted for possible individual differences in patterns of hammer selection by including random slope terms within subjects for all main effects and interactions of a given submodel (Barr et al., 2013; Schielzeth & Forstmeier, 2009). We did not include correlations between random intercepts and slopes nor random slopes within the random effects of location (GPS point) and hammer selection episode to avoid excessively complex models for our sample size. This seems further justified since omitting correlations between random slopes and intercepts do not strongly compromise model validity (Barr et al., 2013) and since it seemed unlikely that the effect of the fixed effects would vary between locations and hammer selection episodes. To get an overall significance of the main effects (weight, weight squared, hardness/material, distance, day in season, ground/tree location of anvil) and circumvent multiple testing issues, we first compared a full model comprising all main effects (with no interactions) with a respective null model comprising only the intercept, the offset term, the random effects and the random slopes of the main effects within subject (Barr et al. 2013; Schielzeth & Forstmeier, 2009), using a likelihood ratio test (Dobson, 2002). Then, the significance of each submodel was established by a likelihood ratio test comparing the full submodel and a null submodel comprising only the intercept, the offset term, the random effects and the respective random slopes. A few hammer selection episodes involved partially overlapping transects, meaning that some available hammers appeared in more than one transect (see 'Study site and data collection'). To account for such repeated occurrences of the same hammers in the data, we initially included hammer identity as a random effect in all models. However, since those hammers appearing more than once in the data set were consistently always selected or not selected by the chimpanzees, and since the vast majority of the hammers were present in the data just once, a complete separation issue arose (Field, 2005), which made the model unstable (fitting algorithm failed to converge). To cope with this problem, we (1) removed hammer identity from the random effects, (2) created subsets of the data in which only one randomly sampled occurrence of each individual hammer was retained, (3) ran each of our submodels on a total of 1000 such subsets, and (4) report as results the averaged coefficients, standard errors, z and P values.

Prior to running the models, we checked all predictors for their distributions. After checking the distributions, we log-transformed hammer distance (both Relative Distance and Distance of the Closest Hammer, both after adding one) and hammer weight, in order to achieve roughly symmetric distributions and avoid influential cases. Moreover, we z-transformed all numeric and ordinal predictors to a mean of zero and a standard deviation of one to get comparable estimates and easier to interpret models with regard to the interactions and squared terms (Schielzeth, 2010). Variance inflation factors (VIF), applied to standard linear models excluding the random effects, did not reveal any multicollinearity issue among predictors (maximum VIF = 1.76; Field, 2005; Quinn & Keough, 2002). To ensure that there were no particularly influential cases in our data set, we checked each submodel's stability by excluding the levels of the identity of the hammer selection episode one at a time and fitting each submodel for the obtained data sets. A comparison of the estimated coefficients showed that the results did not vary drastically.

The threshold for statistical significance was set as $P \leq 0.05$. All statistical analyses were conducted in R version 3.0.1 (R Core Team, 2013). We fitted GLMMs using the function 'glmer' (R package 'lme4' v. 0.999999-2, Bates, Maechler, & Bolker, 2013). Model diagnostics were calculated using the functions 'vif' (R package 'car', Fox & Weisberg, 2011).

RESULTS

Data Summary

We observed 113 hammer selection episodes (mean per individual chimpanzee 22.6, range 19–27), 14 involving the use of an arboreal anvil and 99 a ground anvil. In 52 episodes the chimpanzees used a stone hammer, while they used a wooden hammer in 61 episodes. The 113 transects (see Fig. 3) were placed at 95 different GPS locations (79 GPS locations hosted a single hammer selection episode, 11 locations hosted two, four locations hosted three and one location hosted four hammer selection episodes) and contained a total of 1851 available hammers (mean number of available hammers per selection episode 16.38, median 15, range 2–62). In total, the 113 hammer selection episodes involved 101 unique chosen hammers. The discrepancy between number of hammer selection episodes and the number of unique chosen hammers is because the same hammer was sometimes selected in more than one episode (91 hammers were chosen only once, eight twice and two three times). Fig. 4a reports the distributions of the number of available stones and wooden hammers across hammer selection episodes (transects). The maximum weight for a recorded available hammer was 15.1 kg (a stone chosen by a chimpanzee). A visual comparison of the distribution of weights across available and chosen hammers suggests that chimpanzees preferred heavier hammers (Fig. 4b). Most available hammers were of wood (Fig. 4a) and fell in the softest category (Fig. 4d), whereas stones and hard woods were the most frequently chosen hammers (Fig. 4d). Transport distances were usually short, with the median being

