The spatio-temporal complexity of chimpanzee food:
How a large-brained primate can counteract the ephemeral nature of its foods

1   # The spatio-temporal complexity of chimpanzee food:

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3   # nature of its foods

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23

24   **Short title: The spatio-temporal complexity of chimpanzee food**

25

Abstract

Ecological complexity has been proposed to play a crucial role in primate brain-size evolution. However, detailed quantification of ecological complexity are still limited. Here we quantify the spatio-temporal distribution of tropical fruits and young leaves, two primary chimpanzee (*Pan troglodytes*) foods focusing on the predictability of their availability in individual trees. Using information on up to 20 years of monthly young leaf, unripe and ripe fruit availability in plant species consumed by chimpanzees from tropical forests in East, Central and West Africa, we estimated 1) the forest wide frequency of occurrence of each food type and 2) the predictability of finding ripe fruit-bearing trees, focusing on the timing, frequency, and amount of ripe fruit present. In all three forests, at least half of all encountered trees belonged to species that chimpanzees were known to feed on. However, the proportion of these trees that bore young leaves and fruit fluctuated strongly between months. Ripe fruit was the most ephemeral food source, and trees that had more than half of their crown filled were at least nine times as rare as other trees. In old growth forests only one large ripe fruit crop per 10 km was encountered on average. High levels of inter-individual variation in the number of months that fruit was present existed, and in some extreme cases individuals bore ripe fruit more than seven times as often as conspecifics. Some species showed substantially less inter-individual variation in ripe fruit production frequencies and fruit amount than others. We hypothesize that chimpanzees employ a suite of cognitive mechanisms, such as an ability to 1) generalize or classify food trees, 2) remember the relative metrics of quantity and frequency of fruit production, and 3) flexibly plan monitoring (or return) times to optimize high-energy food consumption in individual trees and efficient travel between them.

INTRODUCTION

Tropical forest habitat and its distribution is thought to have a major impact on primate, and especially great ape, evolution [e.g. Milton, 1981; Sussman, 1991; van Schaik et al., 1993; Potts, 2004; White et al., 2009; Sussman et al., 2013]. One crucial argument for this supposition is that the majority of modern primate species and all great apes forage on foods produced by tropical forest trees [Fleagle, 1988; Fleagle & Reed, 1996; Terborgh, 1986; Potts, 2004; Knott, 2005; Robbins, 2008; Doran-Sheehy et al., 2009]. Given their lack of morphological and/or physiological dietary adaptations, great apes are, in contrast to old world monkeys, unable to digest chemically defended forest foods such as most mature leaves and certain seeds and thereby must increase the consumption of energy-rich food, such as ripe fruit, when more is available [reviewed in Doran-Sheehy et al., 2009]. A low percentage of ripe fruit in the diet has been shown to influence female reproductive physiology and life history traits such as waiting time to conception in great apes [Knott, 2005; Thompson & Wrangham, 2008]. Therefore, detailed investigation of the temporal distribution of food availability in tropical forests has the potential to improve our understanding of great ape evolution and in particular that of their advanced representational skills and larger brain size [Byrne, 1997; Knott, 2005].

The availability of energy-rich plant food throughout the forest is characterized by temporal fluctuations that result in periods of abundance, alternated by variably long periods of scarcity [e.g., Hladik, 1988; van Schaik et al., 1993; Chapman et al., 1999a; Knott, 2005; van Woerden, 2012; Polansky & Boesch, 2013]. Further, not all plant foods are available for equally long periods at specific locations [Milton 1980]. Young leaves and ripe fruit are typically reported to be highly ephemeral [Milton 1980]. Observations that necessary food resources could in fact be scarce but predictable led to the "ecological intelligence hypothesis" [Milton 1981; 1988] - that primates, such as great apes, which rely on ephemeral fruits would need larger ranges and would have evolved advanced cognitive capacities that facilitate optimal food finding strategies [Milton & May, 1976, Milton, 1980]. The hypothesis found support in several comparative studies which found correlations between a variety of brain size measures and levels of frugivory in primates, rodents and bats [Clutton-Brock & Harvey, 1980; Harvey & Krebs, 1990; Barton, 1996]. For example, sympatric primate species that differ considerably in relative brain size show clear dietary differences and those that feed on energy rich and ephemeral ripe fruit for a larger percentage of time have

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86 relatively larger brains [Milton, 1981; Wrangham et al., 1991; Houle et al., 2010;

87 Doran-Sheehy et al., 2006; 2009].

88   Knowledge of the temporal availability of energy-rich tropical forest food has

89 continued to increase, triggering investigations on primate brain size evolution [Allman

90 et al., 1993; Aiello and Wheeler, 1995; van Woerden et al., 2010, 2012]. Larger-brained

91 primate species, such as great apes, in contrast to smaller-brained species, were shown

92 to exhibit less seasonality in food consumption than expected on the basis of

93 environmental seasonality in their dietary consumption [van Woerden et al., 2012]. This

94 finding led to the proposition that larger brains provide a cognitive behavioral flexibility

95 which facilitates the buffering of periods of food scarcity ["the cognitive buffer

96 hypothesis"; Allman et al., 1993; van Woerden et al., 2012]. These buffering effects

97 were thought to be most apparent in large-brained primates, which had cognitive

98 abilities that enabled extractive foraging or exploitation of dispersed food patches [Van

99 Woerden et al., 2012].

100

101 **When does food distribution become complex and what cognitive abilities**

102 **help food finding?**

103 At what point are required food sources ephemeral and dispersed enough to truly create

104 a challenge to the forager? The answer is not well understood, nor easy to quantify. In

105 fact, decades after Milton [1980] developed her hypothesis very few studies have

106 quantified the spatio-temporal distribution of primate food directly, instead relying on

107 other more indirect measures such as the size of the species' ranging area that is not

108 necessarily related with increased complexity of resource distribution [Clutton-Brock &

109 Harvey, 1980; Dunbar 1998]. Although some (e.g. Janson & Chapman, 1999) have

110 recognized this shortcoming and have proposed and analyzed quantitative measures of

111 food abundance, the majority of botanical studies to date typically describe phenological

112 patterns at the population level [Hladik, 1988; van Schaik et al., 1993; Chapman et

113 al.,1999b and Janson & Chapman, 1999, Knott, 2005]. Long-term data on the temporal

114 fruiting patterns of *individual* trees, the actual food sources that primates need to find in

115 daily life, is still limited [but see Janzen, 1978; Milton et al., 1982; Wheelwright,1986;

116 Struhsaker, 1997; Momose, 2004].

117   Besides a general lack of understanding regarding the point at which large-brained

118 primates are challenged by the ephemeral complexity of their resources, there is in

119 particular limited knowledge of what exact cognitive mechanisms would help them to

120 "counteract" the complications of food finding. Two partial exceptions include studies

121 of how visual specialization [e.g., Barton, 1998, 2004; Dominy & Lucas, 2004;

122 Changizi & Shimojo, 2008] and spatial memory [reviewed in Janson & Byrne, 2007;

123 Zuberbuhler & Janmaat, 2010] are used to address ephemeral resource complexity. To

124 develop hypotheses about which other cognitive abilities primates use for finding

125 ephemeral food, it is essential to understand and quantify the difficulty of food finding,

126 here defined as the localization of plant items that are subsequently eaten. It has been

127 argued that food finding becomes cognitively complex when the distribution of food has

128 neither the lowest entropy (ordered), nor the highest entropy (random or chaotic), but

129 rather has a certain level of predictability or pattern that is predictable without perfect

130 knowledge [Grassberger, 1986; Sambrook & Whiten, 1997; Fagan et al., 2013].

131   Milton [1980], described predictability as an important feature that could work to

132 the primates' advantage, in which she proposes "once the location of a particular food

133 tree is known, it becomes a dependable seasonal resource in terms of its location for the

134 lifetime of the primate." Yet, even granting perfect spatial memory of a particular tree,

135 we might ask how dependable through time is such a "known" food tree? Does it

136 always produce food in the same month or simultaneously with other conspecific trees?

137 Will it bear fruits every fruiting season and, if so, will it always produce the same

138 amount? Botanical studies have revealed that primate food production is subject to

139 complex selection processes involving both seasonally variable biotic (e.g. pollinator

140 population dynamics) and abiotic factors [Rathcke & Lacey, 1985; Wheelwright, 1986;

141 van Schaik et al., 1993; Herrera et al., 1998; Janson & Chapman 1999; Sakai, 2001;

142 Milton et al., 2005]. As a result, individual food plants show variation in the *timing*,

143 *frequency* and *amount* of food produced [van Schaik et al., 1993; Chapman et al.,

144 1999b; reviewed in Sakai, 2001; Anderson et al., 2005].

