

## Ecology of culture: do environmental factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*?

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Geographical variation in behaviour may be best explained in terms of culture if ecological and genetic explanations can be excluded. However, ecological conditions and genetic predispositions may in turn also affect cultural processes. We examined the influence of environmental factors on foraging tool use among chimpanzees at the Seringbara study site in the Nimba Mountains, Guinea, where nut cracking and termite fishing are absent, but ant dipping is present. We tested two ecological hypotheses to explain foraging tool use prevalence. The opportunity hypothesis states that encounter rates with nuts, insects or tools explain tool use patterns. We measured the density and distribution of nut trees, nuts, army ants, termites and potential tools in relation to the chimpanzees' ranging patterns. The necessity hypothesis states that tool use is a response to scarcity of preferred foods (i.e. ripe fruit). We measured the temporal availability of nuts, army ants and termites in relation to preferred food sources. Our findings support the opportunity hypothesis: nut trees and *Macrotermes* mounds were rare and peripheral to the chimpanzees' range, whereas army ants were abundant and widespread. The necessity hypothesis did not explain tool-assisted insectivory, as both army ants and termites were available during ripe fruit scarcity, yet neither ant dipping nor termite fishing functioned as fallback strategies. Nuts were absent at times of fruit scarcity and were not available as fallback foods. Our findings highlight the importance of considering environmental conditions in explaining foraging tool use by wild chimpanzees and emphasize the interplay between environment and culture.

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Culture has been identified in a number of animal taxa, including chimpanzees, orang-utans, *Pongo pygmaeus* and *Pongo abelii*, and cetaceans (Whiten et al. 1999; Rendell & Whitehead 2001; van Schaik et al. 2003). A behavioural variant may be termed 'cultural' if it is group-typical and depends on social learning for its maintenance and transmission (adapted from Laland & Hoppitt 2003). The main technique used to demonstrate presence of culture in wild animal populations, especially long-lived species, is the 'method of exclusion' (e.g. Whiten et al. 1999; Krützen et al. 2007), also called the 'geographical method' (van Schaik et al. 2003; van Schaik 2009), 'method of elimination' (van Schaik 2003), 'group comparison method' (Fragazy & Perry 2003) or 'ethnographic method' [sic] (Laland & Janik 2006). This method compares geographical variation in behaviour between populations and seeks to exclude behavioural variants clearly explained by genetic or environmental differences between sites, in order to assess possible cultural variants.

The main criticism of the method of exclusion is the difficulty of ruling out environmental and genetic influences (Laland & Hoppitt 2003; Laland & Janik 2006, 2007; Galef 2009; Laland et al. 2009). However, opponents and supporters of this approach agree that behavioural differences between populations are unlikely to be determined by culture alone, but rather by an interaction between genetics, environmental conditions and opportunities for social learning (e.g. Schöning et al. 2008; Laland et al. 2009; van Schaik 2009; Humle 2010). Importantly, the exclusion method was developed to identify the presence of culture in wild animal populations and not to assess the relative importance of culture in explaining behavioural variation (Krützen et al. 2007; van Schaik 2009). A number of geographically variable behavioural patterns in apes are explained most parsimoniously in terms of culture (Whiten et al. 1999; van Schaik et al. 2003; Krützen et al. 2011), but this does not mean that ecological conditions and genetics have no influence on cultural processes. So rather than focusing on a simplistic, trichotomous distinction between environment, genes and culture, research should shift towards assessing the extent and nature of interactions between genes, environmental conditions and culture. Recent studies on wild apes have made a start at disentangling relative contributions of genes, environment and

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culture in structuring patterns of behavioural variation (e.g. Schöning et al. 2008; Langergraber et al. 2010; Lycett et al. 2011; Krützen et al. 2011; Kamilar & Marshack 2012; Luncz et al. 2012).

Tool use in extractive foraging has been an important focus of animal culture studies, as the use of tools to gain access to food varies extensively among populations in a number of primate species. Across the animal kingdom, tool use is relatively rare (Schumaker et al. 2011) and habitual tool use in the wild is restricted to only a small number of bird species (e.g. New Caledonian crows, *Corvus moneduloides*: Hunt 1996) and mammal species (e.g. bottle-nosed dolphins, *Tursiops* sp.: Mann et al. 2008). The most extensive use of tools is found among the nonhuman primates and regular tool use is observed in some populations of chimpanzees (Whiten et al. 1999), orang-utans (van Schaik et al. 2003), bearded capuchin monkeys, *Cebus libidinosus* (Otoni & Izar 2008) and longtailed macaques, *Macaca fascicularis aurea* (Gumert et al. 2009). Widespread and flexible tool use across a range of contexts is found only in wild chimpanzees (McGrew 2004).

Chimpanzees have played a prominent role in the study of nonhuman culture (e.g. Goodall 1973; McGrew 1992, 2004; Boesch 1996). Cultural variants in wild chimpanzees have been described for subsistence, self-maintenance and social behaviours (Whiten et al. 1999, 2001). Nut cracking, termite fishing and ant dipping are examples of cultural tool use variants (Whiten et al. 1999). Nut cracking involves the use of a hammer and anvil to crack open nuts to expose the edible kernels and is restricted to West African forests (Boesch et al. 1994; Table 1). Termite fishing entails the use of a flexible probe to extract termites (mostly *Macrotermes*) from terrestrial mounds and occurs in a number of chimpanzee populations from Senegal to Tanzania (McGrew et al. 1979; Goodall 1986; Sanz et al. 2004; Bogart & Pruetz 2008). In ant dipping, chimpanzees use a wand to collect aggressive army ants (*Dorylus* spp.) from their temporary underground nests (McGrew 1974) or from surface trails (Sugiyama 1995). Army ants are ubiquitous across Africa, and tool use in army ant predation has been recorded in over a dozen chimpanzee study sites (reviewed in Schöning et al. 2008). However, not all populations of apes sympatric with army ants or termites use tools to harvest these insects, nor do all West African chimpanzee populations crack nuts (Whiten et al. 2001). The presence of cultural variants, such as nut cracking, ant dipping or termite fishing, raises the question as to the influence of environmental conditions on these variants and the extent to which the environment affects the likelihood of innovation and spread of tool use behaviours.

To examine the effects of environmental factors on tool use prevalence, we studied chimpanzees at Seringbara in the Nimba Mountains, Guinea, West Africa. The Seringbara chimpanzees use tools to dip for army ants (Humble & Matsuzawa 2001; Schöning et al. 2008), but show no signs of termite fishing (Humble & Matsuzawa 2001). Nut cracking is also absent at Seringbara, although oil palms, *Elaeis guineensis*, are present (Humble & Matsuzawa 2004). The lack of nut cracking is surprising, since the nearby (only 6 km away) Bossou community relies heavily on cracking of oil palm nuts for subsistence, especially at times of fruit scarcity (Yamakoshi 1998). Furthermore, chimpanzees in Yealé (Ivory Coast), on the other side of the Nimba mountain range (10 km away), crack oil palm and *Coula edulis* nuts (Matsuzawa & Yamakoshi 1996; Humble & Matsuzawa 2004). The Seringbara chimpanzee population thus provides a case study to investigate how environmental factors may influence the emergence and spread, or lack thereof, of cultural tool use variants among wild chimpanzees.

