1   TITLE: Chimpanzee diet composition and food availability in a

2   human-modified landscape at Lagoas de Cufada National Park,

3   Guinea-Bissau

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5   Running title: Chimpanzee diet and food availability in Guinea-Bissau

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16

Abstract

Throughout their range, chimpanzee populations are facing widespread conversion of their suitable habitat to human-modified landscapes dominated by agriculture. Cultivated foods may offer alternative resources to chimpanzees, particularly during periods of wild fruit scarcity. We assessed intra-seasonal variation in dietary composition and diversity of chimpanzees at Lagoas de Cufada Natural Park, Guinea-Bissau, a forest-savannah mosaic disturbed by humans, in relation to food availability. A phenological study was conducted from March 2011 to February 2012 by sampling focal plant taxa. Macroscopic analyses of faecal samples and feeding remains were conducted during the dry season (February-May and October-December) of 2011. More fruits were available in the dry than in the wet season and ripe fruit availability peaked in the late dry season. Chimpanzees showed a fruit-based diet composed of 31 identified plant species. Faecal samples were dominated by wild species (82.38%), while cultivated species were rare (0.87%; 16.75% unidentified). Chimpanzees chose wild fruit species disproportionately to their overall availability. There was no significant association between dietary composition and distances among faeces, suggesting that chimpanzees have access to and largely use the same set of plant species over the entire study area. Moreover, no influence of settlements or roads as proxies for the presence of cultivated areas was found on dietary composition. Our findings highlight that chimpanzees in this human-modified landscape still mostly rely on the consumption of wild fruit species and rarely include cultivated foods in their diet. This underscores the importance of preserving remnants of native vegetation within agriculture-dominated landscapes to ensure persistence of chimpanzee populations and the maintenance of the seed dispersal services they provide.

Introduction

Primates play an important role in ecosystem functioning as both seed consumers and seed dispersers, representing a large part of the frugivore biomass in tropical forests (Lambert and Garber 1998; Wrangham *et al.* 1994). Increasing anthropogenic habitat loss, climate change, human settlement of wild areas and hunting may negatively impact or disrupt these ecosystem services (Levi and Peres 2013). Habitat loss and fragmentation have been reducing the area of suitable environmental conditions for primates (Junker *et al.* 2012). Suitable habitat for chimpanzees is increasingly surrounded by agricultural and agro-forestry areas, especially where human population density is high (Campbell *et al.* 2008). Consequently, chimpanzee populations frequently live in fairly close contact with humans which leads to the transmission of diseases and pathogens (Campbell *et al.* 2008) and often results in chimpanzee-human conflicts as a result of crop-raiding (Hockings *et al.* 2009). Recent studies have provided insights into the diet and feeding ecology of chimpanzees in human-modified landscapes (Hockings *et al.* 2009; Hockings and McLennan 2012; McLennan 2013). They suggest that new feeding opportunities arise from crops, particularly the consumption of cultivated foods by chimpanzees in periods of wild fruit scarcity. However, little is known about whether there are consistent shifts in dietary composition with respect to the proximity to settlements or roads, which often can be regarded as suitable proxies for the presence of agricultural areas (Hockings and Sousa 2012) (Joana Carvalho, personal observation).

As ripe-fruit specialists, chimpanzees show an overwhelmingly fruit-based diet, selecting preferred fruits disproportionately to their overall availability (Conklin-Brittain *et al.* 1998; Hladik 1977; Tutin *et al.* 1997; Wrangham 1977; Wrangham *et al.* 1998). Preferred fruits are high-quality foods that contain low levels of secondary

compounds and high levels of energy (Conklin-Brittain *et al.* 1998; Hladik 1977;

Reynolds *et al.* 1998; Wrangham *et al.* 1998). In periods of scarcity of preferred fruits

chimpanzees supplement their diet with lower-quality foods, such as non-preferred

fruits, foliage, flower, bark, piths, or even honey, mushrooms, insects or arthropods

(Basabose 2002; McGrew *et al.* 1988; Watts *et al.* 2012; Wrangham *et al.* 1998), which

are considered fallback foods (Lambert 2007; Marshall and Wrangham 2007).