145

This study

147 In this commentary, we aim to develop and discuss a number of hypotheses that explain

148 how primates can "counteract" the ephemeral nature of high-energy food. To do so, we

149 use our analyses of long-term data on the temporal food distribution of the exceptionally

150 large-brained primate, the chimpanzee (*Pan troglodytes*), to inspire us. We expand

151 earlier quantifications of ecological complexity (Milton 1980; 1981;1988) by

152 investigating the temporal distribution of the availability of tropical fruit and young

153 leaves [(two primary foods of chimpanzees) in individual trees [e.g., Wrangham, 1977;

154 Medlicott & Thompson, 1985; Matsumoto-Oda & Hayashi, 1999; Goné Bi, 2007],

155 focusing on the primary species of food consumed by chimpanzees. We focused on the

156 availability of young leaves, unripe fruit, and ripe fruit (also see below) because they are

157 known to be important food sources for chimpanzees and other sympatric large-brained

158 primate species and are fed on to fulfill basic energy and protein requirements [Hladik,

159 1977; Rogers et al., 1990; Wrangham et al., 1991; Janson & Chapman, 1999; Doran-

160 Sheehy et al., 2006; 2009; Head et al., 2011].

161   The phenology data analyzed here spans ~ 5 to 20 years of individual trees

162 sampled at monthly intervals, and was collected from three tropical forests located in

163 East, Central, and West Africa. Using this unique amalgamation of long-term datasets,

164 we quantify the difficulty of finding relatively energy-rich young leaves, unripe fruit,

165 and, in particular, large ripe fruit crops. We first describe the probabilities of

166 encountering trees in each of these three plant phenophases forest wide. To provide

167 insight into the potential strategies that chimpanzees could use to maintain a constant

168 intake of energy despite the ephemeral nature of their most energy-rich food, we

169 secondly describe the predictability of the timing, frequency, and quantity of ripe fruit

170 production in individual focal trees.

171

172 **The challenge of finding a tree with ripe and unripe fruit and young leaves**

173 We first estimated the probability of encountering young leaves and unripe and ripe

174 fruit at the forest community level. We measured the availability of these three plant

175 phenophases during monthly phenology checks of chimpanzee food trees growing in

176 their territories. We did this in two ways: (1) by aggregating the data over all time, per

177 site to describe the percentage of individuals showing each phenophase through time,

178 and (2) reporting the minimum and maximum of these percentages. We also provide a

179 detailed description of the temporal availability of large ripe fruit crops. By combining

180 the particularly extensive and long-term dataset on tree density, crown size measures,

181 and ripe fruit availability in individual fruit trees in the old growth forest compartments

182 of Kanyawara with long-term knowledge [Isabirye-Basuta, 1988] on the diet of

183 chimpanzees in this same forest, we also carried out an additional calculation on the

184 encounter rates of (large) ripe fruit-bearing trees per distance travelling in this forest to

185 gain more accurate insight in the challenges faced.

186

187

188   The importance of ripe fruit crops

189   In this study we especially focused on the spatio-temporal distribution of ripe fruit crops

190   for the following reasons. Ripe fruit crops are considered to be a highly energetic food

191   source, with fruit pulp containing high levels of sugars and seeds which are rich in

192   starch and fat [Woodward, 1972; Marriott et al., 1981; Medlicott & Thompson, 1985;

193   Matsumoto-Oda & Hayashi, 1999; Doran-Sheehy et al., 2009; Irwin et al., 2014]. Trees

194   with large ripe fruit crops are considered especially important to chimpanzees, as the

195   high energetic reward is expected to counterbalance the cost of travel and vertical climb

196   [Goodall, 1986; Jurmain, 1997; Pontzer & Wrangham, 2006; Hanna et al., 2008; Kraft

197   et al., 2014]. Primates such as chimpanzees are heavy, and despite the fact that heavier

198   primates are more efficient at climbing and locomotion, absolute costs of travel and

199   vertical climbing, especially that of injury after falling is higher for heavier primates

200   than lighter ones [Goodall, 1986; Jurmain, 1997; Pontzer & Wrangham, 2006; Hanna et

201   al., 2008; Kraft et al., 2014]. Large ripe fruit crops are expected to provide social

202   benefits as they enable individuals traveling in parties to stay together and reduce

203   feeding competition or engage in beneficial social behavior [Isabirye-Basuta, 1988;

204   Chapman et al., 1995; Wrangham, 2000; Wakefield, 2008; Thompson et al., 2014].

205

206   The challenge of finding ripe fruit in "known" trees

207   *The timing of ripe fruit presence*

208   Once a tree is encountered, fed in and known to be reproductively mature, how does a

209   chimpanzee know when it will produce fruit again? Tropical forests have distinct rainy

210   and dry periods, potentially severe enough to limit or stimulate the production of plant

211   phenophases at predictable moments in time [reviewed in Janson & Chapman, 1999].

212   However, tropical wet forests that lack well-developed xeric (dry) periods show less

213   predictability in the timing of fruiting periods [e.g. Frankie et al., 1974; Putz, 1979;

214   Opler et al., 1980]. For example, individual trees of understory plants in ever-wet

215   forests that cannot rely on seasonality in rain or irradiation can produce fruit at any time

216   of year, showing similar asynchronous fruiting patterns as observed in some fig species

217   [*Ficus spp.;* Opler et al.,1980; Milton, 1980, 1991; van Schaik et al., 1993; Sakai, 2001;

218   Koptur et al., 2009]. For other rainforest tree species the timing of peak fruiting for a

219   given species can vary between months, years and areas [Chapman et al., 1999, 2004;

220   Janmaat et al., 2012; Polansky & Robbins, 2013]. Such irregular patterns, it is argued,

221   could lower the success of food finding strategies that predict the particular month that

222 fruit will be available in individual trees based on monitoring photoperiod or stable

223 successions of fruiting seasons [Janmaat et al., 2012].

224   However, many rainforest tree species have reproductive strategies that cause

225 different trees of the same species bear fruit simultaneously within a clustered time [i.e.,

226 fruiting season; Chapman et al., 1999b]. So even if species do not produce fruits at

227 predictable months in the year, this phenomenon could enable chimpanzees to predict

228 the time that fruit is available in a large number of conspecific trees at any moment in

229 time. Based on the immediate discovery of fruit in one tree of a particular species it

230 could then predict the presence of fruit in other trees of that same species [e.g., Milton,

231 1980; Milton et al., 2005; Menzel, 1991; Janmaat et al., 2012]. We expect this strategy

232 may be especially beneficial for chimpanzees as African forests are described as lacking

233 large areas with ever-wet forest [Richards, 1973], which likely results in a larger than

234 expected proportion of conspecific trees producing fruit simultaneously.

235   To understand whether the onset of ripe fruiting periods was predictably linked

236 to particular months of the year we describe the *timing* at which each individual tree

237 within a species bears ripe fruit over time frames of up to 20 years. In addition, we

238 investigate whether and how the fruiting of individual trees were synchronized in time

239 between conspecific trees at given locales to gain insight in the probability that a

240 primate will find conspecific trees that fruit simultaneously. We furthermore,

241 investigated how synchrony levels varied across species in all tree forests by computing

242 a measure of inter-individual fruiting synchrony. Finally, we compare inter-individual

243 fruiting synchrony of ripe fruit with that of unripe fruit and the inter-individual flushing

244 synchrony of young leaves.

245

246 *The frequency and amount of ripe fruit*

247 When chimpanzees search for ripe fruit in tree species that have just started their

248 fruiting season, do all "known" individuals within that species at that locale have a

249 similar probability of bearing fruit and how likely are individuals to bear ripe fruit at the

250 same amount? To gain insight into the predictability of ripe fruit production frequencies

251 and amount we describe the histories of monthly ripe fruit production in individual fruit

252 trees of a total of 190 species that were monitored for up to 20 years.   We also compare

253 the variation in the number of months that ripe fruit was found present across species. In

254 addition, we compare the variation in the number of months when the tree crown was

255 scored as more than half filled with fruit to all the times it had been observed bearing at

256 least some ripe fruit across species.

257   We conclude our commentary by providing a number of hypotheses on potential

258 cognitive strategies and abilities that chimpanzees could use to counteract the ephemeral

259 nature of their most energy-rich food. Some of these hypotheses are very theoretical and

260 perhaps speculative, yet are presented here with the purpose to give guidance and

261 inspiration to future studies in the field of foraging cognition.

