

1 Landscaping the behavioural ecology of primate 2 stone tool use

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17

18 Author contributions

19 KAW is the main author and contributor and was responsible for conceptualization,
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21 original manuscript. TM provided resources and editorial advice. SC provided supervision,
22 data and resources and contributed towards conceptualization, methodology and revisions of
23 the manuscript.

24

25 **Abstract**

26 Ecology is fundamental to the development, transmission, and perpetuity of primate
27 technology. Previous studies on tool site selection have addressed the relevance of targeted
28 resources and raw materials for tools, but few have considered the broader foraging
29 landscape. In this first landscape-scale study of the ecological contexts of wild chimpanzee
30 (*Pan troglodytes verus*) tool-use, we investigate the conditions required for nut-cracking to
31 occur and persist over time at discrete locations in Bossou (Guinea). We examine this at three
32 levels: selection, frequency of use, and inactivity. We find that, further to the presence of a nut
33 tree and availability of raw materials, abundance of food-providing trees as well as proximity
34 to nest sites were significant predictors of nut-cracking occurrence. This suggests that the
35 spatial distribution of nut-cracking sites is mediated by the broader behavioural landscape and
36 is influenced by non-extractive foraging of predictable resources, as well as non-foraging
37 activities. Additionally, the number of functional tools was greater at sites with higher frequency
38 of nut-cracking and was negatively correlated with site inactivity. Our findings indicate that the
39 technological landscape of the Bossou chimpanzees shares affinities with the ‘favoured
40 places’ model of hominin site formation and provides new insights for reconstructing ancient
41 patterns of landscape use.

42

43 **Key words:** behavioural ecology, landscape-use, nut-cracking, primate archaeology, wild
44 chimpanzees

45

46 **Résumé**

47 L'écologie est fondamentale pour le développement, la transmission et la pérennité de
48 la technologie des primates. Des études antérieures ont identifié la disponibilité des
49 ressources cibles ainsi que les matières premières pour les outils comme des facteurs

50 influents dans la sélection des emplacements pour les activités technologiques. Cependant,
51 il y a peu d'études qui abordent cette recherche à l'échelle du paysage et du comportement
52 fourrager. Dans cette première étude paysagère sur l'utilisation d'outils par le chimpanzé
53 sauvage (*Pan troglodytes verus*), nous recherchons les conditions écologiques qui influencent
54 la sélection, l'utilisation et l'inactivité des emplacements utilisés pour le cassage des noix en
55 Bossou, Guinée. Nos résultats montrent qu'en plus de la présence d'un noyer et de la
56 disponibilité des matières premières, l'abondance d'arbres nourriciers ainsi que la proximité
57 des sites de nidification étaient des prédicteurs significatifs de l'occurrence du cassage des
58 noix. Cela suggère que la distribution spatiale des sites de cassage de noix est influencée par
59 le paysage comportemental et est influencée par le fourrage non-extractive de ressources
60 prévisibles, ainsi que par des activités non-fourragers. Nos résultats indiquent que le paysage
61 technologique des chimpanzés de Bossou partage des affinités avec le modèle des « lieux
62 favoris » de la formation des sites hominidés et fournit de nouvelles perspectives pour
63 reconstruire les modes d'utilisation du paysage anciens.

64

65 **Introduction**

66 Ecology plays an important role in shaping non-human primate behaviour from foraging
67 strategies, to ranging patterns, and sociality (Robbins and Hohmann, 2006; Strier, 2011). Tool-
68 use, particularly for extractive foraging, is no exception. Recent studies have highlighted that
69 ecology is key in determining whether tool-use emerges in a population, how it manifests itself,
70 and how it is maintained once it is established (S. Carvalho et al., 2007, 2011; Grund et al.,
71 2019; Koops et al., 2013, 2014).

72 Stone tool-use is often recurrent in spatially discrete locations, frequently involves the
73 reuse of tools, and leaves a recognisable archaeological footprint that can be traced back
74 thousands of years (Falótico et al., 2019; Mercader et al., 2007). However, little is known about
75 the ecological factors influencing selection and repeated use of specific locations for these

76 activities and how they fit within the broader foraging landscape. Lithic-based foraging
77 technology has been recorded in several wild, non-human primate species including
78 chimpanzees (*Pan troglodytes ssp.*; Whiten *et al.*, 1999), bearded capuchin monkeys
79 (*Sapajus libidinosus*; Ottoni and Izar, 2008), Burmese long-tailed macaques (*Macaca*
80 *fascicularis*; Gumert, Kluck and Malaivijitnond, 2009), and, most recently, in white-faced
81 capuchins (*Cebus capuchinus*; Barrett *et al.*, 2018).

82 Chimpanzees are of particular interest because they are our closest living relatives
83 (Langergraber *et al.*, 2012), and they present the largest, most diverse and ecologically
84 adaptable technological repertoire compared to any other non-human species, reflecting a
85 level of cognitive flexibility akin to the earliest hominin toolmakers (S. Carvalho *et al.*, 2013;
86 Pascual-Garrido and Almeida-Warren, 2021; Rolian and Carvalho, 2017). Chimpanzee nut-
87 cracking assemblages have been found to have close similarities to the low-density
88 assemblages characteristic of the early hominin record (S. Carvalho *et al.*, 2008; S. Carvalho
89 and McGrew, 2012). Thus, understanding how patterns of nut-cracking behaviour accumulate
90 across the landscape can provide valuable insights into the formation and spatial distribution
91 of early hominin assemblages and allow the modelling of ancient landscape use and resource
92 exploitation.

93 Previous research on chimpanzee nut-cracking has established that the spatial
94 availability of nut trees and raw materials for tools influences site location and reuse, as well
95 as frequency and distance of tool transport (S. Carvalho *et al.*, 2007, 2011). Nevertheless,
96 nut-cracking assemblages are yet to be explored within the context of the broader ecological
97 and foraging landscape. This requires the study of nut-cracking sites not only in relation to
98 direct ecological correlates such as access to raw materials and nuts, but also in relation to
99 ecological requirements of other daily activities critical to survival such as food, water, and
100 shelter.

101 Chimpanzees living in forested environments spend approximately 50% of their waking
102 hours foraging and travelling between feeding locations (Pruetz and Bertolani, 2009). Recent
103 studies have shown that chimpanzee ranging patterns are dynamic and are influenced by the

104 spatial distribution and seasonality of food (Trapanese et al., 2019), which may also determine
105 where non-foraging activities, such as nesting, take place (Basabose and Yamagiwa, 2002;
106 Hernandez-Aguilar, 2009; Janmaat et al., 2014). Their diet mainly consists of fruit (Morgan
107 and Sanz, 2006), but high-energy foods such as insects, nuts and honey acquired through
108 tool-assisted foraging are also important staples or nutritional supplements for many
109 chimpanzee populations (Sanz and Morgan, 2013). Yet, little is known about how extractive
110 foraging interacts with other feeding activities and the broader behavioural landscape. This
111 study explores this question for the first time in the context of chimpanzee nut-cracking using
112 stone tools.

113 Water is essential to life (Popkin et al., 2010). For non-human primate species living in
114 extremely arid conditions, such as savannah-dwelling chimpanzees and baboons, water is a
115 critical resource that constrains movement patterns and landscape use (Barton et al., 1992;
116 Pruetz and Herzog, 2017; Wessling et al., 2018). It has also featured in many discussions
117 surrounding early hominin evolution and behaviour (Joordens et al., 2019), and has been
118 spatially linked with early stone tool sites (Rogers et al., 1994). Similarly, the location of
119 chimpanzee nut-cracking sites has been suggested to coincide with the proximity to
120 hydrological features, such as streams and rivers (S. Carvalho et al., 2007), possibly because
121 they are the most likely sources of eroded lithic raw materials for tools (S. Carvalho, 2011),
122 although this remains to be empirically tested.

123 Chimpanzees habitually make a sleeping nest at the end of every day, and sometimes
124 make day nests for resting (Koops et al., 2012). They have been an important focus of
125 research since Sept (1992) recognised that they form clusters of debris akin to early hominin
126 assemblages, and saw their potential for understanding patterns of early hominin landscape
127 use and the origins of human shelter (McGrew, 2021). Nesting locations have subsequently
128 been linked with a range of ecological parameters such as tree species and tree architecture,
129 as well as surrounding topography and vegetation types (Badji et al., 2018; J. S. Carvalho et
130 al., 2015; Hernandez-Aguilar, 2009; Hernandez-Aguilar et al., 2013; Koops et al., 2012;
131 Ndiaye et al., 2018; Stewart et al., 2011). Other studies have found additional links between

132 nest sites and proximity to areas of high fruit availability (Basabose and Yamagiwa, 2002;
133 Furuichi and Hashimoto, 2004; Goodall, 1962; Janmaat et al., 2014). While the exact
134 conditions determining nest site suitability appears to be population-specific rather than
135 universal, these findings demonstrate that nesting activities shape chimpanzee landscape
136 use, and, in turn, are shaped by resource distribution and the local environment. Nevertheless,
137 little is known about how nesting relates to other activities such as spatially discrete forms of
138 tool use (e.g., nut-cracking and termite-fishing).

139 This is the first landscape-scale investigation of the ecological drivers of chimpanzee
140 tool-use, where we examine the conditions required for nut-cracking to occur and persist over
141 time in discrete locations at the long-term field site of Bossou (Guinea). This is divided into
142 three points of enquiry: 1) tool site selection; 2) tool site use; 3) tool site inactivity.

143 *Tool site selection* explores the ecological conditions that determine where nut-cracking
144 sites are established within the chimpanzee home-range. This is critical to understanding how
145 technological activities occur within the broader behavioural landscape, and how these
146 activities produce locally discrete assemblages that can remain archaeologically identifiable
147 for thousands of years (e.g. Falótico et al., 2019; Mercader et al., 2007). There is a growing
148 body of research on habitat selection for daily activities such as foraging, travelling, socializing
149 and sleeping, particularly within the context of anthropogenic landscapes and the implications
150 for conservation (Bryson-Morrison et al., 2017; K. B. Potts et al., 2016). However, regarding
151 technological activities, although we are beginning to learn more about raw material selection
152 for tools (S. Carvalho et al., 2008; Pascual-Garrido and Almeida-Warren, 2021), the selection
153 of locations for tool use remains unexplored.

154 *Tool site use* focuses on the ecological factors that influence the frequency with which
155 established sites attract nut-cracking activity. How often a site is used can serve as a proxy
156 for inferring preference in relation to other sites. From an archaeological perspective, generally
157 the more a location is used for debris-generating activities, the larger and more conspicuous
158 an archaeological signature becomes. This has important implications for understanding the
159 spatial clustering of activities and material evidence over time and can offer many insights into

160 the formation and perpetuity of early hominin archaeological assemblages (S. Carvalho and
161 Almeida-Warren, 2019; McGrew, 2010). Ethoarchaeological studies of chimpanzee nests
162 have found that sleeping sites are frequently revisited and the nests themselves may be
163 reused (Hernandez-Aguilar, 2009; Sept, 1992; Stewart et al., 2011). However, comparable
164 literature on the use of tool sites is scarce, except for the reuse of stone tools (S. Carvalho et
165 al., 2009), and sources of perishable raw materials (Pascual-Garrido, 2018; Pascual-Garrido
166 and Almeida-Warren, 2021).

167 *Tool site inactivity* investigates the ecological conditions that may cause the cessation
168 of nut-cracking activity at an established tool site. Chimpanzees live in dynamic landscapes
169 shaped by environmental change. Whether natural or anthropogenic, these shifts often result
170 in changes in resource distributions that may in turn lead to the development of new
171 behavioural adaptations and ranging patterns (e.g. Kalan et al., 2020). New opportunities may
172 arise (e.g., foraging food from crops: Hockings et al., 2015, 2012; nesting in novel plant
173 species: McCarthy et al., 2017), while formerly habitual activities may shift to new locations or
174 become obsolete (Gruber et al., 2012; Köhl et al., 2019). Environmental changes have been
175 identified as important drivers of our own evolutionary history (Bobe et al., 2002; Bobe and
176 Carvalho, 2019; Joordens et al., 2019; R. Potts, 1998; R. Potts et al., 2020; Reed, 1997), but
177 few studies have addressed empirically how these changes may have affected patterns of
178 landscape use and the distribution of early hominin tool sites (e.g. Rogers et al., 1994). Thus,
179 investigating the conditions that influence the cessation of activity at chimpanzee tool sites,
180 can provide important clues as to the factors that lead to their temporary or long-term
181 abandonment.

182 Throughout these steps we assess the effect of ecological parameters that have been
183 found to correlate with nut-cracking activities (nut availability; abundance of raw materials;
184 distance to water) as well as variables that encapsulate two key aspects of chimpanzee activity
185 patterns: non-extractive foraging (abundance of food resources: wild food trees; wild fruit
186 trees; THV - terrestrial herbaceous vegetation) and sleeping (distance to nesting site).