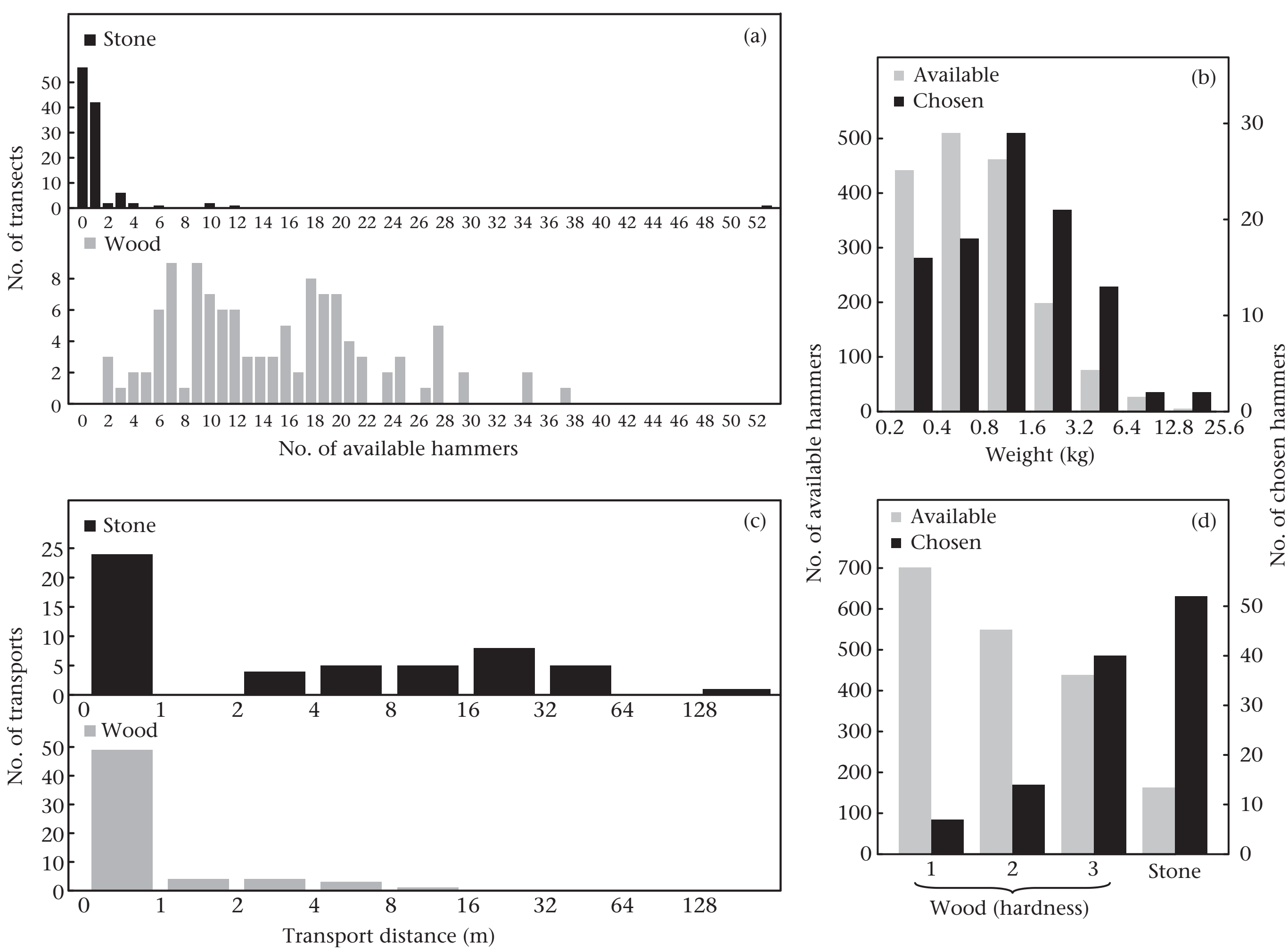


Figure 4. Data summary. (a) Distribution of the number of available stone and wood hammers across transects: mean number of stone hammers per transect 1.44, median 1, range 0–53, mean number of wooden hammers per transect 14.94, median 14, range 2–38. (b) Distribution of weights across available and chosen hammers: mean weight of available hammers 1.13 kg, median 0.7 kg, mean weight of chosen hammers 2.08 kg, median 1.2 (range not given, since this depended on operational definitions). (c) Distribution of observed transport distances for stone and wood hammers: mean transport distance of wooden hammers 1.49 m, median 0.4 m, range 0–13.9 m; mean transport distance of stone hammers 13.1 m, median 3.9 m, range 0–166 m. (d) Distribution of hardness/material across available and chosen hammers (1: soft wood; 2: intermediate wood; 3: hard wood).

0.6 m (Fig. 4c), but transports up to 166 m were observed. Only stones were transported over more than 14 m (Fig. 4c).

In most cases, chimpanzees did not engage in any form of hammer exploration before selecting one (i.e. the animal picked up the hammer and transported/used it). None the less, in approximately 11% of hammer selection episodes we observed the animal touching a hammer (11 cases) or briefly lifting it up (two cases) and then rejecting it.

Tool Selection

Overall, physical properties of the hammer (weight and hardness/material), distance of the hammer to the anvil, day in the season (used as a proxy for nut resistance) and the anvil location (ground versus tree) clearly influenced the probability of a hammer being chosen (comparison of full model and null model: $\chi^2_8 = 75.127$, $P < 0.001$).