262

Methods

Phenology data collection

265 Data was collected at three long-term research sites in tropical forests in East, Central,

266 and West Africa: 1) a moist evergreen tropical forest, transitional between lowland

267 rainforest and montane forest in Kibale National Park, Uganda [Kanyawara; Struhsaker,

268 1997; Chapman and Lambert, 2000], 2) a tropical lowland rainforest in Loango National

269 Park, Gabon [Loango; Head et al., 2011], and 3) a lowland tropical moist forest in Taï

270 National Park, Côte d'Ivoire [Taï; Vooren, 1999, Anderson et al., 2005]. Kanyawara,

271 Loango, and Taï contain 11, 11 and 12 primate species, respectively, each including the

272 chimpanzee, [Janmaat , 2006; Head et al., 2011]. Chimpanzee diet composition was

273 assessed through direct observations of feeding behavior of habituated East and West

274 African chimpanzees [*P. t. schweinfurthii, P. t. verus*] by the Kibale Chimpanzee

275 Project [Isabirye-Basuta, 1988; Wrangham et al., 1991] and the Taï Chimpanzee Project

276 [Boesch & Boesch-Achermann, 2000], during periods of 35 and 33 years, respectively.

277 The central African chimpanzees [*P. t. troglodytes*] in Loango were not habituated and

278 their diet was therefore assessed through analysis of fecal samples and feeding remains

279 over five years [Head et al., 2011].

280   The phenology data collection is based on monthly leaf and fruit production

281 checks of individually marked plants that produced food that was known to be

282 consumed by chimpanzees along a network of forest trails located within the territories

283 of the respective chimpanzee communities. In Kanyawara transects were located inside

284 the territory of one chimpanzee community each, while in Taï and Loango transects

285 were longer in order to represent fruit availability in territories of four and three

286 different communities, respectively. Since the majority of the monitored plants were

287 trees, we will subsequently refer to them as trees (instead of trees, figs, and lianas). In

288 general, monitored trees were selected based on evidence of reproductive maturity and a

289 species-specific diameter at breast height (D.B.H.) threshold (>10cm). The details of

290 tree selection and phenology data collection are provided in previous studies

291 [Kanyawara: Chapman et al., 1999b, Loango: Head et al., 2011, Taï: Anderson et al.,

292 2005, Polansky & Boesch, 2013]. Observations of the monthly production of the three

293 phenophases in individually marked trees were made using binoculars. Ripeness of

294 fruits was estimated based on a combination of the fruits' size and color and whether

295 there was evidence of partially eaten fruit or olfactory cues of ripened fruit on the

296 ground. Determining when a fruit is ripe is sometimes difficult since not all fruits

297 change color during ripening. As a result, for each fleshy-fruited species we defined

298 fruit as ripe when they were first eaten by frugivores after they had reached full size or

299 when olfactory cues of ripe fruit were detected under the tree. For wind dispersed

300 species, we considered a tree to have mature fruit when dehiscent fruits opened and

301 seeds could be found under the focal tree. In all three forests, we evaluated the relative

302 abundance of the three phenophases on a production scale of 0–4. For example, in

303 Kanyawara and Taï, the score 0 for ripe fruit corresponded to no observed ripe fruit, and

304 1, 2, 3, and 4 corresponded to 1–25%, 26–50%, 51–75%, and 76–100% of tree crown

305 filled with ripe fruit, respectively [see Chapman et al. 1992 and Anderson et al. 2005 for

306 details]. In Loango, 1, 2, 3 and 4 corresponded to the median of 1-10, 11-50, 51-100,

307 >101 ripe or unripe fruits measured on three separate branches, respectively [Head et

308 al., 2011]. No young leaf status (old or young) measurements were collected in Loango.

309   The monitored trees existed of trees of 45, 38, and 107 species that chimpanzees

310 were known to feed on in Kanyawara, Loango and Taï, respectively. As chimpanzees in

311 Kanyawara, Loango and Taï were observed to feed on a total of 79, 75, and 150 species,

312 respectively, our data included 50-70% of all chimpanzee food species in each forest

313 (Table 1). The Taï forest is part of the Liberian quaternary refugium and has high

314 species diversity and the highest tree density of all three forests [Table 1; Maley, 2001].

315 Tropical forest in west Gabon is described as a biodiversity hot spot [Hladik, 1978;

316 Maley, 2001], yet the Loango forest is a heterogeneous tropical rainforest which

317 includes savannah and lowland swamp habitat, and therefore has a relatively low tree

318 density. The Kanyawara forest is thought to have appeared later than the Taï and

319 Loango forests (around 12,000 B.P.) and had the lowest tree density, with relatively few

320 endemic species [Olupot et al., 1994; Hamilton et al., 2001].

321

322

323 Data analyses

324 We analyzed data from Kanyawara, Loango, and Taï from April 1990 through May

325 2011, January 2007 through December 2011 and January 1989 through December 2010,

326 respectively. The data concerned monthly phenology checks on 1304, 741 and 3422

327 trees representing 45, 38 and 107 chimpanzee food species, respectively. In Kanyawara

328 the number of individuals decreased to 263 from 1997 onwards. Observation periods

329 were not equal for all trees, since some of them fell down, died or their location got lost

330 due to political unrest; however, the trees had an average total study duration from first

331 to last observation of 94, 38 and 80 months per individual for Kanyawara, Loango and

332 Taï, respectively. We only considered phenology data from trees which produced food

333 items that were known to be fed on by the chimpanzees ranging in the respective

334 forests. However, for calculating the encounter probabilities per distance travelled

335 conducted for the Kanyawara forest, we analyzed data from all mature trees

336 (DBH>10cm) and lianas that were tagged along a 5.2 km long and 10 m wide transect

337 and checked for fruit availability on a monthly basis for a period of 6 years. Since the

338 chimpanzee territory in the Kanaywara forest is a mix of old growth and recently logged

339 forest we made separate calculations for the encounter probability of chimpanzee food

340 trees in the old growth forest compartments (K30 area) within it. To calculate the

341 proportion of trees (DBH <10cm) belonging to species that were known to be consumed

342 by Kanyawara chimpanzees out of the total number of trees encountered we included

343 transects from both areas. To calculate comparable measures for Taï and Loango we

344 used data from separate tree density transects for which the methods are described in

345 Goné Bi 2007; Janmaat et al 2013a and Head et al. 2011 (Table 1).

346

347 *The timing of food production: synchrony levels*

348 The timing of food production was assessed in two ways. First, we simply present

349 graphics showing the monthly phenological state of each individual tree over the entire

350 study. Second, we measured the level of simultaneous food production among tree

351 individuals of the same species within clustered time periods (a fruiting or leaf flushing

352 season). For the latter we calculated each species synchrony level measured as the

353 average of all spearman rank correlation coefficients that could be calculated for the

354 fruiting or young leaf state of all possible pairs of trees within a species [Bjørnstad et

355 al., 1999]. For example, when all tree individuals had the same fruiting state in each

356 month, the mean spearman correlation is equal to 1, and a species was defined as having

357 the highest synchrony level. Low synchrony levels were found if not all trees carried

358 fruit within a fruiting season or when some trees produced fruit in other months (e.g.

359 *Ficus spp.*). The correlations were calculated by comparing the presence or absence of

360 ripe fruit scores between pairs of trees. For calculating synchrony levels we only

361 included species for which we had data from at least five individuals with at least 12

362 months of data to calculate a species level mean. In addition, all analyzed individuals

363 had some variation in their phenophase expression, as computing synchrony between 2

364 individuals involves dividing by the product of their standard deviations; if one of these

365 is zero, then the denominator is zero, which would result in an undefined synchrony.

366

367 *Fruiting frequencies*

368 To get a reliable estimate of the inter-individual variation in species-specific fruiting

369 frequencies we restricted analysis to a selection of three very long uninterrupted

370 periods. These periods concerned 76, 67 and 144 months for Kanyawara, Loango and

371 Taï, respectively. To calculate variation in the number of months that trees bore ripe

372 fruits, we only included species that had data from at least five tree individuals.

373

374 *Fruit amount*

375 The history of fruit amount produced in individual trees was visualized by plotting the

376 fruit production score of each monthly phenology check for all focal trees over the

377 entire period. To investigate the variation in fruit production amount in individual trees

378 we first determined the total number of months that each individual tree was observed to

379 bear ripe fruit. We then calculated the percentage of these months that the tree had a

380 fruit production class of 2 or more. To get a reasonable representation of the productive

381 output of trees and the variability across species we only included trees that produced

382 ripe fruit for a minimum of 5 months and species that had data from a minimum of 5

383 trees.

384

385 **Results**

386 Availability of young leaves, unripe and ripe fruit, and full crowns

387 We found substantial fluctuations in the availability of young leaves, unripe fruit and

388 ripe fruit over time, with ripe fruit being the rarest food source of these phenophases in

389 all three forests (Tables S1-S3). Ripe fruit had the lowest probability of encounter at any

390 moment in time (Fig. 1; Tables S1-S3). Based on all phenology checks (425,836

391 observations), trees carried ripe fruit in 3.4%, 10.9% and 8.6% of the observations in

392 Kanyawara, Loango and Taï, respectively. The lowest percentages of trees bearing ripe

393 fruit were observed in August 1997 in Taï and April 2007 in Loango, when the

394 percentages dropped to 0.3% and 1.1%, respectively (Table S1). In Kanyawara the

395 percentage of trees bearing ripe fruit was only 0.08% in April 1990 and dropped to zero

396 several times after 1997 (partially resulting from the fact that the number of monthly

397 checked chimpanzee food trees dropped in 1997; Table S1). While between-site

398 comparisons could be influenced by differences in classifications, we found that trees

399 with a ripe fruit production score larger than two were at least 9 times as rare as trees

400 bearing fewer fruits for all three forests (Fig. 1). In Kanyawara only 6 and 3 times out of

401 119 and 215 observations, respectively, an abundance score of 3 or 4 for ripe fruit was

402 observed (Fig. 1).