We tested two, not mutually exclusive, ecological hypotheses that may explain the prevalence of foraging tool use (Fox et al. 1999, 2004; Spagnoletti et al. 2012). First, the opportunity hypothesis (sensu Fox et al. 1999) states that encounter rates with resources requiring tool use (i.e. nuts, army ants, termites) and tool materials drive patterns of tool-assisted foraging. The opportunity hypothesis predicts that limited or lack of exposure to nuts or tools explains the absence of nut cracking. Similarly, it predicts that high encounter rates with army ants but limited opportunities to encounter termite mounds leads to the observed patterns of tool-assisted insect eating. We addressed this hypothesis by measuring both density and spatial distribution of nut-producing trees, nuts, army ants and termites, as well as the ranging patterns of the chimpanzees. In addition, we assessed availability of raw materials for tools around nut trees, army ant nests and *Macrotermes* mounds.

Second, the necessity hypothesis (sensu Fox et al. 1999) states that tool use is a response to scarcity of preferred food sources and is thus dependent on the relative value in terms of the availability of nuts and insects relative to preferred foods. The diet of wild chimpanzees is dominated by ripe fruit (e.g. Wrangham 1977). Hence, based on this hypothesis, the (relative) value of nuts and insects is expected to increase at times of ripe fruit scarcity and tool-assisted foraging is consequently predicted to function as a fallback strategy. Fallback foods are defined as foods whose use is negatively correlated with the availability of preferred foods (Marshall & Wrangham 2007). We addressed the second

**Table 1**

Nut species selected for cracking at chimpanzee study sites with confirmed nut cracking versus Seringbara (adapted from Humble 2011)

Study site	Country	<i>Coula edulis</i>	<i>Detarium senegalense</i>	<i>Elaeis guineensis</i>	<i>Panda oleosa</i>	<i>Parinari excelsa/glabra</i>	<i>Sacoglottis gabonensis</i>
Seringbara, Nimba <sup>a,b,c</sup>	Guinea	No	Available	Available	No	Available	No
Bossou <sup>d,e</sup>		No	No	Yes	No	Available	No
Diécké <sup>a,f,g</sup>		Yes	No	Available	Yes	Available	No
Yealé, Nimba <sup>a,b,h,i,j</sup>	Ivory Coast	Yes	Available	Yes	Available	Available	No
Tai <sup>h,k,l</sup>		Yes	Yes	Available	Yes	Yes	Yes
Mt Betro <sup>h,i</sup>		(Available)	(Available)	Available	Yes	(Available)	?
Mt Kope <sup>h</sup>		Yes	No	?	Available	Yes	Available
Mt Zoa (Scio) <sup>h,i</sup>		(Available)	(Available)	(Available)	Yes	Available	(Available)
Monogaga <sup>h,i</sup>		(Yes)	?	(Available)	Yes	(Available)	(Available)
Banco <sup>l</sup>		Yes	(Available)	(Available)	?	(Available)	(Available)
Sapo <sup>m</sup>	Liberia	Yes	?	Available	Yes	Yes	Yes
Cape Palmas <sup>n</sup>		Yes	?	Available	?	Available	?
Mt Kanton <sup>o</sup>		Yes	?	?	?	?	?
Tiwai <sup>p</sup>	Sierra Leone	Available	Yes	No	No	Available	?
Ebo <sup>q,r</sup>	Cameroon	Yes	?	Available	Available	?	No

Yes: species cracked; no: species not available; available; species not cracked but available; ?: availability unknown; ( ): published information inconsistent. Source: <sup>a</sup>Humble & Matsuzawa 2001; <sup>b</sup>Humble & Matsuzawa 2004; <sup>c</sup>this study; <sup>d</sup>Sugiyama & Koman 1979; <sup>e</sup>Sugiyama & Koman 1987; <sup>f</sup>Matsuzawa et al. 1999; <sup>g</sup>Carvalho 2011; <sup>h</sup>Boesch et al. 1994; <sup>i</sup>Joulian 1996; <sup>j</sup>Matsuzawa & Yamakoshi 1996; <sup>k</sup>Boesch & Boesch 1983; <sup>l</sup>Boesch & Boesch 1990; <sup>m</sup>Anderson et al. 1983; <sup>n</sup>Savage & Wyman 1844; <sup>o</sup>Kortlandt & Holzhaus 1987; <sup>p</sup>Whitesides 1985; <sup>q</sup>Morgan & Abwe 2006; <sup>r</sup>B. Morgan, personal communication.

hypothesis by measuring the temporal availability of nuts and insects, compared with the temporal availability of ripe fruits. We tested the prediction that tool use functions to overcome food scarcity by examining whether nuts, army ants and termites were available at times of preferred food scarcity and if they functioned as fallback foods (Yamakoshi 1998; Marshall & Wrangham 2007). We also assessed availability and use of alternative fallback foods, such as terrestrial herbaceous vegetation (THV) and fruits of *Ficus* (figs) and *Musanga cecropioides* (umbrella tree).

## METHODS

### Study Site

The Seringbara study site (07.37°N, 08.28°W) is in the Nimba Mountains in the southeast of the Republic of Guinea, West Africa. It covers about 25 km<sup>2</sup> of steep hills and valleys and is 6 km from Bossou, where a community of 12–23 chimpanzees has been studied for over 30 years (Matsuzawa et al. 2011). The Nimba region has been surveyed intermittently since 1992 (Matsuzawa & Yamakoshi 1996; Shimada 2000; Humle & Matsuzawa 2001; Humle 2003). Since 2003, a near-constant research presence has been maintained at Seringbara, but the study population remains largely unhabituated to human observers. For more information on the study site, see Koops (2011a, b).

### Nut, Termite and Army Ant Availability

Densities of nut-producing trees were calculated based on trees recorded along phenology transects (see [Fruit and THV Availability](#)). We monitored monthly availability of nuts from January to December 2008 along 26.2 km of forest trails (in four loop trails) for a subset of nut trees with diameter at breast height (DBH)  $\geq 10$  cm and within 5 m of the trail (see [Results](#) for details of tree species). We scored the availability of edible nuts (i.e. containing a kernel) on the ground below each tree within a 2 m radius of the trunk: (0) nuts absent; (1) 1–50 nuts; (2) 51–100 nuts; (3) >100 nuts. K.K. and local guides collectively judged the suitability of nuts for cracking by checking whether nuts contained an edible kernel or were rotten (sensu Humle & Matsuzawa 2004). Forest trails were largely based on chimpanzee paths, were distributed evenly across the study area and represented all altitude categories and habitat types (Koops et al. 2012). We segmented trail lengths into 100 m altitude categories and into habitat types and we recorded altitude and habitat type for each nut tree. Habitat types recorded were: (1) primary forest (excluding riverine forest); undisturbed forest; (2) secondary forest: forest burned or cultivated in recent past; (3) riverine forest: forest <30 m wide, along permanent water course; (4) THV-dominated forest: forest with understory dominated by herbaceous plants of the Marantaceae and Zingiberaceae; (5) savannah: low- and high-altitude grasslands.