Submodel 1: weight, distance to anvil and their interaction

Overall, the full model was highly significant as compared to the null model (likelihood ratio test $\chi^2_{11} = 284.97$, $P < 0.001$). Since the interaction including weight squared was not significant ($z = -1.301$, $P = 0.203$) we removed it from the model and tested the interaction between distances and weight as a linear term. We found an effect of both hammer weight and transport distance on chimpanzees' selection (for GLMM results of Submodel 1 see Table 2), with heavier hammers preferred over lighter ones for short distances (Fig. 5c) and with this preference decreasing gradually at increasing transport distances (Fig. 5a, b), and a (weak) preference for lighter hammers appearing at the largest distances (Fig. 5a).

Submodel 2: weight, hardness/material and their interaction

Overall, the full model was highly significant as compared to the null model (likelihood ratio test: $\chi^2_{11} = 5.644$, $P < 0.001$). Specifically, chimpanzees preferred harder hammers (stones over wooden clubs, Fig. 6a, and hard wood over soft wood, Fig. 6b) and selected hammer weight differently according to hardness/material: while heavy stones were strongly preferred over lighter stones (Fig. 6a), intermediate weights were preferred among wooden hammers (Fig. 6b). Detailed results of the GLMM for submodel 2 are reported in Table 3.

Submodel 3: weight, location of anvil, day in season and their interaction

Overall, the full model was highly significant as compared to the null model (likelihood ratio test: $\chi^2_8 = 22.35$, $P = 0.004$). Since the interactions including weight squared were not significant ($z = -1.001$, $P = 0.318$ and $z = 0.515$, $P = 0.607$ for anvil location and day in season, respectively) we removed them from the model and we tested the interactions of weight as a linear term with day in season and ground/tree anvil location. Results showed that chimpanzees selected lighter hammers when cracking nuts in a tree than when on the ground (Fig. 7). In contrast, no significant effect of the season (used as a proxy for nut resistance) on the preference for weight was detected. Detailed results of the GLMM for submodel 3 are reported in Table 4.

Table 1 summarizes the operational ‘rules’ that correspond to the significant terms of the tested submodels. A total of eight such ‘rules’ are required to describe the selection patterns of nut-cracking hammers observed in adult female Taï chimpanzees.

DISCUSSION

Cognitive Complexity in Tool Selection

Our results showed that, when they selected their nut-cracking hammers, chimpanzees were sensitive to the costs and benefits involved in the whole process of nut cracking (transport and use), and could balance the trade-offs between power (heavy hammers), precision (lighter hammers) and cost of transport (lighter hammers) by adjusting their preference for hammer weight according to other properties of the tool (hardness/material) and contextual variables (expected transport distance, ground/tree anvil location). Therefore, we found that chimpanzees selected tools in a multidimensional and conditional fashion. To the best of our knowledge, this is the first time that conditional tool selection on more than two variables has been directly demonstrated. In this regard, our results extend previous observations reporting that the features of tools used by chimpanzees, capuchins and macaques vary according to contextual variables (e.g. hammer size/weight and food type: Boesch & Boesch, 1983; Gumert & Malaivijitnond, 2013; Spagnoletti et al., 2011; hammer size/weight and transport distance: Boesch & Boesch, 1984b; hammer material and nut resistance: Luncz et al., 2012; Visalberghi et al., 2009; size of sticks and structure of termite nest: Sanz, Morgan, & Gulick, 2004; size of sticks and ant behaviour: Möbius et al., 2008). In particular, our study expands our understanding of chimpanzee tool use by explicitly investigating conditional tool selection, based on a direct comparison of tools used with the potential tools actually available at the time and place that the hammer selection episode occurred, and by assessing the effect of multiple variables on the preference for hammer weight. The only other studies aiming at revealing conditional aspects of tool selection, and where the availability of tools was controlled for, consisted of field experiments (Massaro, Liu, Visalberghi, & Fragaszy, 2012) and one ‘quasiexperimental’ field study (Gumert & Malaivijitnond, 2013). The latter authors

Table 2
Results of submodel 1, testing the effect of hammer weight and transport distance on the probability of a hammer being chosen

Effect	Estimate	SE	*z*	*P*
(Intercept)	−2.051	0.329	−6.231	[1]
Weight	−0.201	0.374	−0.537	[1]
Relative Distance	−2.244	0.229	−9.782	[1]
Distance of the Closest Hammer	0.862	0.161	5.352	[1]
Interaction: Weight * Relative Distance	−0.631	0.235	−2.690	[1]
Interaction: Weight * Distance of the Closest Hammer	−0.058	0.191	−0.308	[1]
Interaction: Relative Distance * Distance of the Closest Hammer	0.668	0.124	5.398	[1]
Interaction: Weight * Relative Distance * Distance of the Closest Hammer	0.303	0.164	1.845	0.069

All variables were log- and z-transformed. Random effects: subject, location (GPS), selection episode. Offset term: log-transformed inverse of the number of available hammers per selection episode. Random slopes terms within subjects for all main effects and interactions. Mean ± SD of each variable before log- and z-transformation: weight: 1.192 ± 1.457; Relative Distance: 3.886 ± 3.445; Distance of the Closest Hammer: 5.593 ± 15.069. When random slopes were removed from the model, values for the three-way interaction were: estimate ± SE = 0.262 ± 0.129, $z = 2.038$, $P = 0.047$.
[1]Significance test not indicated because it has no meaningful interpretation.