403

404 Encounter rates of ripe fruit and large ripe fruit crops per distance traveled

405 In all three forests, more than 50% of all encountered trees belonged to a species that

406 chimpanzees feed on (Table 1). For example, in Kanyawara 58% of mature trees (1196

407 out of 2070 trees with a DBH >10cm) that were located along the 5.2 km long old

408 growth and recently logged forest transects belonged to chimpanzee food species (based

409 on 25 years of feeding observations of the Kanyawara chimpanzees; $N_{food species}$=75).

410 The research assistants that walked these transects for 76 months, totaling 395 km,

411 encountered on average one ripe fruit-bearing chimpanzee food tree every 97 m, while

412 passing 37 other reproductively mature trees (of all species) along the transect. In the

413 most fruit scarce month they found one ripe fruit-bearing chimpanzee food tree every

414 1730 m, while passing 687 mature trees. When we considered the availability of large

415 ripe fruit crops (i.e. chimpanzee food trees with a DBH equal to or larger than the

416 average size of a Kanyawara chimpanzee feeding tree (67 cm; Potts 2008) and a crown

417 with at least 50% of the crown filled with ripe fruit), the observers found on average

418 only one such tree every 21 km, while passing 7,992 mature trees.

419 If we only consider the old growth forest compartments, spanning 2.4 km long

420 transects, encounter rates of ripe fruit-bearing trees were slightly increased. Out of 1156

421 trees, 62% belonged to species that were known chimpanzee fruit food. Furthermore,

422 observers found on average 1 ripe fruit-bearing chimpanzee food tree every 79 m,

423 passing 37 other mature trees, and 1 tree with a large ripe fruit crop every 10 km,

424 passing 4,742 other mature trees (Fig. 2). In the most fruit scarce month no trees with

425 ripe fruit were encountered in the entire transect. The encounter rates fluctuated strongly

426 in time and were substantially higher for unripe than for ripe fruit crops (Fig. 2, Fig.

427 S1).

428

429 The timing of ripe fruit presence

430 We found some plant species produced ripe fruit at predictable months (Fig. 3a);

431 however, a high level of variation in the timing of fruit production was detected within

432 species. For example, *Sacoglottis gabonensis* trees in Taï, which appear to bear ripe

433 fruit predictably once a year in September, had a fruiting peak in April in 2009 and in

434 February in 2010. Similarly *Uvariopsis congensis* trees in Kanyawara, which appear to

435 bear ripe fruit once a year in June had a fruiting peak in December in 1991 (Fig. 3b).

436   When we plotted the fruiting patterns in time of all monitored species (that

437 contained at least 5 individual trees), we observed species which produced ripe fruit in a

438 highly synchronous manner, with the majority of individuals bearing ripe fruit at the

439 same time (e.g. *Coula edulis* as shown in Fig. 3a). In other species conspecific trees

440 either produced fruit in different months or failed to produce during certain seasons or

441 years, resulting in low levels of synchrony or asynchrony in fruit production (e.g. *Ficus

442 sansibarica* as shown in Fig. 3c). Comparisons of the range of synchrony levels across

443 species by forest indicated that each forest had a comparable range of intra-specific

444 fruiting synchrony values (Fig. 4). Ripe and unripe fruit, however, showed significantly

445 higher levels of synchrony in production than young leaves in Loango and Taï forest

446 (Loango: Friedman test: $X2= 8.69$, df = 2, P= 0.0130, $N_{species}=32$, median $_{young}$

447 $_{leaves}=0.22$, median $_{unripe\ fruit}=0.34$, median $_{ripe\ fruit}=0.32$; Taï: $X2= 36.52$, df = 2,

448 P<0.0001, $N_{species}=73$, median $_{young\ leaves}=0.23$, median $_{unripe\ fruit}=0.38$, median $_{ripe\ fruit}=$

449 0.38; Fig. 4, S2, S3). In Kanyawara we did not detect a significant difference between

450 the phenotypes ($X2=1$, df = 2, P= 0.6065, $N_{species}=18$, median $_{young\ leaves}=0.26$, median

451 $_{unripe\ fruit}=.0.22$, median $_{ripe\ fruit}= 0.21$; Fig. 4). Synchrony levels of some species

452 occasionally changed through time and space, with proportions of trees bearing ripe

453 fruit within fruiting periods being different across years (Fig.S4) or between forests

454 (Fig.5).

455

456 The frequency of ripe fruit presence

457 Fruiting periods of individual species vary in frequency. Some species bear fruit

458 multiple times a year (continuous), twice a year (bi-annual), once a year (annual), or

459   every other year or more (supra-annual; Fig. S5). Given a species was fruiting, ripe fruit

460   production in individual trees showed high levels of inter-individual variation in the

461   number of times that fruit was produced and the number of months it persisted. For

462   example, in Taï, one individual *Treculia africana* bore ripe fruit for 17 months out of 48

463   consecutive months, while another conspecific tree fruited only 3 months within the

464   same period (Fig. S6). Similarly, in Kanyawara, in *Ficus sansibarica* one individual

465   bore ripe fruit for 28 months out of 132 consecutive months, while another tree fruited

466   only 4 months within that same period (Fig. S6). When we considered a large number of

467   species with all trees monitored for similar time durations we found that for all three

468   forests some species had substantially more inter-individual variation in the number of

469   months that ripe fruits were produced than other species (Fig. 6). The within species

470   variation in percentages of monthly production within these same consecutive time

471   periods differed significantly between the three phenophases with ripe fruit having the

472   lowest variation (Friedman test: $X2=35.03$, df = 2, $P<0.0001$, $N_{species}=56$, median

473   standard deviation of young leaves$_s$=4.28; median standard deviation of unripe fruit

474   =5.48; median standard deviation of ripe fruit=2.50). This is likely due to the quicker

475   depletion or perishing times of ripe fruit, resulting in lower maximum months of ripe

476   fruit presence (See SI; Fig.S7, S8, S9) and thus lower levels of variation.

477

478   *The amount of ripe fruit*

479   The number of months that individual trees were scored as having more than 50% of

480   their crown full of ripe fruit (production score > 2) varied between years (e.g., *Xylia*

481   *evansii* in Fig. S5b). The proportion of months in which the ripe fruit production score

482   was larger than 2, out of all the months that a tree was observed to bear ripe fruit, also

483   varied between individual trees (Fig.7). For example, in *Sarcocephalus pobeguinii* in

484   Taï, one individual produced more than half of what it maximally could ((production

485   score>2) 4 out of 53 months, while another tree only produced small amounts of fruit

486   (all scores ≤ 2) within that same period. However, very few tree individuals produced

487   only large or small amounts of fruit for the entire period (Fig. S5b, S10). In Loango and

488   Taï, some species had substantially more inter-individual variation in the proportion of

489   months with a high productive output than other species (Fig.7). For Kanyawara

490   variation across species was low as trees rarely had more than 50% of their crown filled,

491   even in the old growth forest compartments.

492

Discussion

The challenge of finding a tree with ripe and unripe fruit and young leaves

Due to a combination of fruit size, protection, taste, toxicity and inaccessibility, primates only feed on a fraction of the many hundreds of fruit species in a tropical forest [Janson & Chapman, 1999]. The Taï forest, for example, harbors an estimated 1,300 plant species [Guillaumet, 1967] from which only 150 species produce fruits that are known to be consumed by three neighboring Taï chimpanzee communities [Goné Bi, 1999, KJ unpublished data]. Our study however, reveals that plant species fed on by chimpanzees are surprisingly abundant in space. In all three forests more than half of all encountered trees belonged to a fruiting species that chimpanzees were known to consume. A chimpanzee's challenge is therefore not so much to find plants that belong to an edible species, but to find those that actually produce food, in particular those that produce ripe fruit at a particular time. Similar to Milton's [1980] observations in the neo-tropical forest in Panama, ripe fruit in the forest ecosystems observed here was the most ephemeral food source, with the lowest encounter rates, compared to young leaves and unripe fruit. Finding ripe fruit is inferred to be the most challenging in the absence of the chimpanzee's use of any sensory cues. Observations of trees with more than half of their crown filled with ripe fruit were particularly rare being at least nine times as rare as trees with lower productive outputs.