Macroscopic analysis of faecal samples is a commonly used nonintrusive

method for describing dietary patterns of many taxa (e.g. birds (Loiselle and Blake

1999), bats (García-Morales *et al.* 2012)), including poorly habituated chimpanzee

populations (Basabose 2002; McGrew *et al.* 2009; Morgan and Sanz 2006; Moscovice

et al. 2007; Tutin and Fernandez 1993a). Despite not providing a complete repertoire of

food items (McGrew *et al.* 1988; Tutin and Fernandez 1993a), macroscopic analysis is

useful to expand the variety of known dietary constituents in chimpanzee populations

(McGrew *et al.* 2009; Phillips and McGrew 2013). Also, it allows diet comparisons

between African ape populations if fecal samples are collected and processed in a

similar fashion (Tutin and Fernandez 1993a).

Since food availability may determine spatial and temporal variation in

chimpanzee distribution and abundance, and influence patterns of habitat use,

knowledge about phenological patterns of plant species on which chimpanzees base

their diet is crucial (Baldwin *et al.* 1982; Suzuki 1969; Tutin and Fernandez 1993b).

Phenological events are the plant biological activities over the course of an annual

cycle, representing adaptations to the seasonality of biotic or abiotic factors (van Schaik

et al. 1993), which are often site-dependent (Chapman *et al.* 1999).

We assessed the diet of the western chimpanzee, *Pan troglodytes verus*, in a

protected, but highly human-modified landscape in Guinea-Bissau during the dry

94   season. We expected intra-seasonal variation in dietary richness and diversity of fruit

95   species according to fruit availability. Specifically, we predicted that 1) chimpanzee diet

96   would be fruit-dominated, but less diverse when fruit availability is high, i.e. in periods

97   when ripe fruit abundance is highest chimpanzees should focus on a smaller subset of

98   fruit species, and 2) fruit consumption is non-random with respect to availability and

99   chimpanzees preferentially select certain fruit species from those available. Moreover,

100   we hypothesized that dietary composition shows spatial variation. In particular, we

101   predicted that 3) similarity in diet composition decreases with increasing distance

102   among faecal samples, and 4) the proximity to agricultural areas influences diet

103   composition due to increased consumption of cultivated species.

104

105   **Methods**

106   Ethical Note

107   This research adhered to the legal requirements of the governmental agency that

108   manages the protected areas in Guinea-Bissau (*Instituto da Biodiversidade e das Áreas*

109   *Protegidas*).

110

111   Study Area and Study Species

112   Lagoas de Cufada Natural Park (LCNP, 11º34'-11º51' N and 14º49'-15º16' W)

113   is a protected area in Guinea-Bissau (Fig. 1), a small West African country located

114   between the rainforests of the Gulf of Guinea and the Sahelian and Sudanese semi-arid

115   zone of dry savannahs and open-canopy forests (Catarino *et al.* 2002). Dense-canopy

116   forests are distinguished by higher canopy coverage (ca. 90 %) and an undeveloped

117   understory, and correspond to 9% of the total area of LCNP (Amaro 2011). Open-

118   canopy forests or savannah-woodlands are characterized by lower canopy cover (ca. 60-

6

119   70 % and 20-40 %, respectively) and predominate in the LCNP landscape (35 and 54 %,

120   respectively Amaro 2011). For a detailed description of habitat structure, diversity and

121   composition see Carvalho et al. (2015) and Catarino et al. (2002). Mean annual

122   temperature is 26 ºC and annual rainfall averages 2200 mm, which mostly falls during

123   the wet season (June-October), whereas almost no precipitation (<100 mm) occurs

124   during the dry season (November-May) (Catarino *et al.* 2002;

125   http://sdwebx.worldbank.org/climateportal/index.cfm). LCNP is disturbed by human

126   activities. Approximately 11,000 people belonging to different ethnic groups live inside

127   the park and rely extensively on its natural resources for their survival (IBAP 2008).