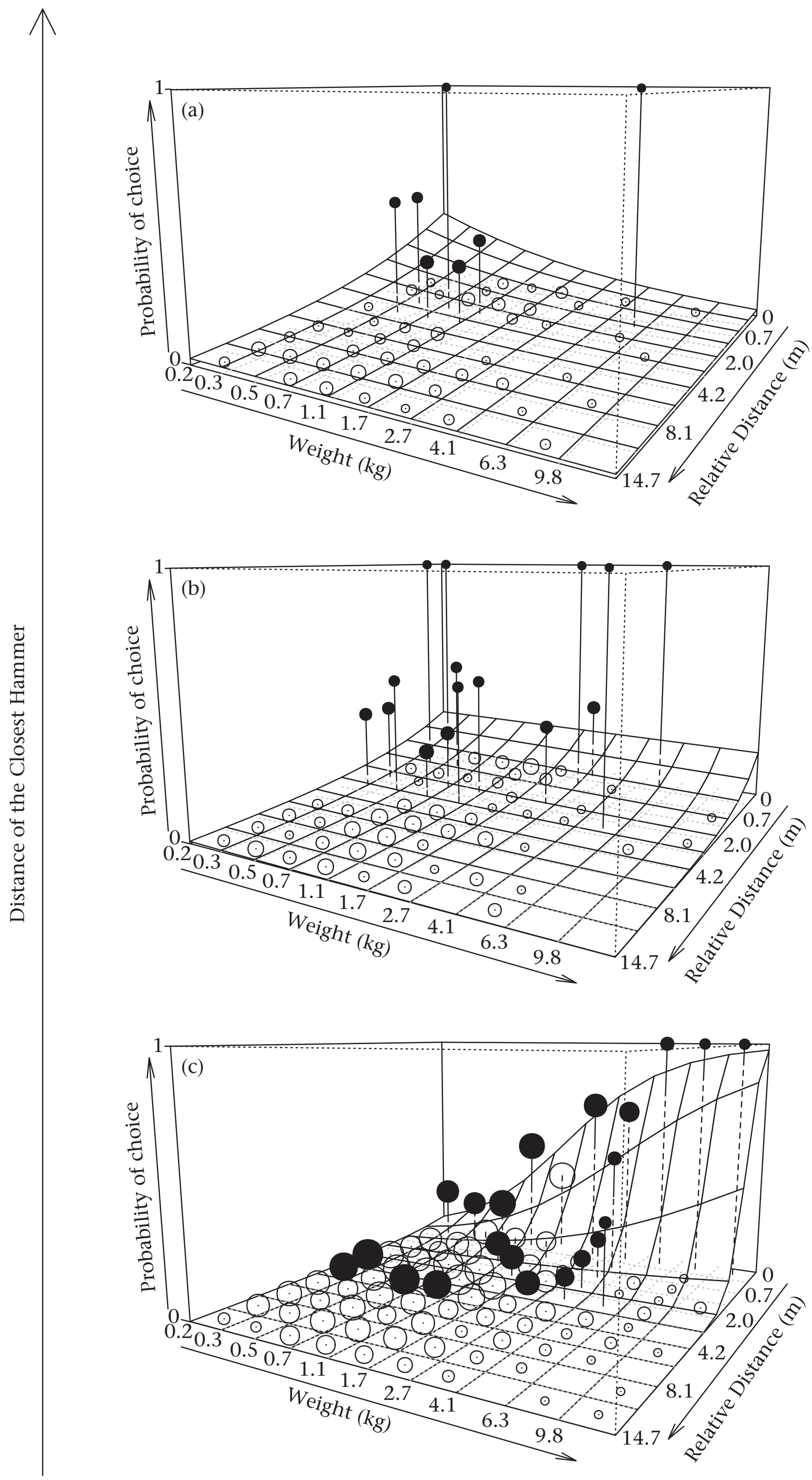


Figure 5. Conditional selection for hammer weight according to transport distance. In each box, surfaces represent fitted probabilities of a hammer being chosen as a function of weight and distance to the anvil relative to the closest available hammer within each transect (Relative Distance). The different boxes (a, b, c) refer to different ranges (intervals with equal widths in log-transformed distance) of the distance of the closest available hammer (Distance of the Closest Hammer). (a) 29–164 m; (b) 4.5–29 m; (c) 0–4.5 m. The height of spheres represents the proportion of hammers actually chosen per combination of weight and Relative Distance. Spheres above the fitted surface are in black; spheres below the surface are in white. The volume of the spheres is proportional to the number of available hammers.