To assess chimpanzee ranging in relation to altitude and habitat type, we monitored the forest trails once per month for chimpanzee signs (i.e. nest, feeding trace, faeces, sighting). Forest trails were monitored during 4 days (i.e. one loop trail per day) in the last week of each month (Koops et al. 2012). We recorded age of nests, feeding traces and faeces in three age classes: (1) fresh ( $\leq 2$  days); (2) recent (>2 days and  $\leq 1$  week); (3) old (>1 week and  $\leq 1$  month). Age classes were assigned using criteria based on chimpanzee evidence of known age at Bossou. Feeding traces and faeces were scored based on decomposition level and moisture content. Nest age was scored as (sensu Tutin & Fernandez 1984): (1) fresh ( $\leq 2$  days): leaves still green and fresh; (2) recent (>2 days and  $\leq 1$  week): leaves still green, but wilted and droopy leaves and

branches; (3) old (>1 week and  $\leq 1$  month): nest mainly made up of dead brown leaves, but still intact (Koops et al. 2012). When a nest was found, we searched for same-aged nests within a 30 m radius to obtain a count of all nests in a group.

We measured termite availability at the end of the dry season (March) and late wet season (October) to assess seasonal variation in termite mound density. We counted all occupied termite mounds within 2 m of forest trails and recorded habitat type and altitude for each mound. We recorded four mound types: (1) *Cubitermes* type: small mushroom-shaped mounds; (2) *Cephalotermes* type: distinctively black mounds; (3) *Allodotermes* type: large, low mounds with prominent ventilation shafts; (4) *Macrotermes* type: irregularly shaped massive mound. In addition, we selected 10 *Macrotermes* mounds and monitored them monthly (January–December 2008) for signs of chimpanzee visits (sensu McBeath & McGrew 1982; McGrew & Collins 1985; McGrew et al. 2007). We took termite samples for species identification and checked mound occupancy in March and October 2008.

To assess availability of army ants (*Dorylus* spp.), we recorded all *Dorylus* columns, swarm raids and visible nests along forest trails during monthly monitoring (see above). In addition, we recorded all army ant encounters during working days in the forest from January to December 2008 (142 days total). For each army ant encounter, we recorded habitat type and altitude. Also, we noted whether columns were: (1) migrating: emigration columns link nests and brood is transported on them from the old to the new nest, i.e. almost all workers carry brood; (2) foraging: foraging columns have workers running in both directions with food items being transported back to the nest. We sampled each column, swarm raid and nest for army ant species identification.

### Tool Material Availability

The availability of potential tools for nut cracking was recorded once (December 2008) as a representative measure of availability for the entire study period. We searched around a subset of trees of nut-bearing tree species for stones and wood items that might function as potential hammers and anvils. We scrutinized the northwest 90° quadrant within a 5 m radius of the tree trunk. We recorded all items with minimum length and width of 5 cm, which was based on minimum length of hammers and anvils at Bossou (S. Carvalho, personal communication). For each stone or wooden item we recorded size (i.e. maximum length) in 4 categories: (1) 5–10 cm; (2) 11–20 cm; (3) 21–30 cm; (4) >30 cm. We noted whether the item was portable (potential hammer or anvil) or nonportable (potential embedded anvil only) and if it had a flat surface with a horizontal surface area of at least 5 × 10 cm and therefore was suitable as a potential anvil. Only items of adequate hardness were recorded, which was established by one person (K.K.) banging portable items five times vigorously on a hard surface (i.e. rock outcrop, tree trunk), or by dropping a 1 kg granite stone five times from a 0.5 m height on nonportable items.

The availability of raw materials (i.e. living plants) for termite-fishing probes was recorded around occupied *Macrotermes* mounds ( $N = 5$ ) in October 2008. We arbitrarily selected the northwest 90° quadrant of a 5 m circle around the mound for scrutiny (sensu McBeath & McGrew 1982; McGrew et al. 2007). We counted all individual plants (i.e. tool sources) capable of providing termite-fishing probes and classified them as twig (tree or shrub), vine, THV or other (monocot or fern).

We recorded the availability of raw materials for ant-feeding tools around all army ant nests exploited by chimpanzees ( $N = 4$ ) that were encountered between November 2007 and December

2008. We measured all potential tool sources in the northwest 90° quadrant of a 5 m circle around the ant nest and classified potential tool sources as described above.

#### Fruit and THV Availability

To monitor temporal variation in fruit availability, we created two 500 m transects (north–south, east–west) on each of eight hills within the site, yielding a total transect length of 8 km. We established transects according to a stratified random design across the chimpanzee home range. We tagged and measured the DBH of all trees and vines belonging to confirmed chimpanzee food species with a DBH  $\geq 10$  cm and with the trunk midpoint within 5 m to each side of the transect line. We noted the presence of ripe and unripe fruit during the first half of each month. Fruit was scored as: (0) fruit absent; (1) 1–25% of canopy in fruit; (2) 26–50%; (3) 51–75%; (4) 76–100%. Phenology data were collected from January to December 2008 for 1147 food trees and vines. To estimate the density of THV, we placed 1 × 1 m quadrats at 100 m intervals to the right- and left-hand side of each phenology transect line ( $N = 192$  quadrats). We counted stems of herbs belonging to the Marantaceae and Zingiberaceae families, recording genus and species whenever possible. THV measurements were done in March, June, October and December 2008.

#### Chimpanzee Diet

To examine the diet of the chimpanzees, we collected faecal samples (<2 days old) below nests and on chimpanzee paths. We determined the wet weight of faecal samples (to the nearest 1 g) with a spring balance. We presoaked faecal samples in water and sieved them with a 1 mm mesh (McGrew et al. 2009). We recorded the number of large fruit seeds (>5 mm) and scored the abundance of small seeds (e.g. *Ficus* spp., *Musanga* sp.), fibre (i.e. THV, leaf) and animal remains (e.g. *Dorylus* spp.): (0) absent; (1) 1–25% of faecal sample; (2) 26–50%; (3) 51–75%; (4) 76–100%.

#### Data Analyses

We tested data for normality using a normal probability plot and a Kolmogorov–Smirnov test (Field 2005). All analyses were two tailed and significance levels were set at 0.05. Statistical tests were performed in SPSS version 16.0 (SPSS Inc., Chicago, IL, U.S.A.). We corrected for multiple comparisons with a Bonferroni correction. Chi-square tests (between altitude and habitat type categories) and binomial tests (within altitude and habitat type categories) were used to compare observed and expected numbers of chimpanzee signs, nut-bearing trees, termites and army ants between habitat types and altitude categories. Expected values were calculated based on the summed distance of forest trails (i.e. survey effort) within altitude categories and habitat types. Chimpanzee altitude and habitat type use was based on distribution of nests and other signs of chimpanzee presence. We considered chimpanzee feeding traces and faeces in the same altitude categories and habitat types to be independent if samples were found during different surveys, or if they belonged to different age classes. When feeding traces or faeces were found in the same altitude category or habitat type as same-aged nests or other traces, we did not consider the evidence as independent and merged same-aged signs of chimpanzee presence into a single data point.

We calculated a monthly fruit availability index (FAI) for chimpanzee food species with the following formula (as given in Takemoto 2004; Hockings et al. 2010):

$$\text{FAI} = \left[ \frac{\sum (P_i \times F_i)}{\sum (P_i \times 4)} \right] \times 100$$

in which FAI is the fruit availability index (%),  $P_i$  is the basal area of the tree ( $\text{cm}^2$ ) and  $F_i$  is the fruiting score of the tree.

In the analyses of chimpanzee diet, multiple same-aged faecal samples collected in the same nest group or along the same chimpanzee trail were not considered statistically independent. First, multiple faecal samples may have belonged to the same chimpanzee. Second, multiple samples from the same nest group or party did not provide independent data points on chimpanzee diet, as the party probably foraged together. Hence, when multiple faecal samples were collected together, we calculated median scores for the variables to be analysed (see *Chimpanzee Diet*) based on all faecal samples in the group (i.e. faecal cluster). This conservative use of median values for multiple faecal samples in a faecal cluster seeks independence of data points, while incorporating information from all samples collected. When only one faecal sample was collected, the value for the faecal cluster equalled the value for the sample.