Encounter rates of trees with ripe fruit crops were substantially lower than that of trees with unripe fruit crops. However, on average observers only had to travel 97 m to find one ripe fruit-bearing tree. In fruit scarce months this distance increased to nearly 20 times (to 1730 m), with observers passing hundreds of trees before encountering one single ripe fruit-bearing chimpanzee food tree in the territory, while none were encountered in the old growth forest compartments. When we considered only trees with large ripe fruit crops, meaning a tree that was at least as large as an average chimpanzee feeding tree, with a crown that was half or more filled with fruit, encounter rates were extremely low. Observers traversing transects located in the chimpanzee territory encountered such a large fruit crop on average only once every 21 km of travelling or every 10 km in old growth forest compartments in the same territory. Considering that the average day journey length of chimpanzees in the Kanyawara forest is 2.1 km [Pontzer & Wrangham, 2004], this encounter rate can be translated into a rate as low as 1 tree per 5 average-length chimpanzee daily routes in old growth forest.

527   Unfortunately, we were unable to make similarly detailed calculations for the

528   Taï and Loango forests, since phenology trees at these sites were selected and did not

529   represent all food trees on a transect as was the case in Kanyawara between 1990 and

530   1996. However, transect data revealed that trees larger than the average feeding tree size

531   of Kanyawara chimpanzees (67 cm) were of similar density [9.8, 8.2 and 11.0 trees ha^{-1},

532   in Kanyawara, Loango and Taï, respectively; Potts et al. 2011]. In addition, the overall

533   proportion of phenology trees carrying ripe fruit was comparable, although slightly

534   higher in Taï and Loango compared to Kanyawara (Fig. 1). Observations of high fruit

535   production scores were rare in all three forests (Table S1).

536   Based on these descriptive findings we hypothesize that chimpanzees in West,

537   Central and East Africa are all considerably challenged in finding ripe fruit crops during

538   some months of the year, and are continuously challenged in discovering large ripe fruit

539   crops which are sizeable enough to feed an averaged sized chimpanzee party. The latter

540   challenge appeared considerably larger for the Kanyawara chimpanzees, which could

541   potentially explain the lower levels of dyadic associations reported in Kanyawara

542   female chimpanzees compared to those in Taï [Wittiger et al., 2013]. Several periods of

543   ripe fruit absence further suggests that the Kanyawara chimpanzees are more challenged

544   than chimpanzees in the other two forests. On the other hand, the lower diversity of tree

545   species in Kanyawara compared to Taï, [the Liberia refugium; Booth, 1957] should

546   make it easier to identify and locate trees belonging to food species, which could

547   potentially limit the complexity and decrease the cognitive challenge [Janson &

548   Chapman, 1999]. Further studies that project fruit availability distributions from

549   phenology transects on simulated forest areas using tree density and diversity data are

550   needed to fully quantify and compare the separate challenges faced at each site.

551

552   Once a tree is "known" to produce fruit, when will it produce ripe fruit again?

553   In all three forests, we detected conspecific trees that produced ripe fruit during

554   predictable months of the year. However, substantial variations in fruiting months were

555   found, making it difficult for chimpanzees to rely on monitoring of photoperiods,

556   climatic variables, or particular orders in fruiting seasons.

557   Levels of ripe fruit synchrony were comparable across the three forests studied

558   here, with some species exhibiting mean intra-specific synchrony correlations of greater

559   than 0.5. We therefore hypothesize that chimpanzees and other primates living in

560   African tropical forests could use the phenomenon of fruiting synchrony to efficiently

561 predict the moment in time that an individual and "known" tree bears ripe fruit. They

562 could use the detection of a ripe fruit bearing tree to predict ripe fruit availability in a

563 large number of conspecific trees.

564   Earlier studies [Janmaat et al., 2012; 2013b] suggest that chimpanzees, and another

565 large-brained rain forest primate (e.g. the gray-cheeked mangabeys (*Lophocebus*

566 *albigena*)), indeed make use of the phenomenon of synchronous fruiting to predict the

567 timing of fruit production in individual trees. Since young leaves showed lower levels of

568 synchrony in their production in two of the three sites, we expect such strategies to be

569 used in particular by fruit-eating primates. However, we do not exclude the possibility

570 that such a strategy will be functional for primates that rely on other highly synchronous

571 plant parts, such as bamboo shoots [*Gorilla gorilla*; Byrne, 1995] or high quality young

572 leaves.

573   Substantial variation in synchrony levels across species in each forest suggest a

574 possible benefit to chimpanzees to learn species-specific differences in synchrony

575 levels. Evidence for such learning abilities has been shown in Taï chimpanzees

576 [Janmaat et al., 2013b]. It remains to be investigated what other primate species have

577 the cognitive abilities to do so, and whether they are aided by an ability to generalize or

578 classify trees in species with high versus low levels of synchrony or, if there is a

579 taxonomic relation to synchrony, if animals can make assessments based on plant type

580 [Janmaat et al., 2013b].

581   Surprisingly, we observed fluctuations in the monthly percentage of trees that

582 bore fruit within the same species across years and between forests. These findings are

583 congruent with results from earlier studies, which indicated that synchrony levels

584 differed between separate parts of a home range or a forest [MacKinnon, 1974;

585 Chapman et al., 1999b; Janmaat et al., 2012]. MacKinnon [1974] suggested that these

586 spatial differences in synchrony levels could be attributable to heavy local rains, which

587 kill both the flowers and pollinators responsible for fertilizing them, inhibiting fruit

588 production locally.

589   Considering these findings, we argue that it is unlikely that chimpanzees rely on a

590 synchronicity-based search strategy that is genetically "hardwired", but that these

591 strategies need to be learned to lead to efficient foraging. We hypothesize that such

592 learning is flexible, enabling primates to update themselves on synchrony levels based

593 on encounter rates of fruit-bearing trees at the start of each season, rather then

594 remembering species-specific levels from previous seasons or feeding locations

595 [Janmaat et al., 2012].

596

597 Once a tree is "known" to produce how often will it produce ripe fruit and how

598 much?

599 Considering the large variation in fruiting frequencies by individual trees during the

600 fruiting time period of the species, we hypothesize that chimpanzees may remember

601 fruit production histories of individual trees, to avoid travelling towards trees that are

602 likely to be empty. However, since some species showed substantially higher levels of

603 inter-individual variation than others, it is unlikely that the advantages of such

604 information will be similar for all tree species. Some species show such small variation

605 in fruiting frequencies that remembering the histories of individual trees may not be

606 worth the effort. Another factor that could result in a low benefit of remembering

607 fruiting histories of individual trees is the species' spatial distribution. If trees are

608 spatially clustered, it could be as efficient to simply remember the fruiting history of a

609 forest patch, than that of each single tree within it [Normand et al., 2009]. Such

610 advantages could potentially explain the higher performance of human and non-human

611 primates in short-term memory tasks when locations are clustered in space compared to

612 when they are not [De Lillo et al., 1997; De Lillo & James, 2012].

613   We found that certain trees had full crowns for a substantially larger proportion of

614 ripe fruit bearing months than others. This was congruent with earlier observations that

615 certain groups of trees in the Taï forest had a yearly maximum fruit score larger than 2

616 for the majority of years, while another much larger group of tree individuals had a

617 yearly maximum class lower than 2 for the majority of years [Janmaat et al., 2013a].

618 The inter-individual variation was however weaker than expected with very few

619 individuals producing only large or only small fruit crops. Moreover, the number of

620 months that trees had high fruit production scores differed between years. This could be

621 explained by the possibility that crop size is not only determined by the age of the plant

622 and its micro-habitat conditions (e.g., soil quality), but also by temporal changes in

623 weather conditions and fruit foragers' densities [e.g. Van Schaik, 1993; Houle, 2004].

624   Extensive observations of habituated chimpanzee females in the Taï forest

625 indicated that inter-annual revisiting and goal-directed monitoring of feeding trees can

626 be extremely rare when territories are large and tree density and diversity is high

627 [Janmaat et al., 2013a, 2013b]. Out of 268 trees that were fed on by one female

628 chimpanzee in Taï in 2009 only 20 and 18 trees were fed on in the same months and

629 fruiting seasons in 2010 and 2011, respectively [Janmaat et al., 2013b]. Out of 118 trees

630 that were fed on by a second female in 2009 none were fed on in the same months of

631 2010, while other trees of the same species were producing fruit. In addition, most trees

632 were inspected for fruit *en route* and only 13% were approached in a goal-directed

633 manner [Janmaat et al., 2013a]. This suggests that the use of an across-seasonal memory

634 of fruiting histories is likely restricted to a very small number of trees that reliably

635 produce fruit or large fruit crops. Yet evidence for an across-seasonal memory has been

636 shown to exist in Taï chimpanzees [Janmaat et al., 2013a]. Based on this study we

637 hypothesize that chimpanzees will target their travels to monitor trees that have a high

638 probability of producing fruit. In addition, we expect them to store and retrieve

639 information on fruiting histories over a large number of years especially when we

640 consider that some inter-fruiting intervals are greater than six years (e.g. *Parinari*

641 *excelsa* in Kanyawara, within 132 months of consecutive observation).