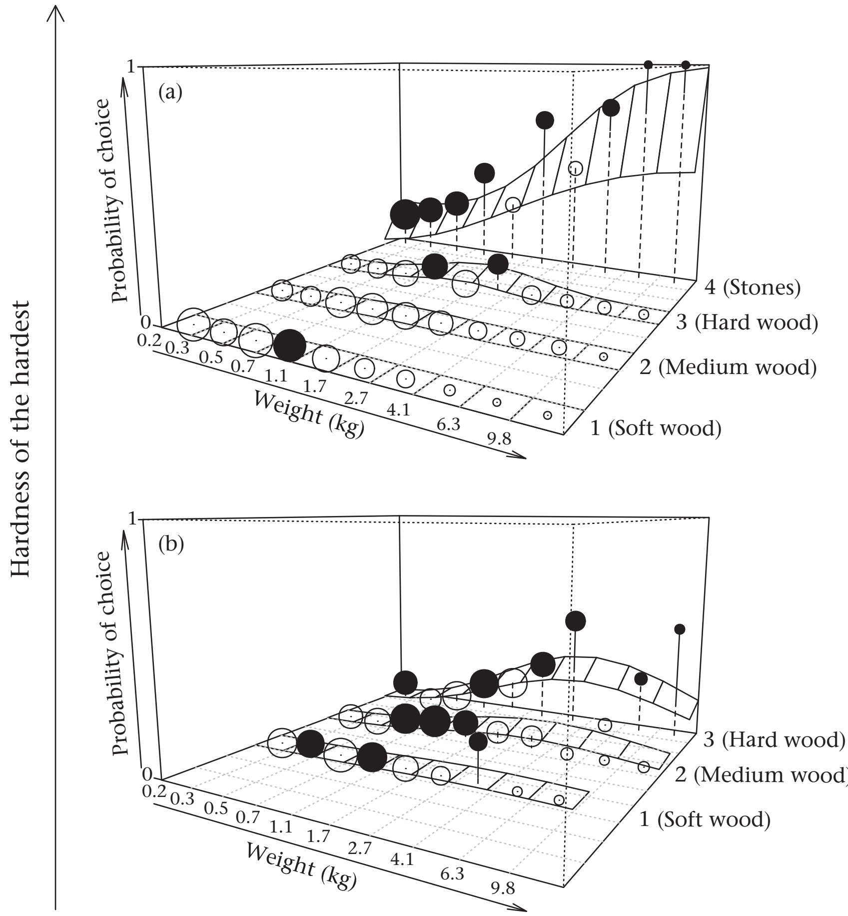


Figure 6. Conditional selection for hammer weight according to hammer hardness/material. Strips represent fitted probabilities of a hammer being chosen as a function of weight and hardness/material. The height of spheres represents the proportion of available hammers that were chosen within each category of hardness/material and range of weights. Spheres above the fitted surface (strips) are in black; circles below the surface are in white. Volume of the spheres is proportional to the number of available hammers. (a) Choices where the hardest available hammer was a stone. (b) Choices where no stone was available, and the hardest hammer available was a hard wooden club.

reported that long-tailed macaques selected stones of different mass according to food type (with episodes of tool selection indirectly inferred rather than directly observed), while Massaro et al. (2012) showed that bearded capuchins preferred different weights depending on how far from the anvil the hammer was placed, thus nicely demonstrating capuchins' ability to appreciate the interacting effect of two variables on the cost–benefit balance of a nut-cracking session. However, these experiments confronted animals with a highly simplified environment. For example in Massaro et al. (2012), capuchins had to choose each time between two values for weight and distance (the anvil was always in view), thus leaving untested whether capuchins can actually apply their ability to flexibly select nut-cracking tools in an ecologically relevant and natural context.

Table 3
Results of submodel 2, testing the effect of hammer weight and hammer hardness/material (‘hardness’ in the table) on the probability of a hammer being chosen

Effect	Estimate	SE	*z*	*P*
(Intercept)	−1.280	0.385	−3.320	[1]
Weight	1.491	0.686	2.174	[1]
Weight^2	−0.941	0.484	−1.941	[1]
Relative Hardness	1.985	0.324	6.118	[1]
Hardness of the Hardest Hammer	−0.274	0.340	−0.805	[1]
Interaction: Weight * Relative Hardness	−0.357	0.513	−0.695	[1]
Interaction: Weight * Hardness of the Hardest Hammer	0.602	0.490	1.228	[1]
Interaction: Weight^2 * Relative Hardness	0.623	0.358	1.739	[1]
Interaction: Weight^2 * Hardness of the Hardest Hammer	−0.780	0.436	−1.791	[1]
Interaction: Relative Hardness * Hardness of the Hardest Hammer	0.733	0.331	2.217	[1]
Interaction: Weight * Relative Hardness * Hardness of the Hardest Hammer	−0.705	0.435	−1.614	[1]
Interaction: Weight^2 * Relative Hardness * Hardness of the Hardest Hammer	0.867	0.351	2.465	0.016

All variables were log- and z-transformed. Random effects: subject, location (GPS), selection episode. Offset term: log-transformed inverse of the number of available hammers per selection episode. Random slopes terms within subjects for all main effects and interactions. Mean ± SD of each variable before log- and z-transformation: weight: 1.192 ± 1.457; Relative Hardness: −1.446 ± 1.053; Hardness of the Hardest Hammer: 2.48 ± 0.574.
[1]Significance test not indicated because it has no meaningful interpretation.