187 **Methods**

188 **Study site and subjects**

189 Bossou (7° 39' N, 8° 30' W) is located in the southeast of the Republic of Guinea (West
190 Africa), 6 km from the foothills of Mount Nimba Strict Nature Reserve (Figure 1) (Humle,
191 2011a; Yamakoshi and Sugiyama, 1995). The chimpanzee community has been studied
192 continuously in both natural (since 1976) and experimental (outdoor laboratory since 1988)
193 settings (Tetsuro Matsuzawa et al., 2011; Sugiyama and Koman, 1979). Between 1976 and
194 2003 the population size ranged from 18 to 23 individuals (Sugiyama, 2004), but has since
195 declined largely due to a catastrophic flu-like epidemic from which it never recovered (Humle,

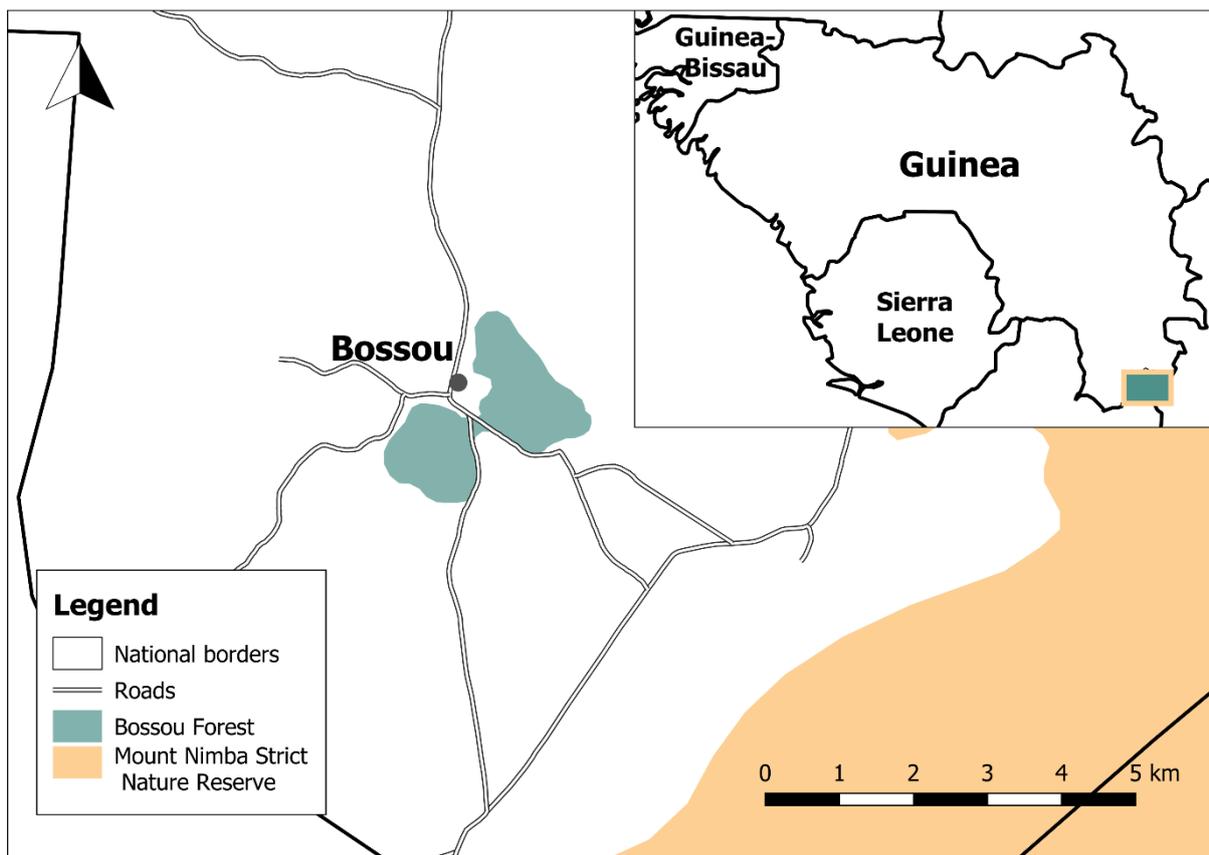


Figure 1 – Map of the Bossou Forest and surrounding area. Mount Nimba Strict Nature Reserve shapefile adapted from the WDPA database (UNEP-WCMC and IUCN, 2019)

196 2011b; Sugiyama and Fujita, 2011). At the time of this study, the population consisted of seven
197 individuals. The Bossou chimpanzees habitually crack and consume oil-palm nuts (*Elaeis*
198 *guineensis*) and are currently the only population known to use portable stones as both
199 hammers and anvils (Carvalho, Matsuzawa and McGrew, 2013; but see Ohashi, 2015 for
200 recent discoveries in Liberia). Bossou has two seasons – a short dry season lasting from
201 November to February, and a long rainy season extending from March to October (Humble,
202 2011a; Yamakoshi, 1998). Nut-cracking occurs year-round, but is most prevalent during peak
203 wet season (June – August) and at the start of the dry season (November – December) when
204 fruit is less abundant (Yamakoshi, 1998).

205 The Bossou forest has an estimated area of 16 km² and is intersected by roads (Figure
206 2; Hockings, Anderson and Matsuzawa, 2006). Within this, the chimpanzees range a core

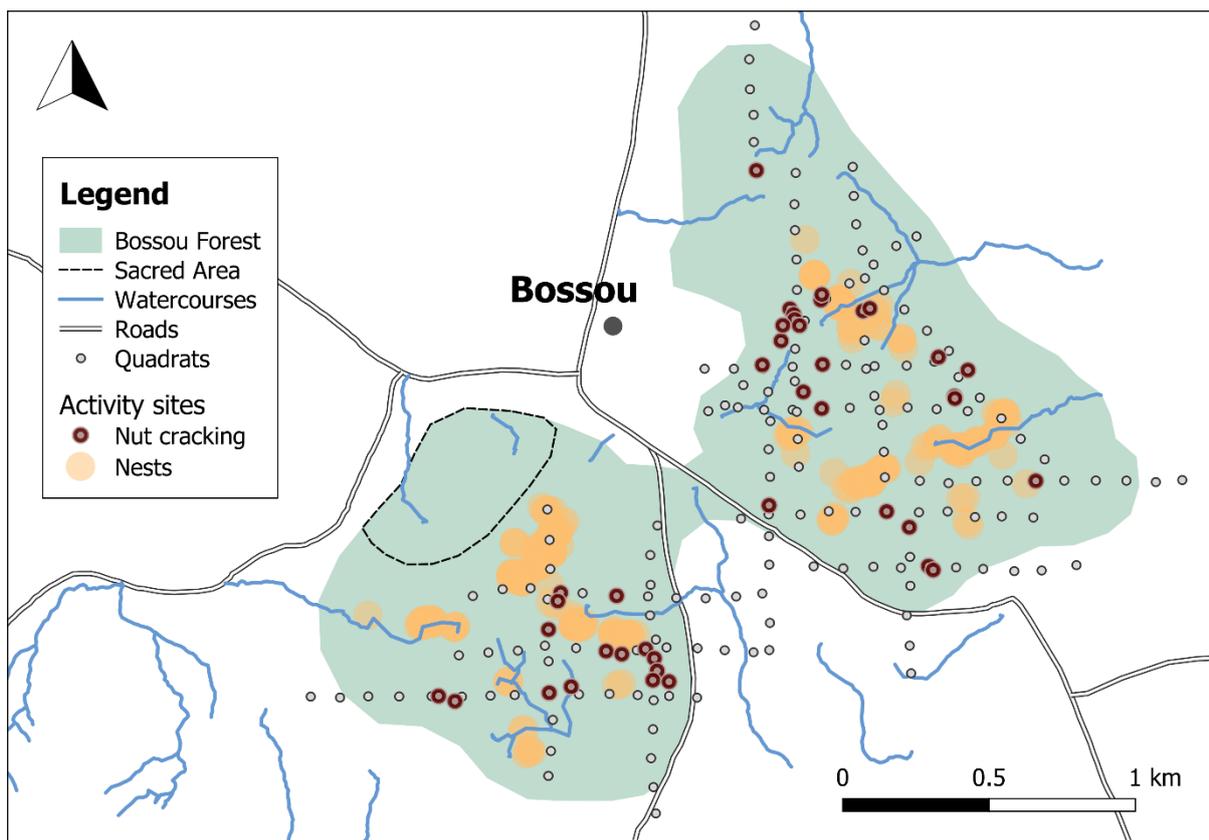


Figure 2 – Map of the study area and surrounding area, highlighting the locations of recorded nut-cracking sites, quadrats, nests, and watercourses.

207 area of approximately 7 km² (Hockings et al., 2006). The habitat is comprised of a composite
208 of primary, secondary and riverine forests, savanna and cultivated fields (Hockings et al.,
209 2012). The northern slope of Mont Gban, in the Eastern part of the forest, is considered a
210 sacred area – forêt sacrée – by the local *Manon* culture, and access is forbidden to outsiders.
211 Out of respect to this tradition, no research was conducted in this area.

212 **Data collection**

213 Data were collected over two field trips: 14DEC17-01MAY18 and 28OCT18-13DEC18,
214 encompassing 160 days of fieldwork. We employed a mixed-method approach that combined
215 direct behavioural observation through active group follows of the chimpanzee population, with
216 archaeological documentation of nut-cracking sites (indirect behavioural observations), and
217 ecological research using the transect and quadrat method. At an initial stage, we targeted
218 nut-cracking sites that had previously been documented by SC in 2006 and 2008-09. Further
219 nut-cracking sites were discovered during surveys and group follows throughout both research
220 seasons. For each nut-cracking site we established 1-km transects intersecting the site datum
221 at 500 metres. Nut-cracking sites within 100 metres of a pre-established transect were either
222 assigned to that transect or became the mid-point of a new perpendicular transect, to ensure
223 even forest coverage. All transects were oriented N-S or E-W, except for two that were
224 oriented NE-SW and NW-SE due to access difficulties (Figure 2). 5-metre radius survey
225 quadrats were established at every 100-metres along the transects starting from the midpoint
226 where the nut-cracking site was located. At each quadrat nut-cracking specific and general
227 ecological and vegetation data were collected (further details below).

228 We employed a fully digital method of data collection. Quadrat datums and all data
229 entries (food-providing vegetation, tools, raw materials) were georeferenced using an Arrow
230 Gold GNSS receiver ($\mu_{HRMS} = 2$ metres; Almeida-Warren et al., 2021; EOS Positioning
231 Systems Inc., 2017). Coordinates were instantly downloaded via Bluetooth to the GeoGرافي-M

232 application (MGISS, 2019) on an android device where further data could be entered through
233 custom made forms.

234 *Oil palms*

235 For each oil palm encountered during quadrat surveys we documented diameter at
236 breast height (DBH), and number of fruit bunches (total and ripe). For 25 of the nut trees
237 associated to nut-cracking sites we also collected information on nut availability and new
238 traces of nut-cracking on a weekly basis during the first field season (22JAN18-03MAY18) and
239 once at the beginning and end of the second season (weeks of 29OCT18; 10DEC18).
240 Additional data was collected by Henry Camara during the weeks of 30SEP19, 27APR20, and
241 25MAY20. As per Koops *et al.* (2013), we scored presence of edible nuts on the ground within
242 a 2-metre radius of the nut tree: (0) nuts absent; (1) 1-50 nuts; (2) 51-100 nuts; (3) > 100 nuts.
243 With aid from field guides, nut suitability was determined by checking a sample of randomly
244 collected nuts for whether the nuts contained an edible kernel or were rotten (following Koops
245 *et al.*, 2013). Nuts were not opened so as not to affect future availability, but the local people
246 also crack oil palm nuts and are able to identify whether or not they are edible (Humble and
247 Matsuzawa, 2004).

248 *Tools and raw materials*

249 All lithic material was recorded for size, raw material type, and portability (whether loose
250 or imbedded in the ground). Adapted from Koops *et al.* (2013), size was scored into six
251 categories: (1) 1-2 cm; (2) 3-5 cm; (3) 6-10 cm; (4) 11-20 cm; (5) 21-30 cm; (6) >30 cm. Tools
252 and bi-products of nut-cracking were defined as stones that showed at least one of the
253 following: a) traces of wear from nut-cracking; b) nutshell remains on or around them; c) could
254 be refitted with another stone with evidence of a) or b). For this study, the variable *Tools*
255 included all lithic materials used for nut-cracking excluding fragments that no longer or could
256 no longer be used for nut-cracking.

257 The collective tool assemblage was also scored for status of nut-cracking activity:
258 (Active) New signs of nut-cracking activity were recorded during the fieldwork period. Nut
259 powder or cracked nut kernels were visible on top of or around tools, and there was at least
260 one hammer and anvil pair with impact points that had not rusted over; (Inactive) There were
261 no signs of recent nut-cracking activity during the entire fieldwork period. Cracked nut kernels
262 were either absent or present but showed clear signs of decay. Iron oxide or moss developing
263 on tool impact points.

264 *Vegetation*

265 We recorded all wild non-THV plants with a DBH > 2cm of species known to be
266 consumed by the chimpanzees of Bossou. We then cross-referenced the recorded species
267 with the current list of chimpanzee food resources to identify those which were sources of fruit
268 – the preferred food-type of chimpanzees. To distinguish permanent food sources from
269 ephemeral food sources, THV was documented separately. Domesticated or crop species
270 were not included in this study.