128   Most of the roads and settlements are surrounded by agricultural areas, particularly

129   cashew plantations (Carvalho *et al.* 2013).

130   *Pan t. verus* has been classified as Endangered on the IUCN Red List since 1988

131   (IUCN 2015). Its range encompasses nine West African countries, although it is already

132   considered rare or close to extinction in four of them, including Guinea-Bissau (Kormos

133   *et al.* 2003). This subspecies showed a considerable population reduction over the last

134   20-30 years as a consequence of the impact of human activities. For LCNP, chimpanzee

135   density was recently estimated to be 0.22 nest builders /km^2 (95% CI 0.08-0.62),

136   corresponding to 137 chimpanzees (95% CI 51-390) (Carvalho *et al.* 2013). The highest

137   density was estimated for dense-canopy forest, which despite being the least available

138   and most threatened habitat type offers the most suitable habitat conditions and

139   protection from human disturbance (Carvalho *et al.* 2013; 2015).

140

141   Dietary Composition and Diversity

142   As chimpanzees in LCNP are very elusive, we relied on macroscopic analysis of

143   faecal samples and feeding remains to describe their diet (Basabose 2002; 2004;

144 Lambert 1999; McGrew *et al.* 2009). Over the dry season of 2011 (February-May and

145 October-December), 210 faecal samples were collected (averaging 30 ± 0.52 SE

146 samples per month, range 7-68) by visiting eleven linear transects that were

147 systematically spread over the study area (five visits between February and May and

148 four visits between October and December, at biweekly sampling intervals). Additional

149 samples were collected along random trails used to access these transects (Fig. 1). The

150 transects included different habitat types such as both forest types, savannah-woodland,

151 herbaceous savannah, agricultural areas and settlements (Carvalho *et al.* 2013). Each

152 sample was collected in a plastic bag and the corresponding geographic location (using

153 a Global Positioning System - GPS Garmin 60) and habitat type recorded. Faeces were

154 sluiced in sieves of 1 mm mesh, stored in a plastic bag and dried in sunlight. For each

155 sample, the contents were divided into the following food items: fruits (including seeds,

156 pulp, and fruit skins), foliage (fibers and digested fragments of leaves), flowers, and

157 non-plant food items (e.g. fragments of insects, hairs, bones). The percentage volume of

158 these items was estimated in intervals of 5 % (Basabose 2002; Phillips and McGrew

159 2014). Each food item was photographed, identified and preserved in paper bags

160 containing silica gel. Identification of food items was carried out to the lowest level of

161 taxonomic resolution possible. Except for figs, we counted all seeds present per sample.

162 Some seeds, such as those of *Aframomum*, *Ficus*, and *Vitex*, were only identified to the

163 genus level.

164   From out of 10 direct chimpanzee observations in 2011, only in three cases

165 feeding remains were found, i.e. wadges (N=29) and partially consumed fruits or foliage

166 (N=9). Most feeding remains were identified on site and photographed. They were only

167 qualitatively considered to provide information on fibrous species that are difficult to

168 identify by faecal analysis (Chancellor *et al.* 2012).

169   Plant species identification was done with help from the park guards and other

170   locals. When necessary, samples were collected for later identification at the herbarium

171   of the *Instituto de Investigação Científica e Tropical* (Lisbon, Portugal). As non-plant

172   food items, such as fragments of insects (N=8), parasites (N=2), bones (N=2), and hairs

173   from small mammals (N=27), were difficult to identify, only plant matter was

174   considered for further analysis.

175

176   Assessment of Food Availability

177   Before the phenological study we compiled a list of wild and cultivated species

178   known to be eaten by chimpanzees based on information provided by park guards and

179   residents, as well as by checking lists from West, Central and East African sites (see

180   Table I). Phenological data on focal plant taxa were recorded monthly (Marshall and

181   Wich 2013), from March 2011 to February 2012. Individuals monitored per species

182   were randomly selected along access trails to the transects which covered both forest

183   types, savannah-woodland and agricultural areas (including settlements and cashew

184   plantations) (Fig. 1). Phenological events on 346 individuals (298 trees with a diameter

185   at breast height, dbh, >10 cm, 16 lianas with dbh >1 cm, 30 herbs, and 2 shrubs) of 25

186   species (N_{wild}=20, $N_{cultivated}$=5) from 14 families were recorded (Table I). We noted the

187   phenophase, i.e. presence or absence of leaves, flowers, and fruits, and the

188   corresponding phenological events (leaves and flowers: new/immature or old/mature;

189   fruits: unripe or ripe).