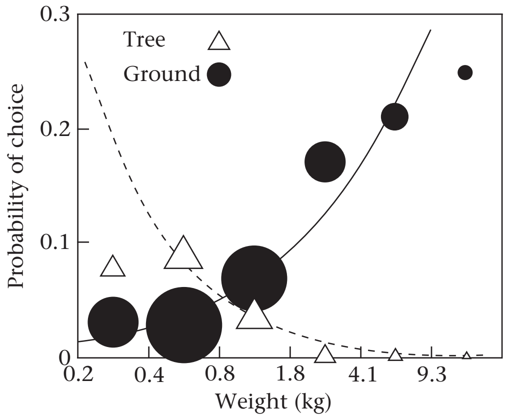


Figure 7. Conditional selection for hammer weight according to the location of the anvil (ground/tree). Fitted probabilities of a hammer being chosen as a function of weight when the chimpanzees were going to crack nuts on the ground (solid line) or on a tree branch (dashed line). The height of symbols (circles: ground; triangles: tree) represents the proportion of available hammers that were chosen within each range of weight for each anvil location. Area of the symbols is proportional to the number of available hammers.

In contrast, we directly investigated foraging optimization by wild chimpanzees in the complexity of their natural environment. In fact, in a natural context, each time chimpanzees select a nut-cracking tool, they must choose from among a large set of different available hammers (Fig. 4a), each characterized by a unique combination of relevant physical properties and distance to the anvil. Chimpanzees must thus form and apply their operational ‘rules’ relying on accumulated experience with a large number of objects and contexts, and a wide spectrum of variable values (Fig. 4) and their often unique combinations.

As we argued above, one measure of the cognitive complexity of a given behaviour could be the number of operational ‘rules’ (see Table 1) that are necessary to describe the behaviour. According to this premise, the tool selection behaviour we report qualifies as an extremely demanding form of foraging optimization from a cognitive point of view. In fact, when selecting their nut-cracking hammers, Taï chimpanzees simultaneously responded to at least two different properties of the hammers (weight and hardness/material) and two contextual variables (distance of hammers to the anvil and location of the anvil on the ground or on a tree). Furthermore, our results showed that the preference ‘rule’ applied by the chimpanzees when selecting hammer weight is not linear (as revealed in submodel 2, see Fig. 6b) and that at least three interactions (weight with hardness/material, transport distance and ground/tree anvil location) are needed to represent the observed pattern of choice. Although we could not fit, owing to our limited data set, a single linear model including all of these effects at the same time, our results correspond to a minimum of eight operational ‘rules’ (four linear terms, one quadratic term and three interactions), out of the 10 we tested, that are needed to describe chimpanzee tool selection patterns (Table 1).

Table 4
Results of submodel 3, testing the effect of hammer weight, anvil location (tree/ground) and day in season (proxy of nut hardness) on the probability of a hammer being chosen

Effect	Estimate	SE	*z*	*P*
(Intercept)	−0.130	0.130	−0.998	[1]
Weight	0.657	0.124	5.313	[1]
Anvil location (tree)	0.070	0.364	0.195	[1]
Day in Season	−0.030	0.131	−0.231	[1]
Interaction: Weight * Anvil location (tree)	−1.275	0.398	−3.203	0.001
Interaction: Weight * Day in season	0.114	0.116	0.985	0.330

Weight was log-transformed and all variables were z-transformed. Random effects: subject, location (GPS), selection episode. Offset term: log-transformed inverse of the number of available hammers per selection episode. Random slopes terms within subjects for all main effects and interactions. Mean ± SD of weight before log- and z-transformation: 1.192 ± 1.457; Anvil location: 14 anvils on tree, 99 on ground.
[1]Significance test not indicated because it has no meaningful interpretation.

Selection for Physical Properties of Hammers

Chimpanzees preferred stone hammers over wooden hammers (Fig. 6a) and harder woods over softer woods (Fig. 6b), a selection pattern consistent with our prediction 1.3 (Fig. 1) indicating chimpanzees were sensitive to the benefits of using harder and/or denser objects. We evaluated the relative importance that chimpanzees might assign to density and hardness by looking at the conditional selection of hammer weight according to hammer density and hardness (predictions 2.1a, 2.1b, Fig. 2). Chimpanzees preferred heavier weights for stones than for woods (Fig. 6), thus showing that the higher density of stones, rather than hardness, is the major driver of this observed interaction. This may also explain why chimpanzees' selection for stones over any kind of wood was much stronger than selection for harder woods over softer woods (Fig. 6). In fact, estimates of energy dissipation with hammers of different hardness suggest that the difference between a stone and a wooden hammer (up to 30%, Boesch & Boesch, 1983) is smaller than the difference between different types of wood (up to 50%, Steiner, 1992). Taken together, these observations show that, at least when it comes to cracking the relatively weak *Coula* nuts, chimpanzees' preference for stones is driven by the higher density of this material (providing the power of a heavy hammer together with the handiness of a compact hammer, and hence better control) even more than by its hardness.