## RESULTS

### Opportunity Hypothesis

To assess the opportunities for chimpanzees to encounter appropriate ecological conditions for tool use, we analysed the spatial distribution of chimpanzee ranging based on signs of chimpanzee presence ( $N = 139$  nests,  $N = 3$  sightings,  $N = 5$  faeces,  $N = 33$  feeding traces) in relation to availability and distribution of nuts, termites, army ants and potential tool sources. Chimpanzee presence differed from expected between habitat types (chi-square test:  $\chi^2_4 = 21.6$ ,  $P < 0.0001$ ) and altitude categories (chi-square test:  $\chi^2_3 = 96.4$ ,  $P < 0.0001$ ). We found fewer signs of chimpanzee presence in riverine forest and savannah (Table 2). Furthermore, we found fewer signs below 800 m and more signs above 900 m (Table 3).

### Nut Cracking

We confirmed the presence of four nut-bearing tree species (Table 4), of which *Detarium senegalense* and *Parinari glabra* were rare, *Elaeis guineensis* occurred at low density and *Parinari excelsa* was common. We found no evidence of nut cracking. *Detarium senegalense* trees ( $N = 4$ ) were found in low-altitude savannah and *P. glabra* trees ( $N = 2$ ) in primary forest. *Elaeis guineensis* ( $N = 23$ )

**Table 2**

Percentage (expected) of forest trail length (26.2 km) compared to percentage (observed) of chimpanzee signs, nut-producing trees (per tree species), termite mounds (early and late wet season) and army ant trails across habitat types

	Primary	Secondary	Riverine	THV	Savannah
Forest trail length	59.1	18.3	11.8	6.9	3.9
Chimpanzee signs ( $N=180$ )	59.8	23.9	4.3*	9.8	0*
Nut-producing trees					
<i>Elaeis guineensis</i> ( $N=23$ )	17.4**	78.3**	0	4.3	0
<i>Parinari excelsa</i> ( $N=61$ )	80.3*	19.7	0*	0	0
<i>Parinari glabra</i> ( $N=2$ )	100	0	0	0	0
<i>Detarium senegalense</i> ( $N=4$ )	0	0	0	0	100
Termite mounds					
Early wet season ( $N=180$ )	66.7	9.4*	11.7	11.1	1.1
Late wet season ( $N=258$ )	70.9**	8.1**	12.8	7.8	0.4*
Army ant trails ( $N=20$ )	50.0	25.0	10.0	15.0	0

THV: terrestrial herbaceous vegetation. Asterisks indicate categories significantly different from expected based on forest trail length (binomial test on frequencies): \* $P < 0.01$ ; \*\* $P < 0.001$ . *Parinari glabra* and *D. senegalense* tree distributions were not statistically testable owing to small sample sizes.



**Table 3**

Percentage (expected) of forest trail length (26.2 km) compared to percentage (observed) of chimpanzee signs, nut-producing trees (per tree species), termite mounds (early and late wet season) and army ant trails across altitude categories

	<800 m	800–900 m	900–1000 m	>1000 m
Forest trail length	39.3	11.0	18.1	31.6
Chimpanzee signs (N=180)	3.8**	14.6	27.0*	51.9**
Nut-producing trees				
<i>Elaeis guineensis</i> (N=23)	95.7**	0	4.3	0
<i>Parinari excelsa</i> (N=61)	0**	3.3	19.7	77.0**
<i>Parinari glabra</i> (N=2)	100	0	0	0
<i>Detarium senegalense</i> (N=4)	100	0	0	0
Termite mounds				
Early wet season (N=180)	66.1**	3.9*	8.3**	21.7*
Late wet season (N=258)	62.8**	5.0*	11.2*	20.9**
Army ant trails (N=20)	50.0	5.0	40.0	5.0*

Asterisks indicate categories significantly different from expected based on forest trail length (binomial test on frequencies): \* $P < 0.01$ ; \*\* $P < 0.001$ . *Parinari glabra* and *D. senegalense* tree distributions were not statistically testable owing to small sample sizes.

occurred less often in primary and more often in secondary forest (Table 2), whereas *P. excelsa* ( $N = 61$ ) occurred more in primary and less often in riverine forest (Table 2). Chimpanzees ranged in habitat types with *E. guineensis*, *P. excelsa* and *P. glabra* trees, but not in savannah, where *D. senegalense* was found. The altitudinal range varied between tree species (Table 3). *Detarium senegalense* and *P. glabra* were found only below 700 m, whereas *E. guineensis* and *P. excelsa* occurred more widely. *Elaeis guineensis* trees were more abundant below 800 m and *P. excelsa* trees were more abundant above 1000 m (Table 3). Thus, chimpanzees had plentiful opportunities to encounter *P. excelsa* trees, but few opportunities to encounter the other nut tree species.

We assessed presence of potential hammers and anvils under a subset of nut-bearing trees (Table 5). At least one potential anvil stone or tree root (i.e. flat surface) together with one potential hammer stone or wooden club (i.e. portable) was present under 64% (35/55) of trees. Wood items were less common than stones under nut-producing trees (Mann–Whitney  $U$  test:  $z = -5.5$ ,  $N_1 = N_2 = 55$ ,  $P < 0.0001$ ). Mean number of stones under nut-producing trees did not differ between tree species (Kruskal–Wallis test:  $H_2 = 2.2$ ,  $N_1 = 20$ ,  $N_2 = 31$ ,  $N_3 = 4$ ,  $P = 0.33$ ), and all tree species had portable and nonportable, flat and nonflat stones present in all size classes. Thus, nut cracking was feasible under all nut-bearing trees species, as both the number of stones and their properties were suitable for use as hammers and anvils.

#### Termite Fishing

We recorded two species of *Macrotermes* (*M. bellicosus*, *M. subhyalinus*) at Seringbara and both of these species are harvested by chimpanzees at other sites with tools (McGrew et al. 1979; Collins & McGrew 1987; Bogart & Pruett 2008). We analysed 107 chimpanzee faecal samples, in 44 faecal clusters, none of which contained termite remains. Most mounds were of the *Cubitermes* type (Table 6). *Macrotermes* mounds were extremely

**Table 4**

Nut-producing tree species at the Seringbara study site

Species	Trees monitored (forest trails)	Density (trees/ha)	Altitude range (m)	Part eaten by chimpanzees
<i>Detarium senegalense</i>	4	+	637–648	None
<i>Elaeis guineensis</i>	20	0.4	662–988	Fruit
<i>Parinari excelsa</i>	29	3.4	816–1134	Fruit
<i>Parinari glabra</i>	2	+	670	Fruit

+ = species present in study area, but not on transects.

rare along forest trails, with only one mound recorded. The distribution of termite mounds between habitat types differed from expected in both early (chi-square test:  $\chi^2_4 = 18.4$ ,  $P = 0.01$ ) and late wet seasons (chi-square test:  $\chi^2_4 = 29.2$ ,  $P < 0.0001$ ). In the early wet season, fewer mounds were found in secondary forest (Table 2). In the late wet season, more mounds were found in primary forest and fewer mounds in secondary forest and savannah (Table 2). The distribution of termite mounds between altitude categories also differed from expected, in both early (chi-square test:  $\chi^2_3 = 29.2$ ,  $P < 0.0001$ ) and late wet seasons (chi-square test:  $\chi^2_3 = 60.3$ ,  $P < 0.0001$ ). In early and late wet seasons, more mounds were found below 800 m and fewer mounds above 800 m (Table 3).