271 *Nests*

272 Because few nests were documented at the quadrat level or along transects, additional
273 forest-wide surveys were conducted through random walks and strategic walks targeting
274 areas that were known nesting locations. When a nest was encountered, elevation and
275 direction of travel were maintained along topographical contours and all nests within 50-metres
276 of the nest and either side of the projected route were documented until no further nests were
277 visible over a 50-metre stretch (modified from Hernandez-Aguilar, 2009). For data analysis,
278 nests were divided into spatial clusters. A cluster was defined as a 50-metre radius area with
279 a minimum of 21 documented nests, representing a minimum of three sleep-events for the
280 collective chimpanzee population (N = 7) as a proxy for a habitual nesting location. This was
281 achieved on QGIS (Version 2.18.4), by creating a 50-metre buffer zone around each nest and

282 using the 'count points in polygon' function to identify zones with a minimum of 21 nests. The
283 *distance to nearest nest cluster* variable used in the following analyses was computed with
284 the 'distance to nearest hub' function and was defined as the distance from a quadrat datum
285 to the centre of the nearest nest cluster.

286 *Watercourses*

287 Watercourse data was collected in 2008/2009 by SC. With the help of field guides,
288 streams and rivers were traced on foot and recorded using the track feature on a Garmin
289 hand-held GPS device. The *distance to nearest river* variable used in the following analyses
290 was computed in QGIS and was defined as the distance between a quadrat datum to the
291 nearest point along the watercourse polylines.

292

293 **Data analysis**

294 *Tool site selection*

295 Initial inspection of the data revealed that no nut-cracking occurred in quadrats where
296 nut trees were absent. This is consistent with previous literature describing that nut-cracking
297 occurs in close proximity to a nut tree (S. Carvalho et al., 2008). Additionally, there was very
298 little variation in the number of oil palms in each quadrat with only 15% of oil palm quadrats
299 documented with more than one oil palm. For these reasons, we restricted data analysis to
300 quadrats where an oil palm was present and did not include the number of oil palms as a
301 predictor, as this would mask the potential effect of the other variables of interest. The final
302 dataset had a total of 82 quadrats, 40 of which had traces of nut-cracking activity. We used a
303 binomial generalized linear model (GLM; Zuur *et al.*, 2009a) with a logit link function to
304 investigate the effect of five main predictors: raw materials, wild food trees, wild food THV,
305 distance to nearest nest cluster, distance to nearest river, on the presence (1) versus absence

306 (0) of a tool site in a given quadrat. We also analysed three sub-models to determine whether
307 more restricted variables yielded a better model fit (Appendix, Table A2). The first sub-model
308 replaced raw materials with a subset of raw materials of size class corresponding to the three
309 most common tool size classes (95% of tools. Size class: 3, 4, 5; Appendix, Table A1). The
310 second sub-model replaced wild food-providing trees with a subset formed only of fruit-
311 providing trees. The third sub-model included raw materials of size class 3-5 and fruit-
312 providing trees. Akaike's Information Criterion for small sample sizes (AICc) was used to
313 compare models (Burnham and Anderson, 2004), whereby the model with the lowest AICc
314 was chosen as the final model.

315 *Tool site use*

316 We investigated whether the hypothesized ecological variables (i.e., nut availability, raw
317 materials, food trees, distance to nearest nest cluster, and distance to nearest river) influenced
318 the frequency a nut-cracking site was used. From a total of 361 monitoring observations, only
319 35 cases of recent nut-cracking events were identified for 17 out of the 25 monitored nut-
320 cracking sites, where frequency of recent activity ranged between 1 and 4. Because of single
321 (N = 1) sample sizes for 2 and 4 events, frequency of activity was recoded as "Low" (≤ 2
322 events; N = 10) and "High" (> 2 events; N = 7). The small sample size (N = 17) was deemed
323 too small to justify a GL(M)M, therefore we only discuss descriptive statistics for this question
324 using two-sample t-tests (or Man-Whitney U tests when assumptions of normality were not
325 met).

326 *Tool site inactivity*

327 We used a binomial GLM with 'logit' link to investigate the effect of mean nut availability,
328 raw materials, and food trees, on tool-site inactivity. The response variable included nut-
329 cracking sites that were classified as active (response = 0; N = 24) with those classified as
330 inactive (response = 1; N = 16). The final dataset included 40 tool sites. Akin the model for

331 tool site selection, we also investigated four sub-models with raw materials of size class 3-5,
332 tools, and fruit tree subsets (Appendix, Table A6). The model with the lowest AICc was then
333 chosen as the final model.

334 *General considerations*

335 All analyses were processed in R Studio (version 1.1.383; R Studio Team, 2016), using
336 R (version 4.1.0; R Core Team, 2021). Data exploration for each GLM, following the protocol
337 described in Zuur, Ieno & Elphick (2010), did not raise any concerns. Collinearity among the
338 explanatory variables was assessed by calculating the Variance inflation factors (VIF) using
339 the function 'vif' of the car package (Jon Fox and Weisberg, 2011). None of the models
340 indicated any multicollinearity issues (Maximum VIF = 1.39, Quinn and Keough, 2002). To
341 assess the significance of the full models and sub-models, we ran likelihood ratio tests (LRT)
342 using the 'anova' function which compared each model to a corresponding null model from
343 which all fixed effects were excluded (Dobson, 2002). We tested the significance of main
344 effects for each model by systematically dropping them one at a time and comparing the
345 resulting model with the full model using the 'drop1' function (Dobson, 2002). P-values for the
346 individual effects were based on the LRT results from the 'drop1' function. The AICc for model
347 selection was calculated using the 'MuMIn' package (Bartón, 2020). Model assumptions were
348 verified by plotting residuals versus fitted values and versus each covariate in the model (Zuur
349 and Ieno, 2016). Influential observations were assessed by calculating and plotting the Cook's
350 distance (Smith and Warren, 2019); all values were under the recommended threshold of 1,
351 suggesting no evidence of influential points (John Fox, 2002; Smith and Warren, 2019).

352 For tool site use, comparisons between low and high frequency of nut-cracking activity
353 were computed for each of the variables of interest using unpaired two-sample t-tests or the
354 non-parametric equivalent, Wilcoxon rank-sum test (i.e., Mann-Whitney U test). Normality
355 assumptions were assessed using the Shapiro-Wilk test. Threshold for statistical significance
356 was set to $p \leq 0.05$.

357 **Data availability**

358 The datasets generated during and/or analysed during the current study will be available
359 from the corresponding author on reasonable request. Source code will be made available at
360 <https://github.com/katarinawarren/bossou-chimps-analysis> [to be replaced with DOI].

361 **Ethical statement**

362 All tool site and ecological data were collected when chimpanzees were absent from the
363 survey locations. Efforts to ensure minimal disturbance of nut-cracking sites included: keeping
364 all tools in their original locations; not removing or cracking nuts; collecting stone samples from
365 existing tool fragments whenever possible. Research was conducted in accordance with all
366 the research requirements of Guinea, and the ethical protocols set out by The University of
367 Oxford, the Kyoto University Primate Research Institute, and the Institut de Recherche
368 Environnementale de Bossou (IREB).

369 **Results**

370 **Tool site selection**

371 The sub-model where raw materials were replaced by a subset of size class 3-5 was the
372 best fitted model according to the AICc (Appendix, Table A3), and had a clear effect on the
373 probability of a nut-cracking site occurring in a location where at least one oil palm was present
374 (full-null model comparison, LRT: $df = 5$, $deviance = 56.52$, $p < 0.001$). Raw materials had a
375 significant positive effect on tool site prediction, as did food trees, while distance to nest cluster
376 had a significant negative effect (Table 1; Figure 3). All other fixed effects were non-significant
377 (Table 1). The sub-model replacing wild food trees with the fruit trees subset yielded the worst
378 model fit in which fruit trees were not a significant predictor (Appendix, Table A3, Table A4).

379

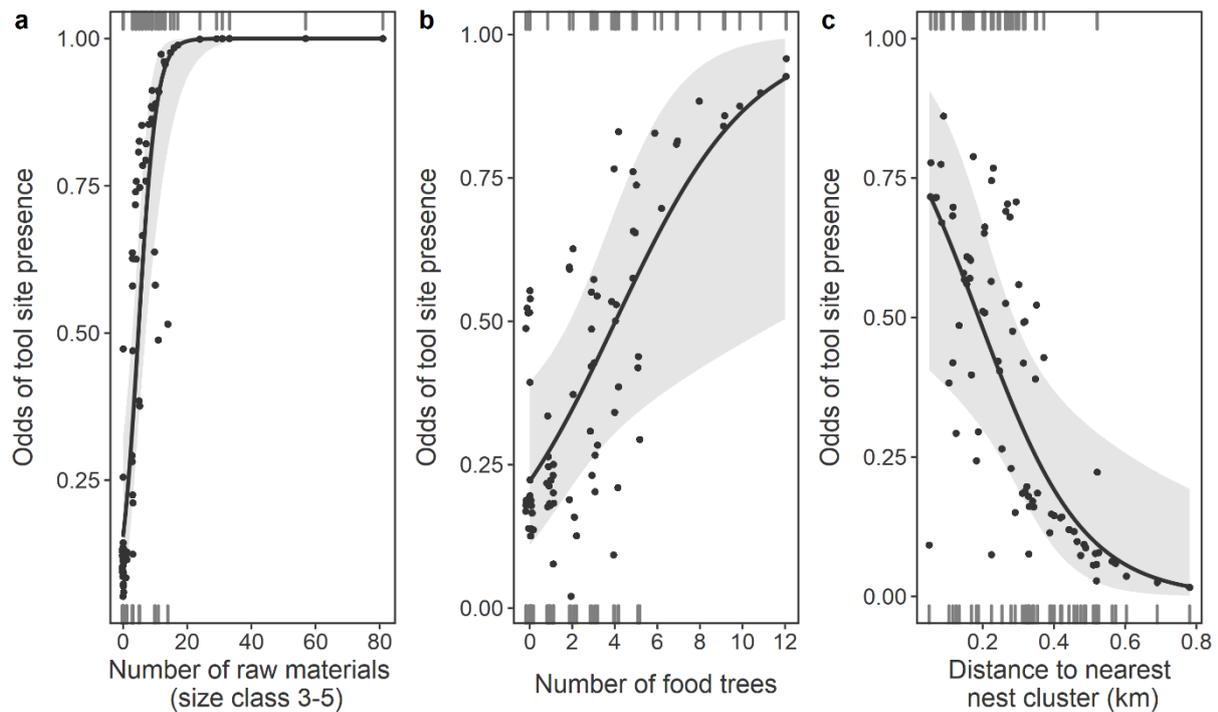


Figure 3 – Probability of tool site presence in response to: a) Raw materials of size class 3 – 5; b) Trees that are sourced by chimpanzees for food; c) Distance to the nearest nest cluster.

380 Table 1 – Results of the final GLM investigating potential predictors influencing tool site
 381 selection

Term	Estimate	SE	χ^2	p^a
Intercept	-1.139	0.472		NI ^b
Raw materials (size class 3-5)	0.358	1.298	21.929	<0.001
Wild food trees	0.313	0.407	5.758	0.016
THV	-0.103	0.383	0.392	0.531
Distance to nearest nest cluster	-0.007	0.485	6.109	0.013
Distance to nearest river	0.005	0.411	1.397	0.237

^a Results from the likelihood ratio test using the ‘drop1’ function.

^b Not indicated because it has a limited interpretation.

382 Tool site use

383 Over a total period of 15 weeks, only 33 cases of nut-cracking were recorded for 17 out
 384 of 25 monitored tool sites. 10 of the 17 sites recorded one or two nut-cracking events (low

385 frequency), with the remaining seven showing recent traces between three and four times
386 during the monitoring period (high frequency). In general, mean nut availability was
387 significantly higher at nut-cracking sites that registered a higher frequency of nut-cracking
388 activity (T-test: $p = 0.03$; Figure 4; Table A5). Furthermore, distance to nearest nest cluster
389 revealed a negative trend, whereby high frequency sites tended to be nearer to nesting
390 locations (Wilcoxon rank-sum test: $p = 0.07$). For all other variables of interest (raw materials,
391 mean fruit bunches, wild food trees and distance to nearest river) there were no significant
392 differences between the groups ($p > 0.15$; Figure 4; Table A5).