It has been argued that, when a behaviour suggesting understanding (e.g. of a causal relation) is highly complex, it becomes unlikely that it can be explained by associative processes alone (e.g. Byrne & Bates, 2006; Seed & Byrne, 2010). Although selection of nut-cracking tools by chimpanzees can be considered highly complex from a quantitative standpoint (at least eight rules need to be invoked, see Table 1), our results, based on the observation of wild animals performing a habitual task, do not, per se, allow us to tell whether chimpanzees select tools based on associations among perceptual stimuli originating from the hammer itself (visual, tactile) and from its use (sensory-motor feedback and the reward of the nut) or whether they have developed abstract ‘concepts’ for weight, hardness, etc. and causal ‘rules’ for their relation to nut-cracking efficiency. Some authors (e.g. Povinelli, 2012) have denied that chimpanzees possess a concept for weight. However, experiments in which the natural correlation of weight and size was removed showed that chimpanzees and capuchin monkeys selected the weight of a nut-cracking hammer regardless of the perceptual context (Schrauf et al., 2012; Schrauf, Huber, & Visalberghi, 2008; Visalberghi et al., 2009), and that chimpanzees may understand that movement is caused by a massive body (Hanus & Call, 2008), thus indicating that they may have a concept-like representation of weight. If chimpanzees trained at cracking nuts with tools (Schrauf et al., 2012) apparently apply a representation of weight independent of perceptual cues, then a parsimonious argument suggests that such a representation also exists for Taï chimpanzees.

Conditional Selection and Planning

We observed conditional selection for weight according to the distance to the anvil, a result qualitatively similar to recent experimental evidence from bearded capuchins (Massaro et al., 2012). In contrast to experimental data, our observations also include several instances when the anvil was more than 30 m away from the selection point, and therefore not visible to the chimpanzee at the moment of hammer selection (Figs 4c and 5a), a situation that has not yet been possible to reproduce in experiments (Byrne & Bates, 2011). In this respect, our results extend observations by Boesch and Boesch (1984b), who, from indirect evidence of hammer transport, reported that chimpanzees most often transported lighter stones to crack *Panda* nuts when the distance was >40 m, whereas they usually preferred heavier stones when carrying them for shorter distances.

Although chimpanzees are known to transport tools out of view from the place where they were selected (Boesch & Boesch, 1984b; Sanz et al., 2004), and this behaviour may appear to be a form of planning for future needs, some authors have pointed out that associative learning may have established the habit, since the tool is selected along the way for the food item, so that the animals may already be motivated to eat the food (e.g. Roberts, 2002; Suddendorf & Busby, 2005; van Schaik et al., 2013). However, although this mechanism would explain the transport itself, it would not explain why chimpanzees should select different weights depending on how far they will (later) transport the hammer. An alternative account, not implying a representation of future goals, would be that chimpanzees pick up hammers according to a fixed preference, and then tend to transport a hammer for a longer distance if they realize that the hammer is not heavy. If this were the case, we should have observed that hammers were picked up and transported for a while, with the probability of being dropped before use being proportional to their weight, a prediction that was not testable by Boesch and Boesch (1983, 1984b). In contrast, through direct observations of the whole behavioural sequence (selection, transport, use), we could assess that this was not the case. In fact we never observed chimpanzees picking up a hammer, transporting it for a while and then dropping it without using it.

None the less, we cannot formally rule out an associative-learning interpretation for our observations of tool selection that is conditional on transport distance (including transport to distant and not visible anvils). Such an associative model would imply that every time an anvil is not in view, an inhibitory association prevents the usual rule for weight (take the heavy hammer, Fig. 5c) to operate. This inhibitory association should have formed through repeated experience with long transports of excessively heavy hammers, which would generate negative feedback stimuli in terms of muscle fatigue. While this prediction could be tested with longitudinal observations of the behaviour's ontogeny, we argue that this associative explanation is hardly more likely than one in which chimpanzees are actually aware of their next steps based on representations of the whole chain of actions (Byrne et al., 2013). The latter interpretation is further supported by experimental evidence that great apes can 'plan' by saving a tool for future needs (Mulcahy & Call, 2006; see also Osvath & Osvath, 2008). In one instance, we witnessed an interval of 7 min 48 s between the selection of a hammer and its use. During this time, the study subject, Narcisse, kept in constant physical contact with the hammer while moving ca. 30 m in two separate bouts and performed other activities not related to nut-cracking, including grooming and resting. On another occasion, we observed Pandora interrupting a nut-cracking session on a *Coula* tree, leaving the tree with the hammer in her hand, feeding on fruits on another tree for 12 min 18 s and then returning to the *Coula* tree to start cracking nuts again with the tool she had carried with her. To our knowledge, this is the longest retention of a tool reported in a natural setting.