*Macrotermes* mounds were restricted to savannah habitat and low altitude (633–651 m), where chimpanzees did not range. Year-round monitoring of *Macrotermes* mounds yielded no signs of chimpanzee visits. Availability of raw materials for termite fishing was measured around five mounds. The typical mound had 12 twig sources (range 1–25), but no vine source (range 0–3). Abundance of grass sources depended on mound location, i.e. mounds in savannah were surrounded by grasses, whereas mounds in savannah–forest edge were not. We confirmed that mounds were fishable by opening an exit hole by finger and inserting a probe. In sum, *Macrotermes* mounds had enough raw materials present to supply termite fishing probes. However, mounds occurred in low-altitude savannah where we recorded no evidence of chimpanzee presence.

#### Ant Dipping

We collected 121 army ant samples. Army ant species included both ‘epigaeic’ and ‘intermediate’ species (Schöning et al. 2007). Samples included *Dorylus emeryi* (50%), *Dorylus nigricans* (24%), *Dorylus mayri* (16%), *Dorylus burmeisteri* (9%) and *Dorylus gribodoi* (4%). Most army ants (90% of samples) encountered were foraging (i.e. foraging trails and swarm raids), whereas migration trails and nests were rarely encountered. Although the distribution of army ant trails between habitat types did not differ from expected (chi-square test:  $\chi^2_4 = 3.5$ ,  $P = 0.48$ ), it varied between altitude categories (chi-square test:  $\chi^2_3 = 11.0$ ,  $P = 0.01$ ). Army ants were encountered less often above 1000 m than expected (Table 3). None the less, chimpanzees and army ants overlapped largely in altitudinal distribution, especially between 900 and 1000 m. On average, 28 potential tool sources were available per northwest 90° quadrant at ant nests ( $N = 4$ , median = 29, range 25–30). Hence, there was no shortage of ant-dipping tools.

#### Necessity Hypothesis

The FAI was negatively correlated with monthly rainfall (Spearman rank correlation:  $r_s = -0.75$ ,  $N = 12$ ,  $P = 0.005$ ). Months of low fruit availability were June–November and of high fruit availability were December–May (Fig. 1). THV densities did not differ between surveys (Friedman ANOVA:  $\chi^2_3 = 2.6$ ,  $P = 0.46$ ), and THV was thus available year-round. Mean stem density  $\pm$  SD was  $4.2 \pm 0.9$  stems/m<sup>2</sup> ( $N = 4$ ) for Marantaceae and  $0.2 \pm 0.1$  stems/m<sup>2</sup> ( $N = 4$ ) for Zingiberaceae plants. No differences in THV densities were found when Marantaceae and Zingiberaceae plants were analysed separately (Friedman ANOVA: Marantaceae:  $\chi^2_3 = 3.1$ ,  $P = 0.381$ ; Zingiberaceae:  $\chi^2_3 = 4.1$ ,  $P = 0.25$ ). All THV species recorded were confirmed to be part of the chimpanzees’ diet based on feeding remains.

#### Nut Cracking

We assessed the temporal availability of nuts by measuring the proportion of nut trees providing nuts per month. Nut availability

**Table 5**  
Mean frequency of stones and wooden items per tree ( $\pm$  SD), according to their qualifying properties (i.e. mobility, flatness, size)

	Total	Movable	Nonmovable	Flat	Nonflat	Size 1	Size 2	Size 3	Size 4
<b>Stones</b>									
<i>Elaeis guineensis</i>	3.6 ( $\pm$ 4.2)	2.2 ( $\pm$ 2.8)	1.4 ( $\pm$ 2.2)	1.9 ( $\pm$ 3.1)	1.7 ( $\pm$ 2.8)	1.5 ( $\pm$ 2.1)	1.4 ( $\pm$ 2.1)	0.4 ( $\pm$ 0.6)	0.4 ( $\pm$ 1.3)
<i>Parinari</i> spp.	5.3 ( $\pm$ 5.0)	2.7 ( $\pm$ 2.6)	2.6 ( $\pm$ 4.0)	2.5 ( $\pm$ 2.2)	2.8 ( $\pm$ 3.8)	1.9 ( $\pm$ 1.8)	2.1 ( $\pm$ 2.0)	0.9 ( $\pm$ 1.9)	0.5 ( $\pm$ 1.4)
<i>Detarium senegalense</i>	8.5 ( $\pm$ 10.0)	5.5 ( $\pm$ 9.7)	3.0 ( $\pm$ 2.2)	5.3 ( $\pm$ 5.5)	3.3 ( $\pm$ 4.6)	3.8 ( $\pm$ 4.3)	3.8 ( $\pm$ 4.3)	0.3 ( $\pm$ 0.5)	0.8 ( $\pm$ 1.5)
Total	4.9 ( $\pm$ 5.2)	2.7 ( $\pm$ 3.5)	2.2 ( $\pm$ 3.3)	2.5 ( $\pm$ 2.9)	2.5 ( $\pm$ 3.5)	1.9 ( $\pm$ 2.2)	1.9 ( $\pm$ 2.3)	0.6 ( $\pm$ 1.5)	0.5 ( $\pm$ 1.3)
<b>Wood</b>									
<i>Elaeis guineensis</i>	0.3 ( $\pm$ 0.6)	0.2 ( $\pm$ 0.5)	0.1 ( $\pm$ 0.3)	0.2 ( $\pm$ 0.4)	0.1 ( $\pm$ 0.2)	0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	0.3 ( $\pm$ 0.6)
<i>Parinari</i> spp.	0.8 ( $\pm$ 1.1)	0.3 ( $\pm$ 0.8)	0.4 ( $\pm$ 0.6)	0.5 ( $\pm$ 0.7)	0.4 ( $\pm$ 0.8)	0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	0.8 ( $\pm$ 1.1)
<i>Detarium senegalense</i>	1.0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	1.0 ( $\pm$ 0.0)	1.0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	1.0 ( $\pm$ 0.0)
Total	0.6 ( $\pm$ 0.9)	0.2 ( $\pm$ 0.7)	0.3 ( $\pm$ 0.5)	0.4 ( $\pm$ 0.6)	0.2 ( $\pm$ 0.7)	0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	0 ( $\pm$ 0.0)	0.6 ( $\pm$ 0.9)

*Elaeis guineensis*:  $N = 20$ ; *Parinari* spp.:  $N = 31$ ; *D. senegalense*:  $N = 4$ . See text for details of categories.

below *E. guineensis* trees peaked in April, but fewer than 50% of trees provided edible nuts (Fig. 2). Availability of nuts below *P. excelsa* trees peaked in January–March, with over 50% of trees providing nuts (Fig. 2), while *P. glabra* trees provided nuts from January to April and *D. senegalense* trees from January to March (Fig. 2). Hence, at times of low fruit availability, few trees provided nuts.

In addition, we measured the quantity of nuts below trees per month. Mean number of edible nuts below *E. guineensis* trees was highest in April and May, but overall availability of nuts below oil palm trees was low (Fig. 3). The mean nut quantity score of *P. excelsa* and *D. senegalense* trees was highest from January to March (Fig. 3). Thus, at times of low fruit availability, the number of nuts below nut-bearing trees was at its lowest.