393

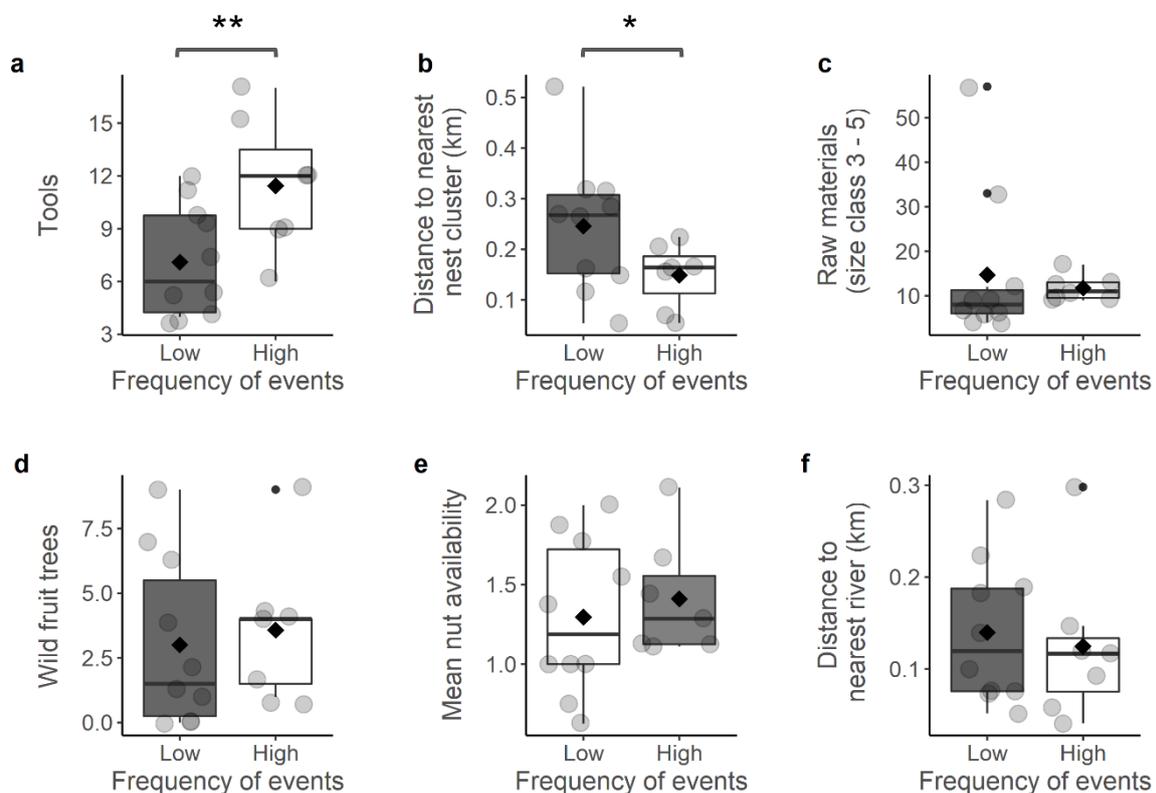


Figure 4 – Frequency of tool site use in relative to: a) Raw materials that have been used as tools; b) Distance to nearest nest cluster (km); c) Raw materials of size class 3 to 5; d) Wild trees that are sourced by chimpanzees for food; e) Wild trees that are sourced by chimpanzees for fruit; f) Distance to nearest river (km). Grey circles represent individual points, and means indicated by diamonds. ** $p < 0.05$; * $p < 0.07$.

394 Tool site inactivity

395 Out of the sub-models, the tool subset model yielded the best fit, although the AICc for
396 the tool and fruit trees model was only marginally higher and produced comparable results
397 (Appendix, Table A7, Table A8). Comparison of the tool subset model with the null model was
398 significant (LRT: $df = 3$, $deviance = 13.20$, $p < 0.01$). Overall, we found that lower values of
399 mean nut availability and a lower number of tools were both significant predictors of tool site
400 inactivity, while wild food trees had no effect (Figure 6; Table 3). However, the data
401 distributions shown in Figure 6 suggest that the model is not very robust.

402

403

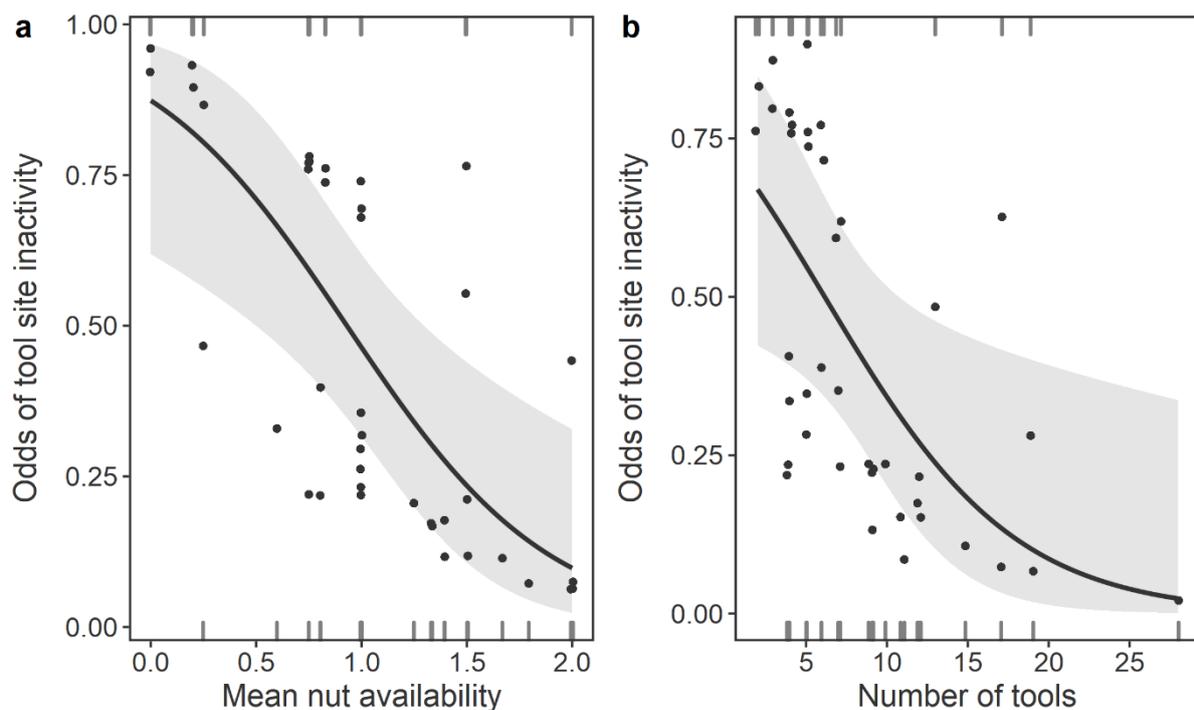


Figure 6 – Probability of tool site inactivity in response to: a) Mean nut availability; b) Raw materials that have been used as tools.

404 Table 3 – Results of the final GLM model investigating potential predictors influencing tool site
405 abandonment

Term	Estimate	SE	χ^2	p ^a
Intercept	2.957	1.263		NI ^b
Mean. nut availability	-2.186	0.851	8.947	0.003
Tools	-0.186	0.093	5.183	0.023
Wild food trees	0.093	0.109	0.752	0.386

^a Results from the likelihood ratio test using the 'drop1' function.

^b Not indicated because it has a limited interpretation.

406

407 Discussion

408 Tool site selection

409 From the initial inspection of the data, it is evident that a minimum of one oil palm,
410 specifically an oil palm in close proximity (within 10 metres), is required for nut-cracking to
411 occur in a given location. Further to this, our results show that the abundance of raw materials
412 and food trees as well as proximity to the nearest nest cluster are also important predictors for
413 whether a tool site is established at an oil palm location. This suggests that, in addition to the
414 *ecological pre-requisites* of nut-cracking, i.e., a producing oil palm and raw materials for tools,
415 other predictable resources that form part of the chimpanzee diet (wild food-providing trees),
416 as well as non-food related activities (sleep sites), are influential in the spatial distribution of
417 nut-cracking locations. In contrast, THV had a negative but non-significant effect on whether
418 tool-sites occurred. While THV is a frequently consumed food item by the chimpanzees of
419 Bossou (Humble, 2011a), it differs from other wild plant foods in that they have low calorific
420 value and an individual plant often can only be sourced once, after which it is permanently
421 depleted. In contrast, food trees are replenishable, often seasonally, and constitute reliable
422 and predictable resources that can be returned to on a seasonal basis. The fact that THV does

423 not bear a clear effect on tool site occurrence suggests that unpredictable food sources are
424 not ecological drivers of tool site selection.

425 Previous research has found that many primate species have goal-orientated foraging
426 trajectories towards spatially permanent resources and that they likely use mental maps to
427 guide their resource exploitation strategies (Trapanese et al., 2019). Our results provide
428 tentative evidence that the chimpanzees of Bossou may behave in a similar way, whereby
429 nut-cracking activities take place within a foraging strategy that primarily targets predictable,
430 high-value foods, while low-energy unpredictable foods like THV act as part of an opportunistic
431 strategy during forage-on-the-go.

432 Distance to nearest nest cluster was a significant predictor in all models, whereby the
433 likelihood of a tool site occurring increased with proximity to nest locations. Previous research
434 has found that nests sites occur in areas of high food availability (Basabose and Yamagiwa,
435 2002; J. S. Carvalho et al., 2015; Furuichi and Hashimoto, 2004; Goodall, 1962; Janmaat et
436 al., 2014). Given that nut-cracking sites are also located in areas with a greater number of
437 food providing trees, and bearing in mind that the Bossou chimpanzees source oil palms for a
438 range or other resources (e.g. fruit, pith, palm heart) and also nest in their crowns (Humble and
439 Matsuzawa, 2001, 2004; Yamakoshi and Sugiyama, 1995), it is possible that the relationship
440 between nut-cracking sites, proximity to nest sites, and food availability, is indicative that these
441 areas are activity hotspots, rich in resources and with habitat characteristics that are suitable
442 for a range of core chimpanzee activities.

443 Distance to the nearest river was not a significant predictor in any of the models. This
444 contradicts previous research in the nearby forest of Diecké, that identified that nut-cracking
445 locations occurred near waterlines (S. Carvalho et al., 2007). Emerging research on the role
446 and importance of water in shaping primate behaviour, adaptations, and landscape use, is
447 providing increasing evidence that there are differences in water-dependence between
448 populations. Rainforest-dwelling apes can usually obtain their daily hydration requirements
449 from the food they consume, and can go several days without drinking (Pontzer et al., 2021).
450 However, for primates that live in year-round or seasonally arid landscapes water is a critical

451 resource that shapes movement patterns and landscape use (Barton et al., 1992; Pruetz and
452 Herzog, 2017; Wessling et al., 2018). Fongoli chimpanzees usually drink water at least once
453 a day and often spend time near water sources during dry months to stay cool (Wessling,
454 pers. comm.; Pruetz and Bertolani, 2009). Conversely, the Bossou forest is much more humid,
455 with a long-wet season. It's many streams, and small forest area provide a hydrological
456 landscape in which chimpanzees are rarely more than 300 metres away from water.
457 Furthermore, during a total of ~500 hours of focal follows, the Bossou chimpanzees were only
458 seen to drink water on eight occasions, suggesting that they can get most of their fluids from
459 the foods they consume, in line with the general trend for non-human apes (Pontzer et al.,
460 2021).

461 While water was not a significant factor for Bossou, we predict that it could be a major
462 ecological driver regarding the spatial distribution and reuse of tool sites by savannah-living
463 chimpanzees. The Fongoli chimpanzees do not crack nuts, but they engage in termite-fishing,
464 which is also a spatially discrete technological activity tethered to the location of termite
465 mounds (Bogart and Pruetz, 2008, 2011), much like nut-cracking.

466 Nevertheless, climatic or hydrological differences cannot explain the differences
467 between Bossou and Diecké. Given the proximity of both field sites (approx. 50 km) and similar
468 climates it is unlikely that this is due to differences in aridity or water availability. However, the
469 chimpanzees of Diecké crack different nut species, *Panda oleosa* and *Coula edulis*, which are
470 absent in Bossou and may be more water dependent than the oil palm. Thus, this discrepancy
471 may be connected to the different plant species exploited and their respective ecology and
472 distribution.

473 **Tool site use**

474 Number of tools was the only variable of interest that differed significantly between sites
475 with low or high frequency of nut-cracking events. This could indicate that the visible traces of
476 nut-cracking found on tools act as visual cues for stimulating further nut-cracking behaviour.

477 The repeated use of discrete locations through stigmergy has been suggested to have led the
478 emergence of persistent places during the Middle Pleistocene (Matthew Pope et al., 2006;
479 Matthew Pope, 2017; Shaw et al., 2016). Similar hypotheses featuring local and stimulus
480 enhancement in chimpanzees have also been discussed as processes of social learning (e.g.
481 in the development of technical skills; Musgrave et al., 2020; Tennie et al., 2020; Whiten,
482 2021) as well why some plants are sourced more intensively than others for the manufacture
483 of termite fishing tools (Almeida-Warren et al., 2017). Conversely, it could indicate that
484 chimpanzees prefer sites with material that they are already familiar with. Previous research
485 in Bossou has demonstrated that chimpanzees reuse hammer-anvil pairs (tool-sets) more
486 often than others, that there is both group- and individual-level preference for certain tool-sets
487 (S. Carvalho et al., 2009), and that chimpanzees are selective of the types of materials they
488 use for nut-cracking (S. Carvalho et al., 2008). Analogous studies on chimpanzee plant
489 technologies, suggests similar patterns in the selection of materials for termite-fishing, ant-
490 dipping, honey gathering and water extraction (Almeida-Warren et al., 2017; Lamon et al.,
491 2018; Pascual-Garrido et al., 2012; Pascual-Garrido and Almeida-Warren, 2021).