That chimpanzees adjust their preference for weight according to the distance to the anvil is reasonable from an energetic standpoint (trade-off between power and cost of transport, see Günther & Boesch, 1993). However, it is less clear why chimpanzees should pick up a hammer when no anvils are in view (very long transports > 30 m), while, in addition, selecting for lighter weights that they do not regard as optimal at a shorter distance (Fig. 5c). Our results, in accordance with previous accounts (Boesch & Boesch, 1983), showed that 67.6% of hammers were collected within 1 m from the anvil, and that transport for long distances was exclusively performed for stone hammers (Fig. 4c). The prevalence of stones in long-distance transports is explained by the fact that they are much rarer in the forest than wooden clubs (Fig. 4a; Boesch & Boesch, 1983; Luncz et al., 2012), but chimpanzees strongly prefer them (see Fig. 6a). Therefore, the likely reason why chimpanzees sometimes pick up a hammer when no anvil is in view is that this hammer is a stone, a rare and valuable tool, providing both power and precision. Because longer transports were only observed with stone hammers (Fig. 4c), one could think that the effect of distance on the preference function for weight depends on a hidden effect of material. Ideally, the best way to tease apart the effects of material and distance on the preference for weight would be to fit a single model including the three variables. Unfortunately, we did not have enough data for such a complex model (see 'Statistical analyses'). However, we have shown that chimpanzees' selection was shifted towards heavier weights when they chose a stone than when they chose among woods (Fig. 6). Therefore, the observed interaction between distance and weight cannot depend upon a preference for lighter weights in the material that is transported for longer distances (stones).

That chimpanzees engage in some form of short-term planning when they select a nut-cracking tool is further strengthened by the observation that chimpanzees selected lighter hammers when they were going to crack nuts on a tree branch than when they were going to crack them on the ground (Fig. 7), an instance of conditional tool selection only anecdotally reported in previous studies (Boesch, 1991; Boesch & Boesch, 1993). In addition to arguments reported in Fig. 2, cracking nuts on a tree can be a very challenging task, since the animal is in an unbalanced position while handling multiple objects at the same time. In fact, when cracking nuts in trees, chimpanzees usually support the target nut with one hand in order to prevent it from bouncing away, so that smaller hammers can be more easily/precisely handled with the remaining free hand. Therefore, the observed conditional selection for weight according to anvil location suggests that chimpanzees may consider and remember the stability of the nut-cracking site as well as their own safety when balancing in the tree and trying to crack a nut at the same time. Here, as well, we note that practically all hammers used on trees were stones (13 stones versus one wooden hammer). This result implies that chimpanzees very rarely venture into a tree before finding a suitable stone. However, as in the case of distance, the observed interaction between anvil location (ground/tree) and weight (lighter weights on trees) cannot depend upon a preference for lighter weights in the material that is used on trees (stones) since chimpanzees preferred heavier weights among stones than among woods (Fig. 6).

Conclusions

Adult female Taï chimpanzees selected their nut-cracking tools according to a multidimensional, conditional strategy, which represents an extremely complex form of foraging optimization, at least from a quantitative cognitive perspective. In fact, chimpanzees must process a large amount of raw information about several physical variables in order to form and retrieve multiple operational 'rules' that account for the interaction among variables. While the observed patterns of hammer selection were consistent with our theoretical predictions for maximization of energetic efficiency, further empirical data (ideally measuring the net energetic intake per unit of time; see Günther & Boesch, 1993 for an approach of this kind) would be necessary to confirm whether chimpanzees select the most efficient hammer in a given situation. Our study also leaves untested whether such patterns of tool selection are shared by adult males, which have been reported to be less efficient than females at nut cracking (Boesch & Boesch, 1984a). Studies addressing this question might also reveal whether such sex differences in efficiency can be explained by a different ability at selecting tools.

Although our study, focusing on wild animals performing habitual tasks, did not directly aim at revealing the nature of chimpanzees' cognitive processes, we argue that abstract representations of an object's physical properties, which chimpanzees have been shown to possess in laboratory experiments (e.g. Hanus & Call, 2008), are likely to be used by chimpanzees in the context of natural tool selection, too. Moreover, our results strongly suggest that chimpanzees may select their tools according to short-term planning involving an anticipation of transport distance and the place where the nuts will be opened (tree or ground). These results are consistent with chimpanzees' planning abilities as revealed in captive studies (Osvath & Osvath, 2008) and in not tool-related field observations (e.g. Janmaat, Polansky, Ban, & Boesch, 2014). Regardless of the particular nature of the cognitive processes, the observation of behaviours that can be shown to be cognitively demanding from a quantitative standpoint in their natural context provides the opportunity to look into the ecological advantage of a species' cognitive abilities. Nut cracking in Taï chimpanzees is certainly one of the most ecologically relevant forms of tool-mediated extractive foraging activity by a nonhuman primate. Therefore, in support of the 'food extraction hypothesis' (Gibson, 1986), we argue that the sophisticated optimization that we have observed represents a compelling example of how ecological selective pressures, in the extractive foraging domain, may have favoured the fixation of powerful cognitive skills in our closest relatives.

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