#### Termite Fishing

We assessed the temporal availability of termite mounds. The number of occupied termite mounds was higher in the late compared to the early wet season (binomial test:  $P < 0.0001$ ), which was mainly due to an increase in *Cubitermes* mounds (Table 6). Overall, termites were available year-round. In March, all *Macrotermes* mounds were occupied and one had fresh exit holes and wings of alates. In October, six mounds remained occupied. Thus, *Macrotermes* were present, and potentially fishable, year-round.

#### Ant Dipping

We assessed temporal variation in both army ant availability and chimpanzee consumption of army ants. Mean monthly army ant column density  $\pm$  SD was  $0.08 \pm 0.06$  columns/km ( $N = 10$ , range 0.04–0.19). Mean encounter rate of army ant columns per day  $\pm$  SD was  $0.7 \pm 0.6$  columns/day ( $N = 10$ , range 0.18–1.65). Both measures of ant abundance were positively correlated with monthly rainfall (Spearman rank correlation: ants/km:  $r_s = 0.81$ ,  $P = 0.005$ ; ants/day:  $r_s = 0.77$ ,  $P = 0.01$ ) and army ants were thus

**Table 6**  
Termite mound frequency and density on forest trails (26.2 km) in early (March) and late (October) wet season

Mound type	Early wet season		Late wet season	
	Mounds	Mound density (per ha)	Mounds	Mound density (per ha)
<i>Cubitermes</i>	173	11.0	244	15.5
<i>Cephalotermes</i>	4	0.3	11	0.7
<i>Allodotermes</i>	2	0.1	2	0.1
<i>Macrotermes</i>	1	0.1	1	0.1
Total	180	11.5	258	16.4

more abundant in wet than dry months. Overall, 36% (38/107) of faecal samples contained army ant remains, which equalled 43% (19/44) of faecal clusters. We confirmed consumption of all five *Dorylus* species. Army ant remains were found in at least one chimpanzee faecal sample in each month during which faeces were found ( $N = 10$  months). The percentage of faecal clusters with army ant fragments was 53% (9/17) in the wet versus 37% (10/27) in the dry season; this difference was not significant (chi-square test:  $\chi^2_1 = 1.1$ ,  $P = 0.36$ ).

#### Fallback Foods

There was no correlation between monthly ant abundance scores in faecal clusters and ripe fruit availability (Spearman rank correlation:  $r_s = -0.23$ ,  $N = 11$ ,  $P = 0.50$ ). Also, no correlation was found between ant abundance scores and number of tree and vine fruit species in faecal clusters (Spearman rank correlation:  $r_s = 0.16$ ,  $N = 44$ ,  $P = 0.29$ ), nor with the number of seeds/g of faeces (Spearman rank correlation:  $r_s = -0.13$ ,  $N = 35$ ,  $P = 0.44$ ). Furthermore, no significant correlation was found between monthly ant abundance scores in faecal clusters and ant trails/km of forest trail (Spearman rank correlation:  $r_s = -0.24$ ,  $N = 10$ ,  $P = 0.50$ ) or ant trails/day (Spearman rank correlation:  $r_s = -0.32$ ,  $N = 10$ ,  $P = 0.37$ ). Hence, army ant consumption did not reflect scarcity of preferred food or availability of army ants. However, ant abundance scores were positively correlated with (pith and leaf) fibre scores in faecal clusters (Spearman rank correlation:  $r_s = 0.37$ ,  $N = 44$ ,  $P = 0.01$ ).

Chimpanzees fed on THV year-round, but there was a nonsignificant negative correlation between FAI and fibre scores (Spearman rank correlation:  $r_s = -0.53$ ,  $N = 11$ ,  $P = 0.09$ ), suggesting that when less ripe fruit was available, more pith and leaf fibre were eaten. No correlation was found between FAI and *Ficus/Musanga* seed scores (Spearman rank correlation:  $r_s = -0.27$ ,  $N = 11$ ,  $P = 0.42$ ). There was a negative correlation between fibre scores and number of seeds/g of faeces (Spearman rank correlation:  $r_s = -0.62$ ,  $N = 35$ ,  $P < 0.0001$ ), providing additional support for the role of THV as a fallback food.

## DISCUSSION

### Opportunity Hypothesis

Opportunities for nut cracking at Seringbara were limited. First, nut-producing tree species were rare, except for *P. excelsa*. Second, skewed spatial distribution of nut-producing trees towards low altitudes further limited opportunities for chimpanzees to encounter nuts other than *P. excelsa*. Moreover, productivity of *E. guineensis* (cracked at nearby Bossou) was extremely low compared to the other nut tree species. Tool availability was not

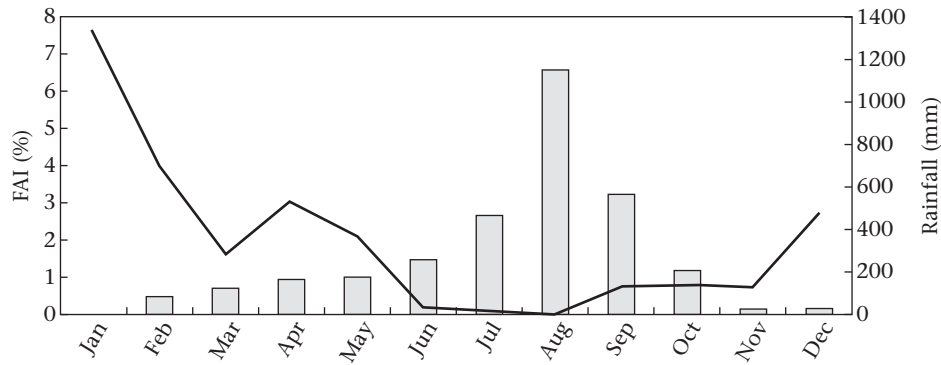


Figure 1. Monthly fruit availability index (FAI) for ripe fruit of chimpanzee food species (black line) and monthly rainfall (grey bars) in 2008.

limited, as availability of potential hammers and anvils was sufficient to allow nut cracking. Thus, overall it is the limited opportunities to find nuts that may account for the absence of nut cracking at Seringbara.

How does availability of nut-bearing trees at Seringbara compare with other chimpanzee sites, with and without nut cracking? We consider sites with research effort exceeding mere surveys and for which consistent information has been published regarding the nut species cracked (Table 7). At Tai, *C. edulis* occurs at high densities compared to other nut species and compared to other study sites and it is also the most cracked species (Boesch & Boesch 1983; Boesch & Boesch-Achermann 2000). Conversely, *E. guineensis* is present at low density and is not cracked at Tai (Boesch & Boesch 1983). At Bossou, *E. guineensis* is present at high density and chimpanzees here rely heavily on cracking of oil palm nuts (Yamakoshi 1998). At Yealé, both *E. guineensis* and *C. edulis* are present at intermediate densities and both species are cracked rarely (Humble & Matsuzawa 2001, 2004). In contrast, nut-producing tree densities at Lopé, Gashaka and Seringbara, where chimpanzees do not crack nuts, are considerably lower (Table 7). In sum, presence or absence of nut-bearing trees does not explain occurrence of nut cracking. However, in line with the opportunity hypothesis, the density and distribution of nut trees contribute to the likelihood of nut cracking being invented, as well as later transmitted, in a population of chimpanzees. The species of nut present may also influence the emergence of nut cracking. That is, presence of a high-value nut species may be more likely to trigger a nut-cracking innovation. After the initial innovation the skill may spread to other nut species. The absence of a nut-cracking ‘trigger’ species, rather than low opportunity, may underlie the absence of *Parinari* nut cracking at Seringbara. In fact, *Parinari* nuts are ignored

at most study sites (Table 1). This suggests that *Parinari* may be less likely to invoke a nut-cracking innovation than are other nut species. Notably, *Parinari* is cracked nowhere unless at least one other nut species is cracked too. *Coula edulis*, on the other hand, is the most frequently cracked species across sites (Table 1). *Coula* nut cracking may be a catalyst for cracking of other nut species, including *Parinari*. It remains to be explored why some nut species are more likely to be cracked than others. Possible avenues of investigation may include a cost and benefit analysis for the different nut species by comparing the calorific and nutritional value, palatability, size of kernel, hardness of nutshell and nut productivity between species and between years.