190

191   Data Analyses

192   All analyses were conducted in R version 3.0.2 (R Development Core Team

193   2013). Reported values are mean ± SE unless otherwise noted**.**

194

Dietary composition and diversity

196   The percentage volume of a food item q for each species s in each faeces f per

197   month m (P_{qsfm}) was assessed as

198    $$P_{qsfm} = \frac{x_{qsfm}}{\sum\limits_{q=1}^{Q}\sum\limits_{s=1}^{S} x_{qsfm}} \times 100 \qquad (1)$$

199   where x_{qsfm} corresponds to the volume of food item q of species s for faeces f in month

200   m ($q=1,\ldots, Q$; $s=1,\ldots, S$; $f=1,\ldots, T$; $m=1,\ldots, M$). We also calculated the mean

201   percentage volume of each food item q for each species s per month m (P_{qsm}) as

202    $$P_{qsm} = \frac{\sum\limits_{f=1}^{T_m} P_{qsfm}}{T_m} \qquad (2)$$

203   where T_m represents the total number of faeces in month m. The percentage volume of

204   food item q in month m (P_{qm}) was calculated as

205    $$P_{qm} = \sum\limits_{s=1}^{S} P_{qsm} \qquad (3)$$

206   Similarly, the percentage volume of species s in month m (P_{sm}) was obtained as

207    $$P_{sm} = \sum\limits_{q=1}^{Q} P_{qsm} \qquad (4)$$

208   Finally, the mean fruit species occurrence in month m (P_m) in faeces was defined

209   as

210    $$P_m = \sum\limits_{s=1}^{S} P_{sm} \qquad (5)$$

211   Because of different faecal sample sizes per month, we used sample-based

212   rarefaction (Gotelli and Colwell 2010) to calculate the fruit species richness expected in

213   a subset of samples. Sample-based rarefaction was computed using EstimateS software

214   (Colwell 2013) and comparisons were made at N=5 faecal samples, the maximum

215   number of faecal samples with fruit species in common across dry season months. We

216   assessed intra-seasonal variation in dietary diversity of fruit species by calculating the

217   exponential form of the commonly used Shannon index, e^H (Jost 2006).

218

219   *Assessment of food availability*

220   The percentage proportion of phenological event k for phenophase p in month m

221   (P_{kpm}) was expressed as

222   $$P_{kpm} = \frac{\sum_{i=1}^{I} y_{kpmi}}{I_m} \times 100 \qquad (6)$$

223   where y_{kipm} represents the phenological event k in phenophase p in month m for

224   individual i and I_m corresponds to the number of individuals in month m (k=1,…, K;

225   p=1,…, O; i=1,…, I).

226   Ripe fruit abundance was estimated based on tree dbh (Chapman *et al.* 1992)

227   and a monthly fruit availability index (F_m) was calculated as

228   $$F_m = \sum_{i=1}^{I} A_s \times \frac{R_{sm}}{I_{sm}} \times dbh_s \qquad (7)$$

229   where A_s represents the abundance of species s found in previous vegetation surveys

230   (see Carvalho *et al.* 2015), R_{sm} corresponds to the number of individuals of species s in

231   month m with ripe fruits during phenological surveys, I_{sm} represents the number of

232   individuals of species s in phenological surveys and dbh_s denotes the mean dbh of

233   species s with ripe fruits. This index was calculated (a) including all ripe fruit species

234   (N=25), (b) only wild species (N=20), (c) only cultivated species (N=5), and (d) only

235   species in common with those identified in faeces (N=11). For all direct comparisons

236   with the faecal data phenological data were restricted to the dry season.