492 Distance to nearest nest cluster showed a weak yet noteworthy difference, whereby the
493 frequency of nut-cracking events was marginally greater at tool sites that were closer to nest
494 locations. These results mirror those found for tool-site selection and offer further tentative
495 support that active tool sites and their frequency of use is influenced by their distribution
496 relative to current activity hotspots.

497 The number of wild food and fruit trees was largely the same for all active nut-cracking
498 sites. This suggest that, while food providing trees are good indicators of tool-site selection,
499 they may not good predictors of site use because the data collected did not capture temporal
500 changes in food availability or frequency of foraging activity. On the other hand, nests are
501 temporary features that rarely preserve for longer than six months in non-savannah
502 environments (Ihobe, 2005; Kamgang et al., 2020; Zamma and Makelele, 2012). Therefore,
503 they are a better spatial proxy for recent ranging patterns and possibly explains why
504 differences were found for nests, but not for vegetation.

505 Some consideration needs to be given as to the low number of weekly traces of nut-
506 cracking events recorded per tool site during the 15-weeks of monitoring. This is partially due
507 to the fact that not all active tool sites were monitored, with a further seven traces were found
508 through indirect observations at non-monitored sites. Our data indicates that a minimum of 40
509 nut-cracking events took place at natural nut-cracking sites during the 15 week monitoring
510 period, averaging approximately three events per week, which may be sufficient for the
511 existing chimpanzee population.

512 Furthermore, out of the nine nut-cracking events witnessed during group follows, six
513 took place at the outdoor laboratory, where nuts and stones were being artificially provisioned
514 for another project. The outdoor laboratory is located at the intersection of several routes which
515 the chimpanzees frequently travel through to access different parts of the forest. As a location
516 that has always experienced a high degree of natural thoroughfare (Tetsuro Matsuzawa,
517 2011), it may represent a pre-existing activity hotspot that has been enhanced by the
518 guaranteed encounter of tools and edible nuts. This could explain why a comparatively higher
519 number of nut-cracking events were observed there, similar to patterns recorded by Hockings
520 et al. (2009).

521 Nevertheless, due to small sample sizes and the limitations of the statistics employed,
522 more data are needed to explore these hypotheses further. For future research, it would be
523 important to investigate over a longer timescale whether and how often chimpanzees visited
524 the part of the forest where the tool site is located. This could make the use of complementary
525 data from camera traps placed in strategic locations, as full-day focal follows are not permitted
526 in Bossou.

527 **Tool site inactivity**

528 Understanding the contexts of tool site inactivity is an important step in investigating the
529 conditions required for nut-cracking to occur and persist over time in a particular location, and
530 the factors that might lead to their abandonment. Our data suggests that mean nut availability,

531 used as a proxy for tree productivity, and a high abundance of tools are important in
532 maintaining the active status of a nut-cracking site. However, there are clear exceptions that
533 appear to not quite fit the model (Figure 6), suggesting that other factors that were not
534 considered in the analysis may also be at play.

535 The Bossou forest suffers from a great deal of human activity, particularly slash-and-
536 burn agriculture, which leads to frequent and rapid changes in the spatial distribution of
537 resources and localized vegetation composition (Hockings, 2011). While oil palms are not cut
538 down during this process and are highly resistant to fire (Yamakoshi, 2011), the changes in
539 the surrounding landscape and the increase in human presence may deter chimpanzees from
540 visiting those areas, especially if they are near the forest boundary. Conversely, cultivated
541 land that contains desirable food items (e.g. banana, mango, papaya) can often attract
542 chimpanzees (Hockings, 2011), and perhaps, under these conditions, the chimpanzees
543 prioritize the prized fruit over nuts that can be found almost anywhere. Site inactivity could
544 also be an artefact of population decline, whereby fewer resources are sufficient to sustain the
545 entire population. Previous literature has suggested that the Bossou forest has a carrying
546 capacity for around 20 chimpanzees (Sugiyama and Fujita, 2011), so it is possible that the
547 current population may no longer need to depend as highly on nuts to supplement their diets.
548 A future longitudinal comparison drawing from historical and contemporary data will help
549 investigate and test this further.

550 **Conclusions**

551 Our results indicate that proximity to a nut tree, an abundance of raw materials and
552 predictable resources, as well as proximity to a nesting site are important ecological
553 parameters for the establishment of a nut-cracking site in a given location. Distance to nearest
554 nest cluster was also correlated with frequency of nut-cracking, which could potentially indicate
555 that nesting sites are important anchors for ranging and activity patterns. Similarly, tool
556 availability was significantly correlated with tool site use, as well as tool site inactivity, suggests

557 that familiarity of materials used for tools or the visual cues of tool use could be important in
558 the persistence of nut-cracking activities once a site has been established. While there was
559 no significant difference in nut availability among oil palms at active sites, the odds of tool site
560 inactivity were greater when mean nut availability was low, potentially indicating that a decline
561 in oil palm productivity at nut-cracking sites is driver of sites disuse. Together, these results
562 postulate that nut-cracking in Bossou is not only tethered to locations that provide the
563 necessary resources for this activity but is also intimately connected to a broader foraging and
564 behavioural landscape that is mediated by the spatio-temporal availability of primary target
565 resources, such as predictable food-providing trees, as well as the distribution of frequently
566 used nesting locations.

567 Preliminary comparisons with other sites regarding the importance of ecological features
568 such as the effect of water on tool use and ranging patterns, suggests that the ecology of
569 chimpanzee technology is context-specific and should be examined with this in mind. Further
570 studies investigating the technological landscapes of other chimpanzee populations, as well
571 as the integration of long-term data, will help better understand the effect of different
572 environmental and demographic contexts on the factors driving the spatial distribution and
573 reuse of tool sites, adding further detail to this picture.

574 While current evidence suggests that early hominin and chimpanzee lithic technologies
575 differ in form and function (Arroyo and de la Torre, 2016; Toth et al., 2006), it is likely they had
576 similar plant-dominated diets supported by insects and sporadic meat consumption (Panger
577 et al., 2003). Thus, it is plausible that, like chimpanzees, early hominin tool-use operated within
578 behavioural landscapes conditioned by localized environmental parameters, where foraging
579 strategies were shaped by the distribution and availability of predictable food sources, the
580 dietary dependence on extractive foraging and the availability of the necessary raw materials,
581 as well as the location of safe places for sleeping. With the aid of primate archaeological
582 inference, visualizing the spatial distribution of hominin lithic assemblages within this
583 framework will be instrumental in providing crucial insights for reconstructing the patterns of
584 landscape use and resource exploitation.

585 The present study suggests that the technological landscape of the chimpanzees of
586 Bossou shares affinities with the ‘favoured places’ model (Schick and Toth, 1993; Shick,
587 1987), which proposed that hominin tool sites formed at the centre of foraging areas where
588 hominins would process and consume food, rest and socialize, with sites being used more
589 intensively in areas with higher resource abundance. Such ‘activity hotspots’ would have acted
590 as ecological tethers, shaping early hominin movement and foraging patterns, which, in turn,
591 would have led to the formation and repeated use of tool sites over time. As the most
592 conspicuous evidence of these locations, stone tool assemblages may hold important clues
593 for uncovering behaviours beyond those associated to lithic technology and serve as starting
594 points to search for traces of other activities, such as sleeping, foraging, and insectivory, that
595 are currently extremely rare in the archaeological record. This research draws upon the work
596 of Glynn Isaac (e.g. Isaac, 1981; Isaac et al., 1981; Isaac and Harris, 1980) who pioneered
597 the application of landscape-scale approaches to the study of hominin assemblages, from
598 which the first concrete models of hominin site formation were developed. Further studies will
599 help guide future human origins research and provide an empirical framework for modelling
600 and testing hypotheses of early hominin behaviour associated to the archaeological record of
601 our earliest ancestors.

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618 **Competing interests**

619 The authors declare no competing interests.

620

621 **Bibliography**

- 622 Almeida-Warren, K., Braun, D. R., and Carvalho, S. (2021). The DistoX2: A methodological
623 solution to archaeological mapping in poorly accessible environments. *Journal of*
624 *Archaeological Science: Reports*, 35, 102688.
625 <https://doi.org/10.1016/J.JASREP.2020.102688>
- 626 Almeida-Warren, K., Sommer, V., Piel, A. K., and Pascual-Garrido, A. (2017). Raw material
627 procurement for termite fishing tools by wild chimpanzees in the Issa valley, Western
628 Tanzania. *American Journal of Physical Anthropology*, 164(2), 292–304.
629 <https://doi.org/10.1002/ajpa.23269>
- 630 Arroyo, A., and de la Torre, I. (2016). Assessing the function of pounding tools in the Early
631 Stone Age: A microscopic approach to the analysis of percussive artefacts from Beds I
632 and II, Olduvai Gorge (Tanzania). *Journal of Archaeological Science*, 74, 23–34.
633 <https://doi.org/10.1016/j.jas.2016.08.003>
- 634 Badji, L., Ndiaye, P. I., Lindshield, S. M., Ba, C. T., and Pruetz, J. D. (2018). Savanna
635 chimpanzee (*Pan troglodytes verus*) nesting ecology at Bagnomba (Kedougou, Senegal).

- 636 *Primates*, 59(3), 235–241. <https://doi.org/10.1007/s10329-017-0647-2>
- 637 Barrett, B. J., Monteza-Moreno, C. M., Dogandžic, T., Zwyns, N., Ibáñez, A., and Crofoot, M.
638 C. (2018). Habitual stone-tool-aided extractive foraging in white-faced capuchins, *Cebus*
639 *capucinus*. *Royal Society: Open Science*, 5(181002).
640 <https://doi.org/10.1098/rsos.181002>
- 641 Bartón, K. (2020). *MuMIn: Multi-Model Inference. R package version 1.43.17*.
- 642 Barton, R. A., Whiten, A., Strum, S. C., Byrne, R. W., and Simpson, A. J. (1992). Habitat use
643 and resource availability in baboons. *Animal Behaviour*, 43(5), 831–844.
644 [https://doi.org/10.1016/S0003-3472\(05\)80206-4](https://doi.org/10.1016/S0003-3472(05)80206-4)
- 645 Basabose, A. K., and Yamagiwa, J. (2002). Factors affecting nesting site choice in
646 chimpanzees at Tshibati, Kahuzi-Biega national park: Influence of sympatric gorillas.
647 *International Journal of Primatology*, 23(2), 263–282.
648 <https://doi.org/10.1023/A:1013879427335>
- 649 Bobe, R., Behrensmeyer, A. K., and Chapman, R. E. (2002). Faunal change, environmental
650 variability and late Pliocene hominin evolution. *Journal of Human Evolution*, 42(4), 475–
651 497. <https://doi.org/10.1006/jhev.2001.0535>
- 652 Bobe, R., and Carvalho, S. (2019). Hominin diversity and high environmental variability in the
653 Okote Member, Koobi Fora Formation, Kenya. *Journal of Human Evolution*, 126, 91–105.
654 <https://doi.org/10.1016/j.jhevol.2018.10.012>
- 655 Bogart, S. L., and Pruetz, J. D. (2008). Ecological context of savanna chimpanzee (*Pan*
656 *troglydytes verus*) termite fishing at Fongoli, Senegal. *American Journal of Primatology*,
657 70(6), 605–612. <https://doi.org/10.1002/ajp.20530>
- 658 Bogart, S. L., and Pruetz, J. D. (2011). Insectivory of savanna chimpanzees (*Pan troglodytes*
659 *verus*) at Fongoli, Senegal. *American Journal of Physical Anthropology*, 145(1), 11–20.
660 <https://doi.org/10.1002/ajpa.21452>
- 661 Bryson-Morrison, N., Tzanopoulos, J., Matsuzawa, T., and Humle, T. (2017). Activity and
662 Habitat Use of Chimpanzees (*Pan troglodytes verus*) in the Anthropogenic Landscape of
663 Bossou, Guinea, West Africa. *International Journal of Primatology*, 38(2), 282–302.