Opportunities for termite fishing at Seringbara also were limited. Termite mound density ranged from 12 to 16 mounds/ha, which is higher than at sites where chimpanzees fish for termites, such as Assirik in Senegal (10.8/ha, McBeath & McGrew 1982), Gombe in Tanzania (5.6/ha, Collins & McGrew 1987), Mahale in Tanzania (13.3/ha, Collins & McGrew 1987) and Fongoli in Senegal (7–10/ha, Bogart & Pruett 2008). However, *Macrotermes* was the least common genus at Seringbara with a density of 0.1 mounds/ha. In comparison, *Macrotermes* was common at two termite-fishing sites, namely 23.6 mounds/ha at Fongoli (Bogart & Pruett 2011) and 10.8 mounds/ha at Assirik (McBeath & McGrew 1982), but relatively rare at Gombe (0.7 mounds/ha; Collins & McGrew 1987) and Mahale-Belingé (0.1 mounds/ha; Collins & McGrew 1987). Hence, low *Macrotermes* mound density alone cannot explain absence of termite fishing.

At Seringbara, *Macrotermes* mounds occurred not only at low density, but also were restricted to low-altitude savannahs, where chimpanzees did not range. Thus, chimpanzees had limited opportunities to interact with mounds and termites, which in turn

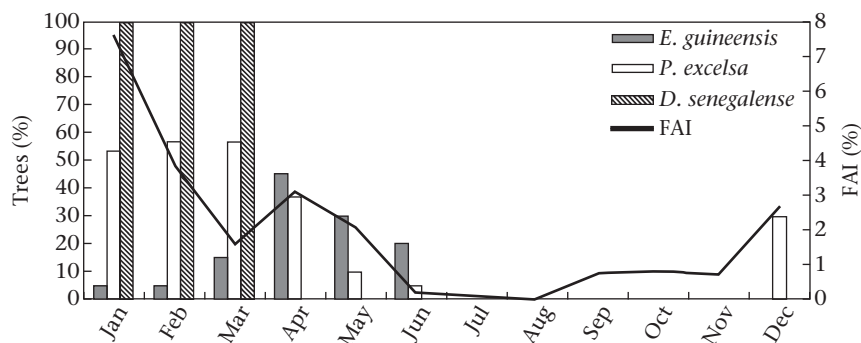
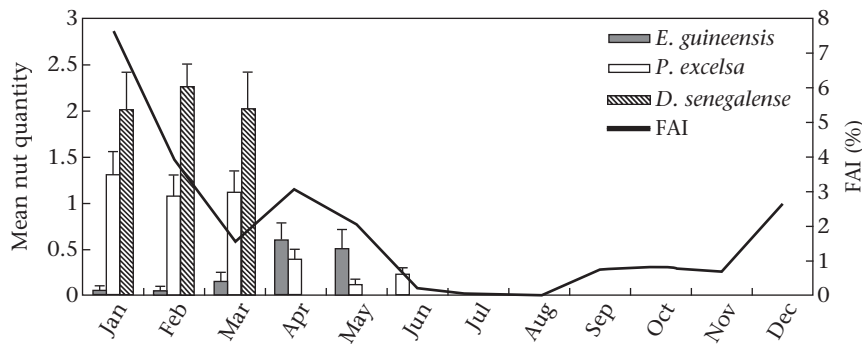


Figure 2. Monthly fruit availability index (FAI) for ripe fruit of chimpanzee food species (black line) and percentage of *E. guineensis* ( $N = 20$ ), *P. excelsa* ( $N = 29$ ) and *D. senegalense* ( $N = 4$ ) trees with edible nuts in 2008.



**Figure 3.** Monthly fruit availability index (FAI) for ripe fruit of chimpanzee food species (black line) and mean nut quantity score +SE for *E. guineensis* ( $N = 20$ ), *P. excelsa* ( $N = 29$ ) and *D. senegalense* ( $N = 4$ ) in 2008.

rendered innovation and spread of termite fishing improbable. Moreover, immigration of a termite-fishing female from a neighbouring community was impossible, as termite fishing is absent in nearby communities at Bossou and Yealé (Humble & Matsuzawa 2001), with only one observation of termite fishing at Bossou in 30 years (Humble 1999). Raw material availability for termite-fishing tools was not a limiting factor, as *Macrotermes* mounds had plentiful twig or grass sources to modify and to use as termite-fishing probes. In sum, low *Macrotermes* mound density and clumped distribution in low-altitude savannahs may explain the absence of termite fishing at Seringbara, which is congruent with the opportunity hypothesis.

Opportunities to encounter army ants were abundant. The average army ant encounter rate at Seringbara (0.08 trails/km) was lower than at Gashaka, Nigeria (0.43 trails/km), where chimpanzees also rely heavily on army ants in their diet year-round (Schöning et al. 2007). However, no comparative data on army ant encounter rates by chimpanzees exist for sites where ant dipping is absent. Army ants were widely distributed at Seringbara, occurring across habitat types and altitude categories. Chimpanzees and army ants had largely overlapping distributions giving plentiful opportunities for them to interact. Also, raw material availability for ant-dipping tools was not limiting around ant nests. Chimpanzees not only had plentiful opportunities to encounter army ants, but also tool-assisted army ant predation is common in neighbouring communities (Humble & Matsuzawa 2001, 2002). Hence, opportunities for an ant-dipping innovation, or diffusion from a neighbouring group, followed by spread and maintenance of the behaviour were abundant, providing further support for the opportunity hypothesis.

#### Necessity Hypothesis

Nuts were present only when fruit availability was high and thus could not serve as a fallback food. At times of fruit scarcity, chimpanzees relied instead on THV. High nut availability during the peak

fruiting period may impede the exploration of these embedded foods and the innovation of nut-cracking behaviour. Furthermore, it is possible that the relative value of nuts versus ripe fruit at Seringbara may have been too low for nut cracking to be beneficial. However, Tai chimpanzees do not eat nuts at times of low fruit availability, but do at times of high nut availability (Boesch & Boesch 1984). One possible explanation could be that the nutritional value of *Coula* nuts exceeds that of *Parinari* nuts, so that even at times of high fruit availability, it pays to crack *Coula* nuts, thus increasing the likelihood of a nut-cracking innovation and subsequent spread. In addition, environmental factors (e.g. tree density and distribution) may further influence social opportunities for learning and transmission of nut-cracking skills.