642

643 What cognitive abilities could facilitate the localization of ephemeral food and

644 maximize energy intake when times are lean?

645 The most energetically rewarding and cognitive flexible behavior proposed to be used

646 by large-brained primates to buffer periods of food scarcity is extractive foraging and

647 tool use [Van Woerden et al., 2010; 2012]. Our extensive assessment of the spatio-

648 temporal complexity and predictability of chimpanzee plant foods allows us to propose

649 an additional important set of flexible behaviors that large-brained primates can use to

650 maximize their energy intake when times are lean. We propose that chimpanzees can

651 use behavioral strategies to outcompete sympatric animals in exploiting easily

652 accessible energy-rich foods, such as ripe fruit, by optimizing their arrival time. It could

653 be argued that the timing of arrival is of little importance as chimpanzees can simply

654 chase away competitors from ripe fruit sources through direct (contest) competition,

655 likely facilitated by a larger body size [Anderson, 1984; Houle, 2004; Houle et al.,

656 2010; but see Zuberbühler & Janmaat, 2010]. However, such chases will not stop

657 competitors from consuming all ripe fruit prior to the arrival of chimpanzees. Hence, we

658 hypothesize that chimpanzees can still benefit by actively reducing indirect (scramble)

659 competition for dispersed and ephemeral foods through adjusting their timing of arrival.

660 Chimpanzees could employ cognitive strategies that enable them to forage more

661 efficiently, either by facilitating early discoveries of large amounts of energy-rich foods,

662   or by optimizing return times to previous feeding locations. A variety of studies have

663   found evidence that primates use spatial memory to relocate ephemeral food sources

664   and can keep track of changes in fruit availability [reviewed in Janson & Byrne, 1997;

665   Janson & Chapman, 1999; Janmaat et al., 2006a; Janmaat et al., 2006b; Martin-Ordas et

666   al., 2010; Zuberbühler & Janmaat, 2010; Sayers & Menzel, 2012; Ban et al., 2014].

667   Robert Barton [1998, 2004] furthermore suggested that the advanced visual

668   specialization of primates, despite short average detection distances within dense forest

669   vegetation, facilitates ripe fruit discovery [Janson & Di Bitetti, 1997; Janmaat et al.,

670   2013a]. Knowledge on what other cognitive strategies are used to discover newly

671   produced and ephemeral food is limited and in need of further investigation.

672   Based on the results of this study we hypothesize that to improve the efficiency of

673   fruit discovery, chimpanzees continuously update their knowledge regarding both the

674   synchrony levels of their food in time and space and the species-specific differences of

675   these levels as well as the fruiting histories of individual trees belonging to species with

676   high levels of inter-individual variation or patches of trees. We further hypothesize that

677   chimpanzees have an ability to use the following suite of cognitive mechanisms in

678   combination with search by use of sensory cues and spatial memory of "known" trees:

679   1) An ability to learn to generalize or classify food plants as belonging to a species (with

680   or without the presence of food), or a class with high and low levels of synchrony, food

681   persistence duration (ephemerality levels) or food production frequencies. 2) An ability

682   to flexibly learn to acquire, store, integrate, order and retrieve information on a) the

683   frequency of phenophase occurrences, b) the relative amounts of fruit and young leaves

684   and variables that influence changes in these amounts in individual plants, as well as c)

685   sensory information emitted by plants (e.g., the smell of ripe fruits) and other sympatric

686   foragers, including group members that indicate the availability of food. 3) An ability to

687   plan or anticipate efficient monitoring (or return) times and efficient travel paths

688   between food producing plants.

689   We expect that chimpanzees will use a combination of these cognitive abilities to

690   reach their goals. For example, once a chimpanzee discovers the first fruit in a highly

691   synchronous plant species that has high variation in fruiting frequencies, it could plan its

692   approach towards a specific tree of the same species – a tree for which its long-term

693   memory informs the chimpanzee that the tree had a good fruiting history and a high

694   probability of bearing a large amount of fruit within season. The chimpanzee could then

695   use this ability in combination with one that can use the sounds of other foragers and

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696 smell of the fruit, to confirm whether the tree has not been depleted, once it arrives in

697 the vicinity, and a spatial memory (using a variety of cognitive maps or orientation

698 skills) to efficiently travel towards the respective tree.

699   In short, ecological intelligence is so much more than solely remembering the

700 spatial location of a number of food trees within a large home range. We conjecture that

701 successful foraging depends on a combination of a large variety of cognitive skills,

702 especially an ability to obtain, store and retrieve knowledge on temporal availability of

703 food in individual trees. Here, we hypothesized on the existence of a suite of cognitive

704 strategies that chimpanzees could employ to maximize food finding efficiency in

705 periods of scarcity by using individual and species specific information on the

706 predictability of their food in individual trees. We challenge cognitive scientists to test

707 whether chimpanzees indeed employ the proposed strategies and whether other primates

708 with smaller brains are able to do the same. Lastly, we hope that our quantification of

709 the temporal complexity of primate food in the three African tropical forests will help

710 future primatologists to further elaborate on and test hypotheses on the cognitive

711 abilities of a wide variety of primate species to provide new insight and ideas on the

712 comparative studies that test the role of ecological complexity in primate brain size

713 evolution.

714

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737

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1046   **Figure legends**

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1048   **Fig.1. The availability of young leaves, unripe fruit and ripe fruit in the focal phenology**

1049   **trees situated in three chimpanzee territories.** Panel a) shows the proportion of all

1050   observations amongst trees were found to bear ripe fruit, unripe fruit, young leaves or none of

1051   the above (N=425,836). Panel b) focuses on the ripe fruit phenophase, showing the proportion

1052   of observations in each of the four ripe fruit production scores given that ripe fruit was

1053   observed**.**

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1055   **Fig. 2 The encounter rates of large ripe and unripe fruit crops in old growth rain forest.**

1056   The open and filled squares represent the average number of trees found along one km of

1057   transect in the old growth forest of the Kanyawara chimpanzee community that bore a large ripe

1058   or unripe fruit crop, respectively. Trees with large fruit crops are defined as trees with a trunk

1059   size equal or larger than the average feeding tree of Kanyawara chimpanzees and a crown that is

1060   more than 50% filled (rank core >2) with ripe fruit.

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1062   **Fig. 3 The timing of ripe fruit availability in individual trees.** Examples of frequency and

1063   intra-specific synchrony (see Fig. 4) of ripe fruit availability of individual trees. Black and grey

1064   dots represent ripe fruit presence and absence, respectively; no dot represents missing data. The

1065   size of the dots are propotional to the fruit production scores; blank white spaces denote no data

1066   collected. Panel a) shows the fruiting pattern for trees of *Coula edulis* in Taï forest, for which it

1067 is relatively easy to predict which individual will bear fruit in season (high synchrony level) and

1068 in which month the season starts (fixed timing). Panel b) shows the pattern for *Uvariopsis*

1069 *congensis* in Kanyawara forest, for which it is relatively easy to predict which individual will

1070 bear fruit in the season (high synchrony level), but where the timing of the season is less

1071 predictable (fluctuating timing). Panel c) shows the pattern for *Ficus sansibarica* in Taï forest,

1072 in which it is difficult to predict which individuals will fruit in which month (asynchronous and

1073 fluctuating timing).

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1075 **Fig.4. Intra-specific ripe fruit mean synchrony by species at each of the three sites.**

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1077 **Fig. 5. Ripe fruit patterns for *Erythroxylum mannii* in two forests, a) Loango (mean**

1078 **synchrony=0.33) and b) Taï (mean synchrony=0.65), illustrating that the same species can**

1079 **have contrasting levels of intra-specific synchrony.** Black and grey dots represent ripe fruit

1080 presence and absence, respectively; no dot represents missing data. The size of the dots are

1081 propotional to the fruit production scores; blank white spaces denote no data collected.

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1083 **Fig. 6. Inter-individual variation in ripe fruit production frequencies in individual trees**.

1084 The number of months that individual trees bore ripe fruit within a consecutive uninterrupted

1085 observation periods of a) 76 months in Kanyawara, b) 67 months in Loango, and c)144 months

1086 in Taï forest. At least 5 trees per species were monitored. Bars represent median values of the

1087 proportions; upper and lower boundaries of boxes represent the upper and lower quartiles.

1088 Whiskers represent the lowest and highest data points still falling within 1.5 times the

1089 interquartile range; Points represent outliers.