- 664 <https://doi.org/10.1007/s10764-016-9947-4>
- 665 Burnham, K. P., and Anderson, D. R. (Eds.). (2004). *Model Selection and Multimodel*
666 *Inference* (2nd ed). Springer. <https://doi.org/10.1007/b97636>
- 667 Carvalho, J. S., Meyer, C. F. J., Vicente, L., and Marques, T. A. (2015). Where to nest?
668 Ecological determinants of chimpanzee nest abundance and distribution at the habitat
669 and tree species scale. *American Journal of Primatology*, 77(2), 186–199.
670 <https://doi.org/10.1002/ajp.22321>
- 671 Carvalho, S. (2011). Diécké Forest, Guinea: Delving into Chimpanzee Behavior Using Stone
672 Tool Surveys. In T Matsuzawa, T. Humle, and Y. Sugiyama (Eds.), *The Chimpanzees of*
673 *Bossou and Nimba* (pp. 301–312). Springer Japan. [https://doi.org/10.1007/978-4-431-](https://doi.org/10.1007/978-4-431-53921-6_31)
674 [53921-6_31](https://doi.org/10.1007/978-4-431-53921-6_31)
- 675 Carvalho, S., and Almeida-Warren, K. (2019). Primate Archaeology. In J. Chun Choe (Ed.),
676 *Encyclopedia of Animal Behavior* (2nd ed., Vol. 1, pp. 397–407). Elsevier.
677 <https://doi.org/10.1016/B978-0-12-809633-8.90156-0>
- 678 Carvalho, S., Biro, D., McGrew, W. C., and Matsuzawa, T. (2009). Tool-composite reuse in
679 wild chimpanzees (*Pan troglodytes*): Archaeologically invisible steps in the technological
680 evolution of early hominins? *Animal Cognition*, 12(1 SUPPL), S103–S114.
681 <https://doi.org/10.1007/s10071-009-0271-7>
- 682 Carvalho, S., Cunha, E., Sousa, C., and Matsuzawa, T. (2008). Chaînes opératoires and
683 resource-exploitation strategies in chimpanzee (*Pan troglodytes*) nut cracking. *Journal of*
684 *Human Evolution*, 55(1), 148–163. <https://doi.org/10.1016/j.jhevol.2008.02.005>
- 685 Carvalho, S., Cunha, E., Sousa, C., and Matsuzawa, T. (2011). Extensive surveys of
686 chimpanzee stone tools: from the telescope to the magnifying glass. In Tetsuro
687 Matsuzawa, T. Humle, and Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba*
688 (1st ed., pp. 145–155). Springer Japan.
- 689 Carvalho, S., Matsuzawa, T., and McGrew, W. C. (2013). From pounding to knapping: How
690 chimpanzees can help us to model hominin lithics. In C. Sanz, J. Call, and C. Boesch
691 (Eds.), *Tool Use in Animals* (pp. 225–241). Cambridge University Press.

- 692 <https://doi.org/10.1017/CBO9780511894800.015>
- 693 Carvalho, S., and McGrew, W. C. (2012). The origins of the Oldowan: Why chimpanzees (*Pan*
694 *troglydytes*) still are good models for technological evolution in Africa. In M. Domínguez-
695 Rodrigo (Ed.), *Stone Tools and Fossil Bones: Debates in the Archaeology of Human*
696 *Origins* (pp. 201–221). Cambridge University Press.
697 <https://doi.org/10.1017/CBO9781139149327.010>
- 698 Carvalho, S., Sousa, C., and Matsuzawa, T. (2007). New Nut-Cracking Sites in Diecké Forest,
699 Guinea: An Overview of the Surveys. *Pan Africa News*, 14(1).
- 700 Dobson, A. J. (2002). An introduction to generalized linear models. In *New York*. Chapman &
701 Hall/CRC.
- 702 EOS Positioning Systems Inc. (2017). *Arrow Gold*. [https://eos-gnss.com/wp-](https://eos-gnss.com/wp-content/uploads/2017/11/eos-arrow-gold-revC-v4.pdf)
703 [content/uploads/2017/11/eos-arrow-gold-revC-v4.pdf](https://eos-gnss.com/wp-content/uploads/2017/11/eos-arrow-gold-revC-v4.pdf)
- 704 Falótico, T., Proffitt, T., Ottoni, E. B., Staff, R. A., and Haslam, M. (2019). Three thousand
705 years of wild capuchin stone tool use. *Nature Ecology & Evolution*, 3(7), 1034–1038.
706 <https://doi.org/10.1038/s41559-019-0904-4>
- 707 Fox, John. (2002). *An R and S-Plus companion to applied regression*. Sage Publications.
- 708 Fox, Jon, and Weisberg, S. (2011). *An R Companion to Applied Regression*. In *Sage* (2nd
709 ed.). Sage.
- 710 Furuichi, T., and Hashimoto, C. (2004). Botanical and Topographical Factors Influencing
711 Nesting-Site Selection by Chimpanzees in Kalinzu Forest, Uganda. *International Journal*
712 *of Primatology* 2004 25:4, 25(4), 755–765.
713 <https://doi.org/10.1023/B:IJOP.0000029121.25284.7F>
- 714 Goodall, J. M. (1962). Nest building behavior in the free ranging chimpanzee. *Annals of the*
715 *New York Academy of Sciences*, 102(2), 455–467. [https://doi.org/10.1111/j.1749-](https://doi.org/10.1111/j.1749-6632.1962.tb13652.x)
716 [6632.1962.tb13652.x](https://doi.org/10.1111/j.1749-6632.1962.tb13652.x)
- 717 Gruber, T., Potts, K. B., Krupenye, C., Byrne, M. R., Mackworth-Young, C., McGrew, W. C.,
718 Reynolds, V., and Zuberbühler, K. (2012). The influence of ecology on chimpanzee (*Pan*
719 *troglydytes*) cultural behavior: A case study of five ugandan chimpanzee communities.

- 720 *Journal of Comparative Psychology*, 126(4), 446–457. <https://doi.org/10.1037/a0028702>
- 721 Grund, C., Neumann, C., Zuberbühler, K., and Gruber, T. (2019). Necessity creates
722 opportunities for chimpanzee tool use. *Behavioral Ecology*, 30(4), 1136–1144.
723 <https://doi.org/10.1093/beheco/arz062>
- 724 Gumert, M., Kluck, M., and Malaivijitnond, S. (2009). The Physical Characteristics and Usage
725 Patterns of Stone Axe and Pounding Hammers Used by Long-Tailed Macaques in the
726 Andaman Sea Region of Thailand. *American Journal of Primatology*, 608(71), 594–608.
727 <https://doi.org/10.1002/ajp.20694>
- 728 Hernandez-Aguilar, R. A. (2009). Chimpanzee nest distribution and site reuse in a dry habitat:
729 implications for early hominin ranging. *J. Hum. Evol.*, 57(4), 350–364.
730 <https://doi.org/10.1016/j.jhevol.2009.03.007>
- 731 Hernandez-Aguilar, R. A., Moore, J., and Stanford, C. B. (2013). Chimpanzee nesting patterns
732 in savanna habitat: Environmental influences and preferences. *American Journal of*
733 *Primatology*, 75(10), 979–994. <https://doi.org/10.1002/ajp.22163>
- 734 Hockings, K. J. (2011). The crop-raiders of the sacred hill. In Tetsuro Matsuzawa, T. Humle,
735 and Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 211–220).
736 Springer Japan.
- 737 Hockings, K. J., Anderson, J. R., and Matsuzawa, T. (2006). Road crossing in chimpanzees:
738 A risky business. In *Current Biology* (Vol. 16, Issue 17).
739 <https://doi.org/10.1016/j.cub.2006.08.019>
- 740 Hockings, K. J., Anderson, J. R., and Matsuzawa, T. (2009). Use of wild and cultivated foods
741 by chimpanzees at Bossou, Republic of Guinea: feeding dynamics in a human-influenced
742 environment. *American Journal of Primatology*, 71(8), 636–646.
743 <https://doi.org/10.1002/ajp.20698>
- 744 Hockings, K. J., Anderson, J. R., and Matsuzawa, T. (2012). Socioecological adaptations by
745 chimpanzees, *Pan troglodytes verus*, inhabiting an anthropogenically impacted habitat.
746 *Animal Behaviour*, 83(3), 801–810. <https://doi.org/10.1016/j.anbehav.2012.01.002>
- 747 Hockings, K. J., McLennan, M. R., Carvalho, S., Ancrenaz, M., Bobe, R., Byrne, R. W.,
32

- 748 Dunbar, R. I. M., Matsuzawa, T., McGrew, W. C., Williamson, E. A., Wilson, M. L., Wood,
749 B., Wrangham, R. W., and Hill, C. M. (2015). Apes in the Anthropocene: Flexibility and
750 survival. In *Trends in Ecology and Evolution* (Vol. 30, Issue 4, pp. 215–222). Elsevier Ltd.
751 <https://doi.org/10.1016/j.tree.2015.02.002>
- 752 Humle, T. (2011a). Location and Ecology. In Tetsuro Matsuzawa, T. Humle, and Y. Sugiyama
753 (Eds.), *The Chimpanzees of Bossou and Nimba* (1st ed., pp. 13–22). Springer Japan.
- 754 Humle, T. (2011b). The 2003 Epidemic of a Flu-Like Respiratory Disease at Bossou. In
755 Tetsuro Matsuzawa, T. Humle, and Y. Sugiyama (Eds.), *The Chimpanzees of Bossou*
756 *and Nimba* (pp. 325–333). Springer Japan.
- 757 Humle, T., and Matsuzawa, T. (2001). Behavioural Diversity among the Wild Chimpanzee
758 Populations of Bossou and Neighbouring Areas, Guinea and Côte d'Ivoire, West Africa.
759 *Folia Primatologica*, 72(2), 57–68. <https://doi.org/10.1159/000049924>
- 760 Humle, T., and Matsuzawa, T. (2004). Oil palm use by adjacent communities of chimpanzees
761 at Bossou and Nimba Mountains, West Africa. *International Journal of Primatology*, 25(3),
762 551–581. <https://doi.org/10.1023/B:IJOP.0000023575.93644.f4>
- 763 Ihobe, H. (2005). Life Span of Chimpanzee Beds at the Mahale Mountains National Park,
764 Tanzania. *Pan Africa News*, 12(1), 10–12.
- 765 Isaac, G. L. (1981). Stone Age visiting cards: approaches to the study of early land use
766 patterns. In I. Hodder, G. L. Isaac, and N. Hammond (Eds.), *Pattern of the past: studies*
767 *in honour of David Clarke* (pp. 131–155). Cambridge University Press.
- 768 Isaac, G. L., and Harris, J. W. K. (1980). A method for determining the characteristics of
769 artefacts between sites in the Upper Member of the Koobi Fora Formation, East Lake
770 Turkana. In R. E. F. Leakey and B. A. Ogot (Eds.), *Proceedings of the 8th Panafrican*
771 *Congress on Prehistory and Quaternary Studies* (pp. 19–22).
- 772 Isaac, G. L., Harris, J. W. K., and Marshall, F. (1981). Small is informative: the application of
773 the study of mini-sites and least effort criteria in the interpretation of the Early Pleistocene
774 archaeological record at Koobi Fora, Kenya. In B. Isaac (Ed.), *The Archaeology of Human*
775 *Origins: Papers by Glynn Isaac* (pp. 101–119). Cambridge University Press.

- 776 Janmaat, K. R. L., Polansky, L., Ban, S. D., and Boesch, C. (2014). Wild chimpanzees plan
777 their breakfast time, type, and location. *Proceedings of the National Academy of*
778 *Sciences*, 111(46), 16343–16348. <https://doi.org/10.1073/pnas.1407524111>
- 779 Joordens, J. C. A., Feibel, C. S., Vonhof, H. B., Schulp, A. S., and Kroon, D. (2019). Relevance
780 of the eastern African coastal forest for early hominin biogeography. *Journal of Human*
781 *Evolution*, 131, 176–202. <https://doi.org/10.1016/J.JHEVOL.2019.03.012>
- 782 Kalan, A. K., Kulik, L., Arandjelovic, M., Boesch, C., Haas, F., Dieguez, P., Barratt, C. D.,
783 Abwe, E. E., Agbor, A., Angedakin, S., Aubert, F., Ayimisin, E. A., Bailey, E., Bessone,
784 M., Brazzola, G., Buh, V. E., Chancellor, R., Cohen, H., Coupland, C., ... Kühl, H. S.
785 (2020). Environmental variability supports chimpanzee behavioural diversity. *Nature*
786 *Communications*, 11(1), 4451. <https://doi.org/10.1038/s41467-020-18176-3>
- 787 Kamgang, S. A., Carme, T. C., Bobo, K. S., Abwe, E. E., Gonder, M. K., and Sinsin, B. (2020).
788 Assessment of in situ nest decay rate for chimpanzees (*Pan troglodytes ellioti* Matschie,
789 1914) in Mbam-Djerem National Park, Cameroon: implications for long-term monitoring.
790 *Primates*, 61(2), 189–200. <https://doi.org/10.1007/s10329-019-00768-3>
- 791 Koops, K., McGrew, W. C., de Vries, H., and Matsuzawa, T. (2012). Nest-Building by
792 Chimpanzees (*Pan troglodytes verus*) at Seringbara, Nimba Mountains: Antipredation,
793 Thermoregulation, and Antivector Hypotheses. *International Journal of Primatology*,
794 33(2), 356–380. <https://doi.org/10.1007/s10764-012-9585-4>
- 795 Koops, K., McGrew, W. C., and Matsuzawa, T. (2013). Ecology of culture: do environmental
796 factors influence foraging tool use in wild chimpanzees, *Pan troglodytes verus*? *Animal*
797 *Behaviour*, 85(1), 175–185. <https://doi.org/10.1016/j.anbehav.2012.10.022>
- 798 Koops, K., Visalberghi, E., and van Schaik, C. P. (2014). The ecology of primate material
799 culture. *Biology Letters*, 10(11), 20140508. <https://doi.org/10.1098/rsbl.2014.0508>
- 800 Kühl, H. S., Boesch, C., Kulik, L., Haas, F., Arandjelovic, M., Dieguez, P., Bocksberger, G.,
801 McElreath, M. B., Agbor, A., Angedakin, S., Ayimisin, E. A., Bailey, E., Barubiyo, D.,
802 Bessone, M., Brazzola, G., Chancellor, R., Cohen, H., Coupland, C., Danquah, E., ...
803 Kalan, A. K. (2019). Human impact erodes chimpanzee behavioral diversity. *Science*,
34