Termites were available at times of food scarcity. In East Africa, chimpanzees are seasonal termite feeders, which is linked to the termite reproductive cycle (McGrew et al. 1979; McGrew & Collins 1985). In Central Africa, chimpanzees eat termites year-round (Rio Muni, Equatorial Guinea: McGrew et al. 1979; Campo, Cameroon: Muroyama 1991; Ndoki, Congo: Suzuki et al. 1995; Goulougo, Congo: Sanz et al. 2004; Dja, Cameroon: Deblauwe 2009). However, chimpanzees at Dja ate more termites at times of fruit scarcity when termites probably complemented protein from low-quality THV (Deblauwe 2009). In Senegal, chimpanzees fish for termites seasonally at Assirik (McGrew et al. 1979) versus year-round at Fongoli (Bogart & Pruetz 2008). Moreover, termite fishing at Fongoli coincides with the period of high fruit availability, rather than fruit scarcity (Bogart & Pruetz 2008, 2011). In sum, termites (including *Macrotermes*) at Seringbara were available when ripe fruit was scarce, but chimpanzees failed to consume them. Evidence from other sites further suggests that termites are generally eaten as a preferred food source and not as a fallback food.

Army ants were available year-round but were most abundant in the wet season, that is, when ripe fruit availability was low. Army ants were an important part of the Seringbara chimpanzees' diet, as 36% of faecal samples contained army ant fragments, which is among the highest rates reported (Gashaka, Nigeria: 42.3%,

**Table 7**

Nut-producing tree density (trees/ha) at study sites with nut cracking (Tai North, Tai South, Yealé, Bossou) and without nut cracking (Seringbara, Gashaka, Lopé)

Species	Tai North <sup>a</sup> Ivory Coast	Tai South <sup>a</sup> Ivory Coast	Yealé <sup>a,b</sup> Ivory Coast	Bossou <sup>b,c</sup> Guinea	Seringbara <sup>b,d</sup> Guinea	Gashaka <sup>e</sup> Nigeria	Lopé <sup>f</sup> Gabon
<i>Coula edulis</i>	<b>17.7</b>	<b>38.8</b>	<b>2.4<sup>a</sup></b>	–	–	–	6.7 (S), 0.3 (L)
<i>Detarium</i> spp.	<b>0.2</b>	<b>0.1</b>	0.3 <sup>a</sup>	–	+	+	0.05 (L)
<i>Elaeis guineensis</i>	?	?	<b>4.2<sup>b</sup></b>	<b>7.2<sup>b</sup>, 13.5<sup>c</sup></b>	1.0 <sup>b</sup> , 0.4 <sup>d</sup>	0.3	0.9 (S)
<i>Parinari</i> spp.	<b>1.3</b>	<b>1.5</b>	1.5 <sup>a</sup>	?	3.4 <sup>d</sup>	–	–
<i>Panda oleosa</i>	<b>0.5</b>	<b>1.1</b>	0.2 <sup>a</sup>	–	–	–	0.1 (S)
<i>Sacoglottis gabonensis</i>	<b>6.3</b>	1.2	–	–	–	–	0.8 (S), 0.3 (L)

+ = species present in study area, but not on transects; – = absent from study area; ? = density not reported; S = small (DBH  $\geq 10$  cm,  $< 70$  cm); L = large (DBH  $\geq 70$  cm). Confirmed nut cracking of species at study site is indicated in bold. Source: <sup>a</sup>amended from Boesch et al. 1994; <sup>b</sup>amended from Humle & Matsuzawa 2004; <sup>c</sup>calculated from Hockings 2007; <sup>d</sup>this study; <sup>e</sup>calculated from Fowler & Sommer 2007; <sup>f</sup>amended and calculated from McGrew et al. 1997.



Schöning et al. 2007; Bossou, Guinea: 37.4%, Takemoto 2000; Dja, Cameroon: 14.5%, Deblauwe & Janssens 2008; Kalinzu, Uganda: 8.6%, Hashimoto et al. 2002; Gombe, Tanzania: 3%, McGrew 1992; Assirik, Senegal: 2%, McGrew 1992; Bwindi, Uganda: 1.8%, Stanford & Nkurunungi 2003). We found no seasonal variation in *Dorylus* consumption, nor was there a correlation between army ant availability and consumption. However, ant availability was based on *Dorylus* activity and not on nest density, and Seringbara chimpanzees appear only rarely to harvest ants from columns (T. Humle, personal communication). Schöning et al. (2007) proposed that army ant colony density remains more constant than column density, which might explain relatively constant levels of army ant consumption.

Year-round consumption of army ants does not preclude a role as a fallback food (Marshall & Wrangham 2007). However, army ant consumption at Seringbara showed no correlation with ripe fruit availability or with fruit consumption. None the less, consumption of army ants increased when more fallback foods (i.e. THV pith and leaf) were eaten, suggesting that army ants may be part of the chimpanzees' fallback food repertoire. Chimpanzees at Kahuzi-Biega (Democratic Republic of Congo) consumed honeybees and ants (with tools) as filler fallback foods in addition to THV (Yamagiwa & Basabose 2009). Likewise, chimpanzees at Dja ate more insects, including *Dorylus*, when fewer succulent fruits were eaten. However, army ants were only a small part of the Dja chimpanzees' diet and were harvested without the use of tools (Deblauwe & Janssens 2008). The relative importance of tool-assisted consumption of adult ants versus harvesting of grubs by hand at Seringbara remains to be elucidated, especially since pupae and larvae do not appear in faeces. Furthermore, more extensive faecal sampling may be required to draw more definitive conclusions about the role of army ants in the diet of Seringbara chimpanzees.

In sum, tool-assisted harvesting of army ants was not a direct response to scarcity of preferred foods, although army ant eating was correlated with THV consumption. Hence, the observed patterns of army ant eating did not provide support for the necessity hypothesis. Consumption of army ants may provide additional protein and micronutrients, but their nutritional value may not provide an appropriate replacement for ripe fruits, which are high in carbohydrates. Nutritional analyses of fruits, THV, leaves and insects may help to reveal the nutritional role of army ants in the chimpanzees' diet. The lack of support for the necessity hypothesis is in agreement with recent findings on tool use in wild bearded capuchins (Spagnoletti et al. 2012). Stone tool use in capuchins did not vary in relation to food availability, but was instead explained by exposure to appropriate ecological opportunities (Spagnoletti et al. 2012). The necessity hypothesis was up to now widely accepted despite lack of critical assessment. These are the first two studies to test systematically both the opportunity hypothesis and the necessity hypothesis.

### Conclusions

The absence of nut cracking was in line with the opportunity hypothesis, as low density and skewed spatial distribution of nut-producing trees (except *P. excelsa*) rendered a nut-cracking innovation and spread unlikely. Opportunities to encounter *P. excelsa* nuts were plentiful, but nuts were present only at times of high ripe fruit availability, thus providing some indirect support for the necessity hypothesis. However, the necessity hypothesis did not explain prevalence of tool-assisted insectivory. Army ants and *Macrotermes* were available when ripe fruit was scarce, yet neither was consumed as a fallback food. The opportunity hypothesis was congruent with patterns of tool-assisted insectivory. *Macrotermes*

were rare and peripheral to the chimpanzees' range, whereas army ants were abundant and widespread. Our findings suggest that environmental opportunity, rather than necessity, may be the mother of invention. The next step will be to examine to what extent environmental factors can explain patterns of foraging tool use across primate populations. By considering an explicit role for ecological conditions in explaining tool use in nonhuman primates, we may shed light on the potential importance of environmental factors in the evolution of technology in the hominin lineage.

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