Fruit consumption and availability

239   Linear regression was used to evaluate whether fruit consumption over the dry

240   season (dietary richness of fruit species per month or monthly dietary diversity of fruit

241   species) was correlated with the F_m index. Separate regressions were performed, one

242   including all ripe fruit species and one including only ripe fruit species in common with

243   those identified in faeces.

244   A randomization test was implemented in R to investigate if the consumption of

245   fruit species deviates significantly from a random selection of the ripe fruit species

246   available. Samples of fruit species randomly selected from those available (random

247   species: RS) were compared with fruit species eaten by chimpanzees (consumed

248   species: CS). Random sampling with replacement was used to obtain RS samples

249   (N=700.00, corresponding to the monthly occurrence of CS in faeces) from the ripe fruit

250   availability data (N=819.75, corresponding to the F_m index including all ripe fruit

251   species). This procedure was repeated 1000 times to evaluate how far from the expected

252   proportion given random consumption (p_{RS}) each observed proportion (p_{CS}) was. For

253   each fruit species, we obtained the distribution of consumption if that species were

254   chosen at random (p_{RS}). Plotting the expected p_{RS} distribution as a function of observed

255   p_{CS} allows one to distinguish preferred ($p_{CS}>p_{RS}$) fruit species from those consumed less

256   frequently than expected based on their availability ($p_{CS}<p_{RS}$), depending on whether the

257   distribution lies entirely below or above the 1:1 line, respectively. Overlap of the

258   randomization distribution p_{RS} with the 1:1 line indicates that the observed p_{CS} might be

259   observed as a result of random choice.

260

Spatial variation in dietary composition

262   Using ARCMAP 9.3, the Euclidean distance was calculated among faecal

263   samples, and between each faeces and settlements and roads (including main and

264   secondary roads). On average, nearest neighbor distances between faecal samples were

265   small (0.15 ± 0.05 km), but distances between faeces and roads (1.12 ± 0.08 km) and

266   faeces and settlements (2.94 ± 0.11 km) were greater (Electronic Supplementary

267   Material [ESM] Appendix S1). All spatial layers were projected into Universe

268   Transverse Mercator Zone 28N. Environmental digital data were made available

269   through the CARBOVEG project (http://carboveg-gb.dpp.pt/).

270   To assess whether dietary composition was spatially structured, we tested

271   whether the matrix of Bray-Curtis distances calculated based on the occurrence of plant

272   species in faecal samples was correlated with the matrix of distances among faecal

273   samples. We controlled for an effect of sampling month (matrix of Gower's distances)

274   using a partial Mantel test with 999 permutations (Legendre and Legendre 1998).

275   Canonical correspondence analysis (CCA), a multivariate direct gradient analysis

276   technique, was used to examine the relationship between dietary composition and two

277   explanatory variables: distances to roads and to settlements. This eigenvector ordination

278   technique was used to test for the amount of variation in chimpanzee diet explained by

279   the canonical axes, i.e. linear combinations of these variables correlated with the

280   occurrence of plant species (Legendre and Legendre 1998; ter Braak and Verdonschot

281   1995; Zuur *et al.* 2007). Overall statistical significance of the CCA was evaluated by a

282   permutation test by comparing the observed CCA result with the distribution of CCA

283   results from 1000 randomly shuffled data matrices (Legendre and Legendre 1998).

284   Partial Mantel test and CCA were performed using the R package *vegan* (Oksanen *et al.*

285   2012).

286

287 **Results**

288 Dietary Composition and Diversity

289   Overall, faecal samples were predominantly composed of fruit items (71.92 ±

290 0.67 %), followed by foliage (26.95 ± 0.57 %) and flowers (0.71 ± 0.14 %). Fruits

291 dominated faecal samples during October-November and March-May, but were

292 replaced by a higher proportion of foliage and flowers during December-February (Fig.