- 804 363(6434), 1453–1455. <https://doi.org/10.1126/science.aau4532>
- 805 Lamon, N., Neumann, C., Gier, J., Zuberbühler, K., and Gruber, T. (2018). Wild chimpanzees
806 select tool material based on efficiency and knowledge. *Proceedings of the Royal Society*
807 *B: Biological Sciences*, 285(1888), 20181715. <https://doi.org/10.1098/rspb.2018.1715>
- 808 Langergraber, K. E., Prufer, K., Rowney, C., Boesch, C., Crockford, C., Fawcett, K., Inoue, E.,
809 Inoue-Muruyama, M., Mitani, J. C., Muller, M. N., Robbins, M. M., Schubert, G., Stoinski,
810 T. S., Viola, B., Watts, D., Wittig, R. M., Wrangham, R. W., Zuberbühler, K., Paabo, S.,
811 and Vigilant, L. (2012). Generation times in wild chimpanzees and gorillas suggest earlier
812 divergence times in great ape and human evolution. *Proceedings of the National*
813 *Academy of Sciences*, 109(39), 15716–15721. <https://doi.org/10.1073/pnas.1211740109>
- 814 Matsuzawa, Tetsuro. (2011). Field Experiments of Tool-Use. In T Matsuzawa, T. Humle, and
815 Y. Sugiyama (Eds.), *The Chimpanzees of Bossou and Nimba* (pp. 157–164). Springer
816 Japan.
- 817 Matsuzawa, Tetsuro, Humle, T., and Sugiyama, Y. (Eds.). (2011). *The Chimpanzees of*
818 *Bossou and Nimba*. Springer Japan.
- 819 McCarthy, M. S., Lester, J. D., and Stanford, C. B. (2017). Chimpanzees (*Pan troglodytes*)
820 Flexibly Use Introduced Species for Nesting and Bark Feeding in a Human-Dominated
821 Habitat. *International Journal of Primatology*, 38(2), 321–337.
822 <https://doi.org/10.1007/s10764-016-9916-y>
- 823 McGrew, W. C. (2010). In search of the last common ancestor: New findings on wild
824 chimpanzees. In *Philosophical Transactions of the Royal Society B: Biological Sciences*
825 (Vol. 365, Issue 1556, pp. 3267–3276). The Royal Society.
826 <https://doi.org/10.1098/rstb.2010.0067>
- 827 McGrew, W. C. (2021). Sheltering Chimpanzees. *Primates*, 1, 3.
828 <https://doi.org/10.1007/s10329-021-00903-z>
- 829 Mercader, J., Barton, H., Gillespie, J., Harris, J., Kuhn, S., Tyler, R., and Boesch, C. (2007).
830 4,300-year-old chimpanzee sites and the origins of percussive stone technology.
831 *Proceedings of the National Academy of Sciences of the United States of America*,
35

- 832 104(9), 3043–3048. <https://doi.org/10.1073/pnas.0607909104>
- 833 MGISS. (2019). *GeoGrafi-M - MGISS*. <https://mgiss.co.uk/product/geografi-m/>
- 834 Morgan, D. B., and Sanz, C. (2006). Chimpanzee feeding ecology and comparisons with
835 sympatric gorillas in the Goulougo Triangle, Republic of Congo. In H. Gottfried, M. M.
836 Robbins, and C. Boesch (Eds.), *Feeding Ecology in Apes and Other Primates* (pp. 97–
837 122). Cambridge University Press.
- 838 Musgrave, S., Lonsdorf, E., Morgan, D., Prestipino, M., Bernstein-Kurtycz, L., Mundry, R., and
839 Sanz, C. (2020). Teaching varies with task complexity in wild chimpanzees. *Proceedings*
840 *of the National Academy of Sciences*, 117(2), 969–976.
841 <https://doi.org/10.1073/pnas.1907476116>
- 842 Ndiaye, P. I., Badji, L., Lindshield, S. M., and Pruett, J. D. (2018). Nest-Building Behaviour by
843 Chimpanzees (*Pan troglodytes verus*) in the Non-Protected Area of Diaguiri (Kedougou,
844 Senegal): Implications for Conservation. *Folia Primatologica*, 89(5), 316–326.
845 <https://doi.org/10.1159/000490945>
- 846 Ohashi, G. (2015). Pestle-pounding and nut-cracking by wild chimpanzees at Kpala, Liberia.
847 *Primates*, 56(2), 113–117. <https://doi.org/10.1007/s10329-015-0459-1>
- 848 Ottoni, E. B., and Izar, P. (2008). Capuchin monkey tool use: Overview and implications.
849 *Evolutionary Anthropology*, 17(4), 171–178. <https://doi.org/10.1002/evan.20185>
- 850 Panger, M. A., Brooks, A. S., Richmond, B. G., and Wood, B. (2003). Older than the Oldowan?
851 Rethinking the emergence of hominin tool use. *Evolutionary Anthropology: Issues, News,*
852 *and Reviews*, 11(6), 235–245. <https://doi.org/10.1002/evan.10094>
- 853 Pascual-Garrido, A. (2018). Scars on plants sourced for termite fishing tools by chimpanzees:
854 Towards an archaeology of the perishable. *American Journal of Primatology*, 80(9),
855 e22921. <https://doi.org/10.1002/ajp.22921>
- 856 Pascual-Garrido, A., and Almeida-Warren, K. (2021). Archaeology of the Perishable. *Current*
857 *Anthropology*, 62(3), 333–362. <https://doi.org/10.1086/713766>
- 858 Pascual-Garrido, A., Buba, U., Nodza, G., and Sommer, V. (2012). Obtaining raw material:
859 Plants as tool sources for Nigerian Chimpanzees. *Folia Primatologica*, 83(1), 24–44.

- 860 Pontzer, H., Brown, M. H., Wood, B. M., Raichlen, D. A., Mabulla, A., Harris, J. A., Dunsworth,
861 H., Hare, B., Walker, K., Luke, A., Dugas, L. R., Schoeller, D., Plange-Rhule, J., Bovet,
862 P., Forrester, T. E., Thompson, M. E., Shumaker, R. W., Rothman, J. M., Vogel, E., ...
863 Ross, S. R. (2021). Evolution of water conservation in humans. *Current Biology*, 31, 1–
864 7. <https://doi.org/10.1016/j.cub.2021.02.045>
- 865 Pope, Matthew. (2017). Thresholds in behaviour, thresholds of visibility: landscape processes,
866 asymmetries in landscape records and niche construction in the formation of the
867 Palaeolithic record. In M Pope, C. Gamble, and J. McNabb (Eds.), *Crossing the Human*
868 *Threshold Dynamic Transformation and Persistent Places During the Late Middle*
869 *Pleistocene*. Routledge.
- 870 Pope, Matthew, Russel, K., and Watson, K. (2006). Biface form and structured behaviour in
871 the Acheulean. *Lithics: The Journal of the Lithic Studies Society*, 27, 44–57.
- 872 Popkin, B. M., D’Anci, K. E., and Rosenberg, I. H. (2010). Water, hydration, and health.
873 *Nutrition Reviews*, 68(8), 439–458. <https://doi.org/10.1111/J.1753-4887.2010.00304.X>
- 874 Potts, K. B., Baken, E., Levang, A., and Watts, D. P. (2016). Ecological factors influencing
875 habitat use by chimpanzees at Ngogo, Kibale National Park, Uganda. *American Journal*
876 *of Primatology*, 78(4), 432–440. <https://doi.org/10.1002/AJP.22513>
- 877 Potts, R. (1998). Environmental hypotheses of hominin evolution. *American Journal of*
878 *Physical Anthropology*, 107, 93–136. [https://doi.org/10.1002/\(SICI\)1096-](https://doi.org/10.1002/(SICI)1096-8644(1998)107:27+<93::AID-AJPA5>3.0.CO;2-X)
879 [8644\(1998\)107:27+<93::AID-AJPA5>3.0.CO;2-X](https://doi.org/10.1002/(SICI)1096-8644(1998)107:27+<93::AID-AJPA5>3.0.CO;2-X)
- 880 Potts, R., Dommain, R., Moerman, J. W., Behrensmeyer, A. K., Deino, A. L., Riedl, S., Beverly,
881 E. J., Brown, E. T., Deocampo, D., Kinyanjui, R., Lupien, R., Owen, R. B., Rabideaux,
882 N., Russell, J. M., Stockhecke, M., deMenocal, P., Faith, J. T., Garcin, Y., Noren, A., ...
883 Uno, K. (2020). Increased ecological resource variability during a critical transition in
884 hominin evolution. *Science Advances*, 6(43), eabc8975.
885 <https://doi.org/10.1126/sciadv.abc8975>
- 886 Pruetz, J. D., and Bertolani, P. (2009). Chimpanzee (*Pan troglodytes verus*) Behavioral
887 Responses to Stresses Associated with Living in a Savannah-Mosaic Environment:

- 888 Implications for Hominin Adaptations to Open Habitats. *PaleoAnthropology*, 2009, 252–
889 262. <https://doi.org/10.4207/pa.2009.art33>
- 890 Pruetz, J. D., and Herzog, N. M. (2017). Savanna Chimpanzees at Fongoli, Senegal, Navigate
891 a Fire Landscape. *Current Anthropology*, 58(16), S337–S350.
892 <https://doi.org/10.1086/692112>
- 893 Quinn, G. P., and Keough, M. J. (2002). *Experimental Design and Data Analysis for Biologists*.
894 R Studio Team. (2016). *RStudio: Integrated Development for R* (1.1.383). RStudio, Inc.
- 895 Reed, K. E. (1997). Early hominid evolution and ecological change through the African Plio-
896 Pleistocene. *Journal of Human Evolution*, 32(2–3), 289–322.
897 <https://doi.org/10.1006/jhev.1996.0106>
- 898 Robbins, M. M., and Hohmann, G. (2006). Primate feeding ecology: an integrative approach.
899 In G. Hohmann, M. M. Robbins, and C. Boesch (Eds.), *Feeding Ecology in Apes and*
900 *Other Primates* (pp. 1–13). Cambridge University Press.
- 901 Rogers, M. J., Harris, J. W. K., and Feibel, C. S. (1994). Changing patterns of land use by
902 Plio-Pleistocene hominids in the Lake Turkana Basin. In *Journal of Human Evolution* (Vol.
903 27, Issues 1–3, pp. 139–158). <https://doi.org/10.1006/jhev.1994.1039>
- 904 Rolian, C., and Carvalho, S. (2017). Tool use and manufacture in the last common ancestor
905 of Pan and Homo. In M. Muller, R. Wrangham, and D. Pilbeam (Eds.), *Chimpanzees and*
906 *Human Evolution* (pp. 602– 644). Belknap Press of Harvard University Press.
- 907 Sanz, C., and Morgan, D. B. (2013). Ecological and social correlates of chimpanzee tool use.
908 *Phil Trans R Soc B*, 268, 20120416. <https://doi.org/10.1098/rstb.2012.0416>
- 909 Schick, K. D., and Toth, N. (1993). *Making silent stones speak*. Simon and Schuster.
- 910 Sept, J. M. (1992). Was there no place like home?: A new perspective on early hominid
911 archaeological sites from the mapping of chimpanzee nests. *Current Anthropology*, 33(2),
912 187–207. <https://doi.org/10.1086/204050>
- 913 Shaw, A., Bates, M., Conneller, C., Gamble, C., Julien, M.-A., McNabb, J., Pope, M., and
914 Scott, B. (2016). The archaeology of persistent places: the Palaeolithic case of La Cotte
915 de St Brelade, Jersey. *Antiquity*, 90(354), 1437–1453.