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1091 **Fig. 7. Inter-individual variation in the amount of fruit produced during ripe fruiting**

1092 **bouts.** The percentage of months individual trees had a fruit production score larger than 2 out

1093 of all the months individual trees bore ripe fruit. Each species includes data on at least 5

1094 individuals that bore fruit for at least 5 months. Bars represent median values of the proportions;

1095 upper and lower boundaries of boxes represent the upper and lower quartiles. Whiskers

1096 represent the lowest and highest data points still falling within 1.5 times the interquartile range;

1097 Points represent outliers.

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Table 1. Tree and species distribution in three tropical forests

|	Kanyawara	Taï	Loango
# trees/ha (DBH>10cm)	406	507	321
# chimpanzee fruit trees/ha	237	325	162*
# average sized chimpanzee fruit trees/ha (DBH>67cm)	9.81	11.00	8.18*
# chimpanzee fruit species	75	150	79*
# monitored chimpanzee fruit species	45	107	38

* These numbers may be underestimations as diet composition was based on 5 years of observation and dung analysis of non-habituated chimpanzees, compared to 30 and 25 years of feeding observations for the Taï and Kanyawara chimpanzee communities, respectively

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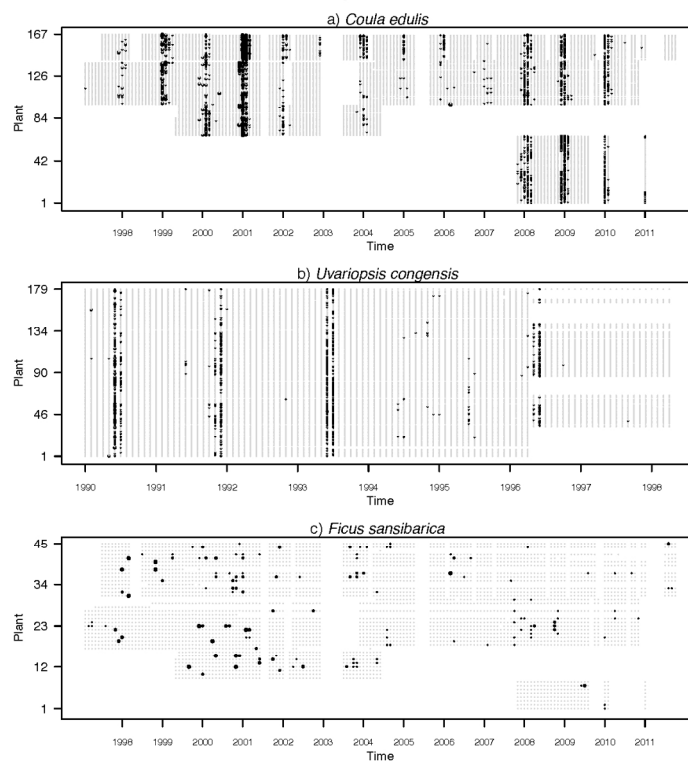51
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Figure 1
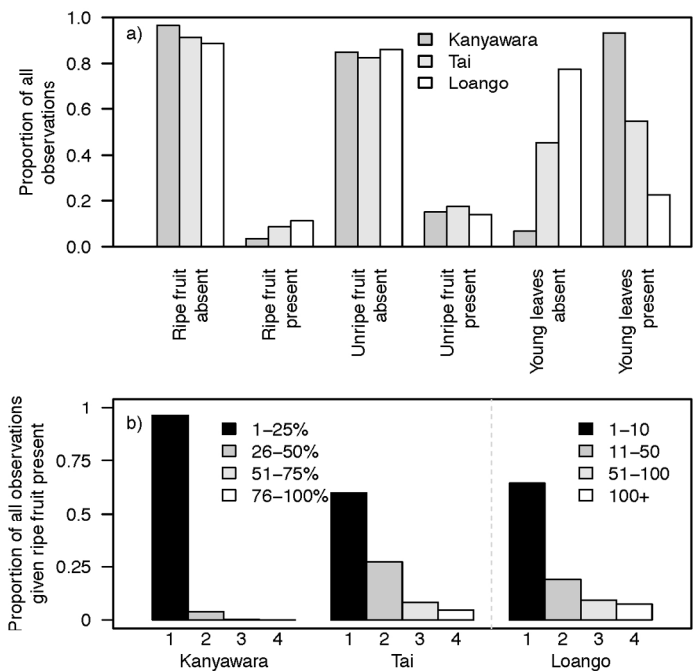
The availability of young leaves, unripe fruit and ripe fruit in the focal phenology trees situated in three chimpanzee territories. Panel a) shows the proportion of all observations amongst trees were found to bear ripe fruit, unripe fruit, young leaves or none of the above (N=425,836). Panel b) focuses on the ripe fruit phenophase, showing the proportion of observations in each of the four ripe fruit production scores given that ripe fruit was observed.
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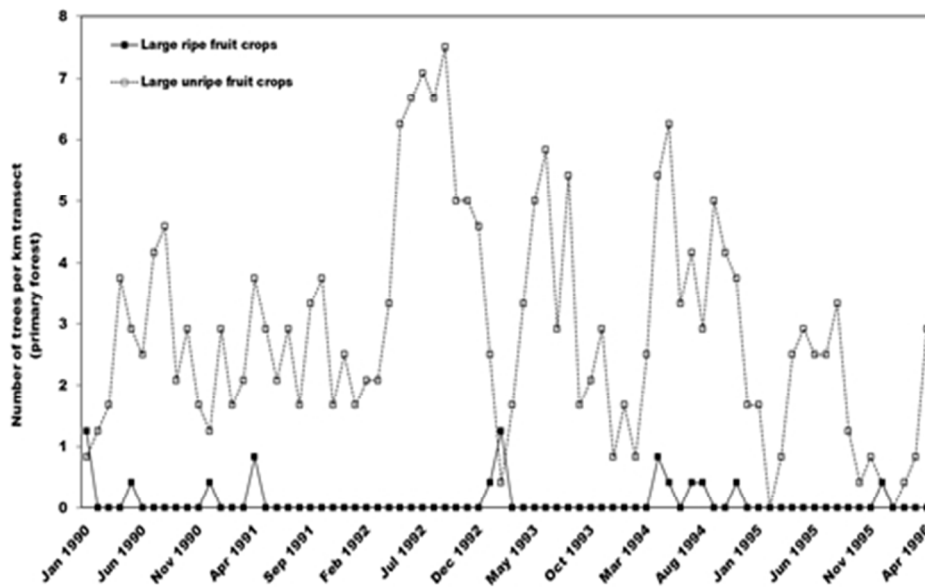
The encounter rates of large ripe and unripe fruit crops in old growth rain forest. The open and filled squares represent the average number of trees found along one km of transect in the old growth forest of the Kanyawara chimpanzee community that bore a large ripe or unripe fruit crop, respectively. Trees with large fruit crops are defined as trees with a trunk size equal or larger than the average feeding tree of Kanyawara chimpanzees and a crown that is more than 50% filled (rank core >2) with ripe fruit.
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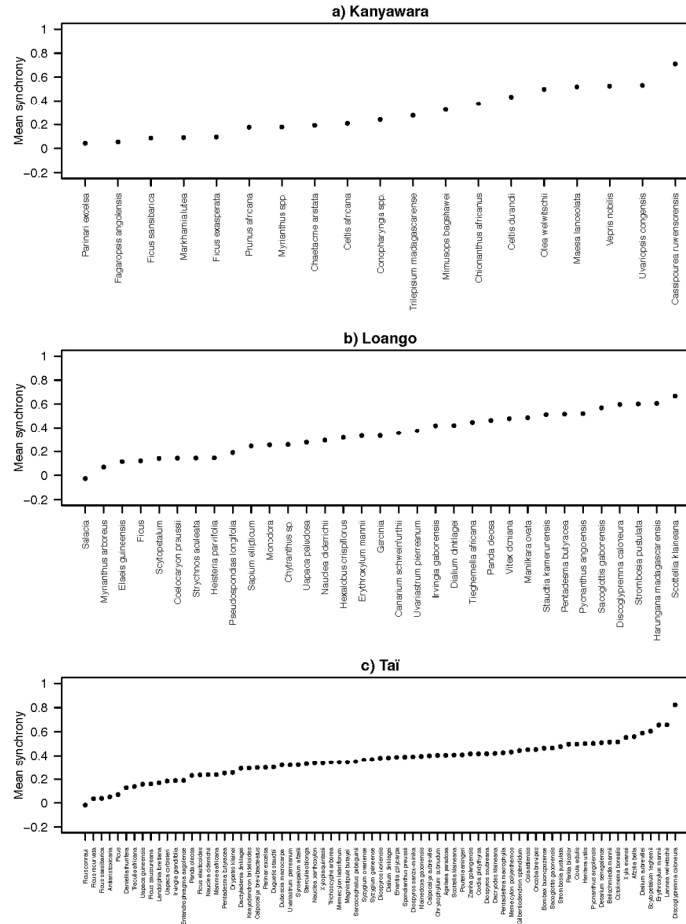21
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Figure 3

The timing of ripe fruit availability in individual trees. Examples of frequency and intra-specific synchrony (see Fig. 4) of ripe fruit availability of individual trees. Black and grey dots represent ripe fruit presence and absence, respectively; no dot represents missing data. The size of the dots are propotional to the fruit production scores; blank white spaces denote no data collected. Panel a) shows the fruiting pattern for trees of Coula edulis in Taï forest, for which it is relatively easy to predict which individual will bear fruit in season (high synchrony level) and in which month the season starts (fixed timing). Panel b) shows the pattern for Uvariopsis congensis in Kanyawara forest, for which it is relatively easy to predict which individual will bear fruit in the season (high synchrony level), but where the timing of the season is less predictable (fluctuating timing). Panel c) shows the pattern for Ficus sansibarica in Taï forest, in which it is difficult to predict which individuals will fruit in which month (asynchronous and fluctuating timing).
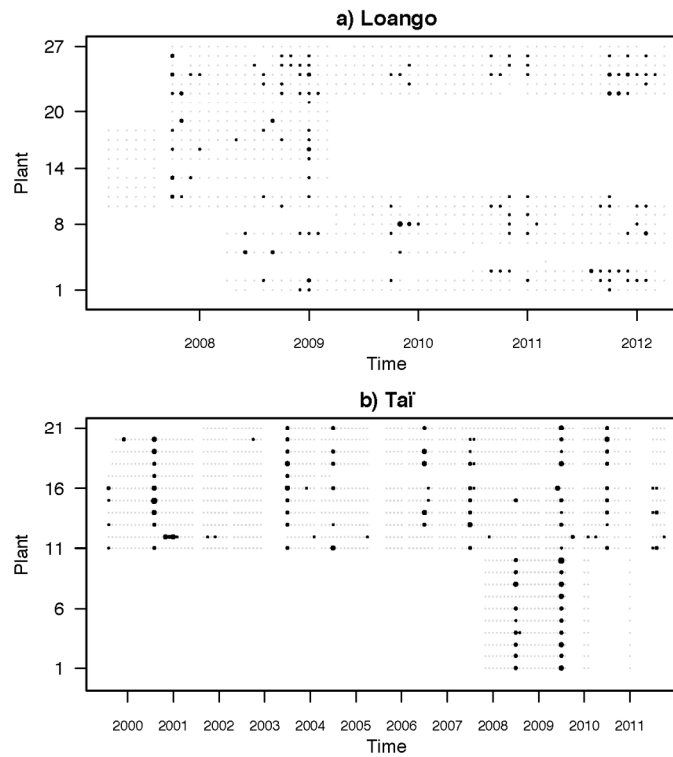215x279mm (200 x 200 DPI)

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Figure 4

Intra-specific ripe fruit mean synchrony by species at each of the three sites.
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Figure 5

Ripe fruit patterns for Erythroxylum mannii in two forests, a) Loango (mean synchrony=0.33) and b) Taï (mean synchrony=0.65), illustrating that the same species can have contrasting levels of intra-specific synchrony. Black and grey dots represent ripe fruit presence and absence, respectively; no dot represents missing data. The size of the dots are propotional to the fruit production scores; blank white spaces denote no data collected.
215x279mm (200 x 200 DPI)
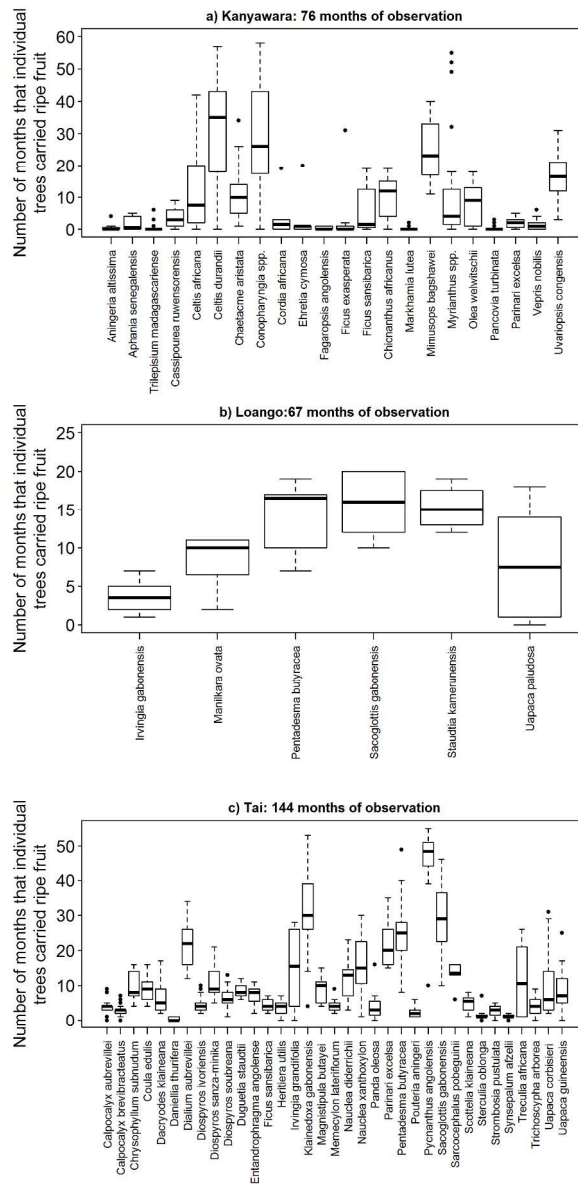
Inter-individual variation in ripe fruit production frequencies in individual trees. The number of months that individual trees bore ripe fruit within a consecutive uninterrupted observation periods of a) 76 months in Kanyawara, b) 67 months in Loango, and c)144 months in Taï forest. At least 5 trees per species were monitored. Bars represent median values of the proportions; upper and lower boundaries of boxes represent the upper and lower quartiles. Whiskers represent the lowest and highest data points still falling within 1.5 times the interquartile range; Points represent outliers.

149x299mm (300 x 300 DPI)
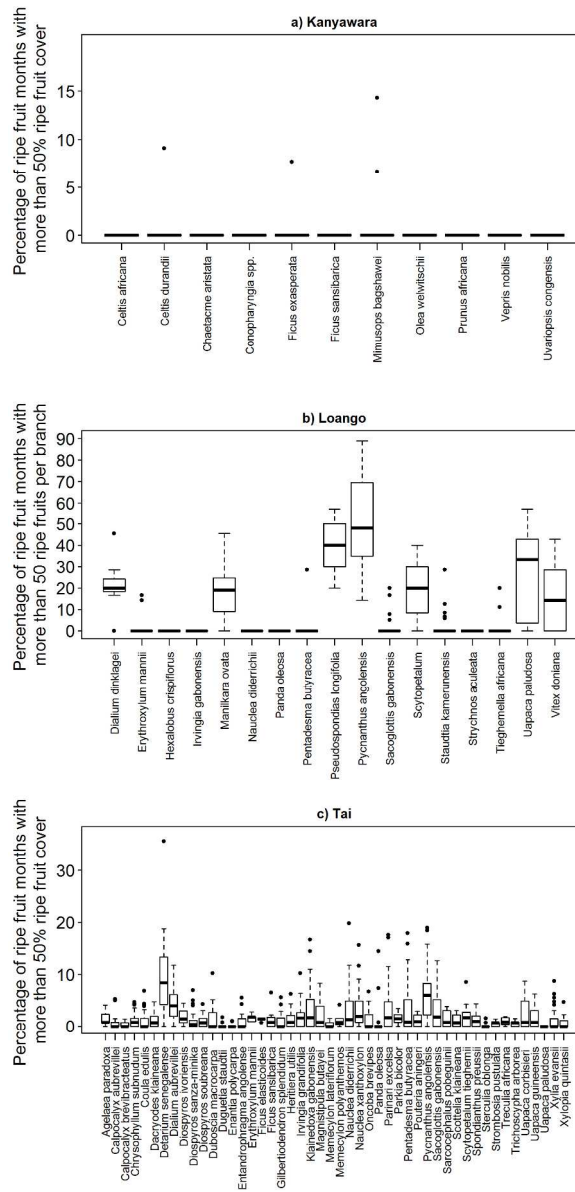
Inter-individual variation in the amount of fruit produced during ripe fruiting bouts. The percentage of months individual trees had a fruit production score larger than 2 out of all the months individual trees bore ripe fruit. Each species includes data on at least 5 individuals that bore fruit for at least 5 months. Bars represent median values of the proportions; upper and lower boundaries of boxes represent the upper and lower quartiles. Whiskers represent the lowest and highest data points still falling within 1.5 times the interquartile range; Points represent outliers.

149x299mm (300 x 300 DPI)