- 916 <https://doi.org/10.15184/aqy.2016.212>
- 917 Shick, K. D. (1987). Modeling the formation of Early Stone Age artifact concentrations. *Journal*
918 *of Human Evolution*, 16(7–8), 789–807. [https://doi.org/10.1016/0047-2484\(87\)90024-8](https://doi.org/10.1016/0047-2484(87)90024-8)
- 919 Smith, C., and Warren, M. (2019). *GLMs in R for Ecology*. Amazon Publishing.
- 920 Stewart, F. A., Piel, A. K., and McGrew, W. C. (2011). Living archaeology: Artefacts of specific
921 nest site fidelity in wild chimpanzees. *Journal of Human Evolution*, 61(4), 388–395.
922 <https://doi.org/10.1016/j.jhevol.2011.05.005>
- 923 Strier, K. B. (2011). *Primate behavioral ecology*. Allyn and Bacon.
- 924 Sugiyama, Y. (2004). Demographic parameters and life history of chimpanzees at Bossou,
925 Guinea. *American Journal of Physical Anthropology*, 124(2), 154–165.
926 <https://doi.org/10.1002/ajpa.10345>
- 927 Sugiyama, Y., and Fujita, S. (2011). The Demography and Reproductive Parameters of
928 Bossou Chimpanzees. In Tetsuro Matsuzawa, T. Humle, and Y. Sugiyama (Eds.), *The*
929 *Chimpanzees of Bossou and Nimba* (pp. 23–34). Springer Japan.
- 930 Sugiyama, Y., and Koman, J. (1979). Tool-using and -making behavior in wild chimpanzees
931 at Bossou, Guinea. *Primates*, 20(4), 513–524. <https://doi.org/10.1007/BF02373433>
- 932 Team, R. C. (2021). *R: A language and environment for statistical computing* (4.1.0). R
933 Foundation for Statistical Computing.
- 934 Tennie, C., Bandini, E., van Schaik, C. P., and Hopper, L. M. (2020). The zone of latent
935 solutions and its relevance to understanding ape cultures. *Biology and Philosophy*, 35(5),
936 55. <https://doi.org/10.1007/s10539-020-09769-9>
- 937 Toth, N., Schick, K. D., and Semaw, S. (2006). A comparative study of the stone tool-making
938 skills of Pan, Australopithecus, and Homo sapiens. In N. Toth and K. Schick (Eds.), *The*
939 *Oldowan: case studies into the earliest Stone Age* (pp. 155–222). Stone Age Institute
940 Press.
- 941 Trapanese, C., Meunier, H., and Masi, S. (2019). What, where and when: spatial foraging
942 decisions in primates. *Biological Reviews*, 94(2), 483–502.
943 <https://doi.org/10.1111/brv.12462>

- 944 UNEP-WCMC, and IUCN. (2019). *Protected Planet: The World Database on Protected Areas*
945 *(WDPA)*. www.protectedplanet.net
- 946 Wessling, E. G., Kühl, H. S., Mundry, R., Deschner, T., and Pruetz, J. D. (2018). The costs of
947 living at the edge: Seasonal stress in wild savanna-dwelling chimpanzees. *Journal of*
948 *Human Evolution*, 121, 1–11. <https://doi.org/10.1016/j.jhevol.2018.03.001>
- 949 Whiten, A. (2021). The burgeoning reach of animal culture. *Science*, 372(6537), eabe6514.
950 <https://doi.org/10.1126/science.abe6514>
- 951 Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., Tutin, C. E.
952 G., Wrangham, R. W., and Boesch, C. (1999). Cultures in chimpanzees. *Nature*,
953 399(6737), 682–685. <https://doi.org/10.1038/21415>
- 954 Yamakoshi, G. (1998). Dietary responses to fruit scarcity of wild chimpanzees at Bossou,
955 Guinea: Possible implications for ecological importance of tool use. *American Journal of*
956 *Physical Anthropology*, 106(3), 283–295. [https://doi.org/10.1002/\(SICI\)1096-](https://doi.org/10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O)
957 [8644\(199807\)106:3<283::AID-AJPA2>3.0.CO;2-O](https://doi.org/10.1002/(SICI)1096-8644(199807)106:3<283::AID-AJPA2>3.0.CO;2-O)
- 958 Yamakoshi, G. (2011). Pestle-pounding behavior: the key to the coexistence of humans and
959 chimpanzees. In Tetsuro Matsuzawa, T. Humle, and Y. Sugiyama (Eds.), *The*
960 *Chimpanzees of Bossou and Nimba* (pp. 107–115). Springer Japan.
- 961 Yamakoshi, G., and Sugiyama, Y. (1995). Pestle-pounding behavior of wild chimpanzees at
962 Bossou, Guinea: A newly observed tool-using behavior. *Primates*, 36(October), 489–500.
963 <https://doi.org/10.1007/BF02382871>
- 964 Zamma, K., and Makelele, M. (2012). Comparison of the Longevity of Chimpanzee Beds
965 between Two Areas in the Mahale Mountains National Park, Tanzania. *Pan Africa News*,
966 19(2), 25–28. <https://doi.org/10.5134/168176>
- 967 Zuur, A. F., and Ieno, E. N. (2016). A protocol for conducting and presenting results of
968 regression-type analyses. *Methods in Ecology and Evolution*, 7(6), 636–645.
969 <https://doi.org/10.1111/2041-210X.12577>
- 970 Zuur, A. F., Ieno, E. N., and Elphick, C. S. (2010). A protocol for data exploration to avoid
971 common statistical problems. *Methods in Ecology and Evolution*, 1(1), 3–14.

972 <https://doi.org/10.1111/j.2041-210X.2009.00001.x>

973 Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A., and Smith, G. M. (2009). *GLM and GAM*
974 *for Absence–Presence and Proportional Data* (pp. 245–259).

975 https://doi.org/10.1007/978-0-387-87458-6_10

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977 **Appendix**

978 Table A1 – Summary of the response variables used in this study and their descriptions.

Variable	Description	Units	Range
Raw materials	Total number of stones in the survey quadrat	Counts	0-99
Raw materials (size class 3-5)	Number of stones with sizes within the 95% confidence interval of tools used of nut-cracking	Counts	0-81
Tools	Total number of stones used for cracking nuts; Excludes unused fragments	Counts	0-28
Food trees	Total number of plants know to provide food sources to Bossou chimpanzees; Excludes plants with diameter at breast high (DBH) under 2 cm	Counts	0-12
Fruit trees	Total number of plants know to be sources of fruit to Bossou chimpanzees; Excludes plants with diameter at breast high (DBH) under 2 cm	Counts	0-9
THV	Total number of individual terrestrial herbaceous vegetation (THV) plants that are part of the Bossou chimpanzee diet	Counts	0-10
Nut availability	Approximate amount of nuts with edible kernels; Mean nut availability used in analysis	Categorical	0 (none); 1 (< 50); 2 (50 – 100); 3 (> 100)
Distance to nearest nest cluster	Distance, in metres, to nearest cluster of 21 nests; Cluster defined as nests within a 50-metre radius	Metres	50.01-781.06
Distance to nearest river	Distance, in metres, to nearest water course	Metres	6.92-399.84

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981 Table A2 – Likelihood ratio test results of the Full-Null model comparisons of the site selection
 982 models.

Model	Resid. df	Resid. Dev	df	Deviance	p
~1 (Null model)	81	113.627			
~Raw materials + Wild food trees + THV + Nest +River	76	59.289	5	54.338	<0.001
~ Raw materials (size class 3-5) + Wild food trees + THV + Nest +River	76	57.109	5	56.519	<0.001
~Raw materials + Wild fruit trees + THV + Nest +River	76	62.480	5	51.147	<0.001
~Raw materials (size class 3-5) + Wild fruit trees + THV + Nest +River	76	61.817	5	51.810	<0.001

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984 Table A3 – Results of the AICc-Based Model Selection of the GLM for the predictors of tool
 985 site selection. Subset variables highlighted in bold.

Model	df	AICc
~Raw materials + Wild food trees + THV + Nest +River	6	72.409
~ Raw materials (size class 3-5) + Wild food trees + THV + Nest +River	6	70.229
~Raw materials + Wild fruit trees + THV + Nest +River	6	75.599
~Raw materials (size class 3-5) + Wild fruit trees + THV + Nest +River	6	74.937

991 Table A4 – Results of the additional GLMs investigating potential predictors of tool site
 992 selection. Subset variables highlighted in bold.
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Model	Term	Estimate	SE	χ^2	P ^a
~Raw materials + Wild food trees + THV + Nest +River	Intercept	-0.575	1.076		NI ^b
	Raw materials	0.195	0.057	19.748	<0.001
	Wild food trees	0.303	0.155	4.944	0.026
	THV	-0.101	0.159	0.419	0.518
	Distance to nearest nest cluster	-0.007	0.003	7.377	0.007
	Distance to nearest river	0.004	0.004	0.887	0.346
~Raw materials + Wild fruit trees + THV + Nest +River	Intercept	-0.305	1.052		NI ^b
	Raw materials	0.203	0.059	20.316	<0.001
	Wild fruit trees	0.241	0.193	1.753	0.185
	THV	-0.031	0.136	0.051	0.821
	Distance to nearest nest cluster	-0.008	0.003	8.469	0.004
		0.005	0.004	1.270	0.260
~Raw materials (size class 3-5) + Wild fruit trees + THV + Nest +River	Intercept	-0.700	1.079		
	Raw materials (size class 3-5)	0.351	0.102	20.978	0.000
	Wild fruit trees	0.199	0.202	1.049	0.306
	THV	-0.017	0.141	0.014	0.905
	Distance to nearest nest cluster	-0.007	0.003	7.715	0.005
	Distance to nearest river	0.006	0.004	1.967	0.161

^a Results from the likelihood ratio test using the 'drop1' function.

^b Not indicated because it has a limited interpretation.

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998 Table A5 – Descriptive statistics and test results of the comparison between tool sites with low
 999 frequency (N = 10) and high frequency (N = 7) of nut-cracking events.

Variable	Low frequency		High frequency		Test results			
	Mean	SD	Mean	SD	Test ^a	t	df	p
Tools	7.100	3.143	11.429	3.780	tt	2.487	11.429	0.029
Distance to nearest nest cluster (m)	245.660	132.760	148.714	64.047	tt	-2.000	13.707	0.066
Raw materials (size class 3-5)	8.000 ^b	5.250 ^c	11.000 ^b	3.500 ^c	wt	50.000 ^d	-1.430 ^e	0.154
Raw materials	8.000 ^b	14.500 ^c	14.000 ^b	4.000 ^c	wt	49.000 ^d	-1.320 ^e	0.186
Mean nut availability	1.296	0.489	1.410	0.371	tt	0.547	14.835	0.593
Wild fruit trees	3.000	3.300	3.571	2.760	tt	0.387	14.401	0.704
Distance to nearest river (m)	139.613	77.486	124.710	84.836	tt	-0.369	12.265	0.718
Mean fruit bunches	1.252	0.630	1.188	0.630	tt	-0.204	13.069	0.842
Wild food trees	4.000	3.916	4.286	2.690	tt	0.178	15.000	0.861

^a Test used: tt =t-test; wt = Wilcoxon rank sum test

^d Reported as median

^e Reported as inter-quartile range (IQR)

^b Reported as w-statistic for Wilcoxon rank sum tests

^c Reported as z-score for the w-statistic

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1003 Table A6 – Likelihood ratio test results of the Full-Null model comparisons of the site inactivity
 1004 models.

Model	Resid. df	Resid. Dev	df	Deviance	p
~1 (Null model)	81	113.627			
~Mean nut availability + Raw materials + Wild food trees	36	46.532	3	8.017	0.046
~Mean nut availability + Raw materials (size class 3-5) + Wild food trees	36	46.518	3	8.030	0.045
~Mean nut availability + Tools + Wild food trees	36	41.350	3	13.198	0.004
~Mean nut availability + Raw materials (size class 3-5) + Wild fruit trees	36	46.621	3	7.928	0.048
~Mean nut availability + Tools + Wild fruit trees	36	41.968	3	12.581	0.006

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1006 Table A7 – Results of AICc-Based Model Selection of the GLM for the predictors of tool site
 1007 inactivity. Subset variables highlighted in bold.

Model	df	AICc
~Mean nut availability + Raw materials + Wild food trees	4	55.675
~Mean nut availability + Raw materials (size class 3-5) + Wild food trees	4	55.661
~Mean nut availability + Tools + Wild food trees	4	50.493
~Mean nut availability + Raw materials (size class 3-5) + Wild fruit trees	4	55.764
~Mean nut availability + Tools + Wild fruit trees	4	51.110

1013 Table A8 – Results of the additional GLM models investigating potential predictors of tool site
 1014 inactivity. Subset variables highlighted in bold.

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Model	Term	Estimate	SE	χ^2	P ^a
~Mean nut availability + Raw materials + Wild food trees	Intercept	1.275	0.927		
	Mean nut availability	-1.909	0.788	7.757	0.005
	Raw materials (size class 3-5)	0.001	0.017	0.001	0.973
	Wild food trees	0.083	0.111	0.567	0.452
~Mean nut availability + Raw materials (size class 3-5) + Wild food trees	Intercept	1.310	0.923		NI ^b
	Mean nut availability	-1.911	0.787	7.796	0.005
	Raw materials (size class 3-5)	-0.003	0.022	0.015	0.903
	Wild food trees	0.086	0.109	0.625	0.429
~Mean nut availability + Raw materials (size class 3-5) + Wild fruit trees	Intercept	1.838	0.971		NI ^b
	Mean nut availability	-1.895	0.773	7.757	0.005
	Raw materials (size class 3-5)	0.004	0.022	0.036	0.849
	Wild fruit trees	-0.104	0.145	0.522	0.470
~Mean nut availability + Tools + Wild fruit trees	Intercept	3.282	1.268		NI ^b
	Mean nut availability	-2.077	0.812	8.491	0.004
	Tools	-0.170	0.088	4.689	0.030
	Wild fruit trees	-0.053	0.144	0.135	0.714

^a Results from the likelihood ratio test using the 'drop1' function.

^b Not indicated because it has a limited interpretation.

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