293 2). Consequently, for the following analyses we separated the dry season into early dry

294 season (EDS, October-November), mid dry season (MDS, December-February) and late

295 dry season (LDS, March-May). A total of 31 plant species were identified (N=28 from

296 faecal samples; N=3 exclusively from feeding remains) representing 16 families (Table

297 I). Most of these species belonged to the legume subfamily Caesalpinioideae as well as

298 to Euphorbiaceae and Gramineae. Wild species were the most recorded (82.38 ± 0.84

299 %) whereas cultivated species were rarely found (0.87 ± 0.14 %); the remainder were

300 unidentified species (16.75 ± 2.12 %). Most of the food items of wild and cultivated

301 species belonged to trees (67.23 ± 0.74 %), followed by shrubs (9.31 %), herbs (4.85 ±

302 0.36 %), and lianas (1.87 ± 0.14 %). A total of 14 species were identified in feeding

303 remains (N=38 samples), 11 of which were also found in faecal samples (Table I).

304   Dietary richness of fruit species was greater in EDS (N=19) than in MDS (N=16)

305 or LDS (N=10) (ESM Appendix S2). Sample-based rarefaction, however, suggested no

306 statistically significant difference in fruit species richness among dry season periods

307 (ESM Appendix S3). Similarly, intra-seasonal variation in dietary diversity (e^H) of fruit

308 species was not significant (Kruskal-Wallis test, χ^2 =2.00, df =2, P=0.37).

309

310 Assessment of Food Availability

14

311   To better distinguish patterns of food availability and consumption, we separated

312 the dry season as described above (EDS, MDS and LDS), and the wet season into early

313 and late wet season (EWS, June-July; LWS, August-September). Leaf shedding and leaf

314 flushing peaked during the EDS and MDS, respectively (ESM Appendix S4). Overall,

315 flower availability was greatest between MDS and LDS. Fruit availability was in line

316 with the increase in fruit species richness over the dry season and the decrease over the

317 wet season, and ripe fruit abundance peaked in LDS (ESM Appendix S4-S5). The F_m

318 index including all ripe fruit species generally followed the previously described pattern

319 (Fig. 3). Also, wild and cultivated species showed highest availability of ripe fruits in

320 LDS (Fig. 3).

321   Individual species varied considerably in terms of the amount of ripe fruits

322 provided and how fruit availability was temporally distributed over the annual cycle

323 (ESM Appendix S5). Only four species provided fruits year-round: *Landophia*

324 *heudelotii*, *Saba senegalensis*, *Elaeis guineensis*, and *Musa paradisiaca*.

325

Fruit Consumption and Availability

327   There was no significant association between the F_m index and monthly dietary

328 richness of fruit species when all ripe fruit species were included (linear regression:

329 R^2=0.13, F=0.89, P=0.38). Also, no association was found between F_m index and

330 dietary diversity (e^H) of fruit species (R^2=0.04, F=0.24, P=0.64).

331   Of the 25 fruit species monitored in phenological surveys, all of which fruited

332 during the dry season (ESM Appendix S5), only about half (N=11, 44 %) were also

333 confirmed to be eaten by chimpanzees based on faecal analysis (Table I, Fig. 4),

334 corresponding to wild species. When analysis was restricted to these consumed species,

335 a significant association between the F_m index and monthly dietary richness was found

336 (R^2=0.51, F=6.34, P<0.05) (Fig. 4). There was also a marginally significant association

337 between F_m index and dietary diversity (R^2=0.47, F=5.29, P=0.06).

338   Based on the resampling procedure, we found evidence for non-random

339 selection of fruit species by chimpanzees for five wild species: *Antiaris toxicaria*, *Ficus*

340 spp*., *Parinari excelsa*, *Spondias mombin*, and *Uvaria chamae*, which were consumed at

341 higher proportions than expected based on their availability (located below the 1:1 line,

342 Fig. 5).

343

Spatial Variation in Dietary Composition

345   Dietary composition was not correlated with distances among faecal samples

346 (partial Mantel test: r= 0.002, P=0.44). The CCA indicated that the constraining

347 explanatory variables (i.e. distances to settlements and to roads) accounted for only 0.96

348 % of variation in dietary composition, and the first canonical axis accounted for 59.90

349 % of this variability. The explanatory variables were not significantly associated with

350 dietary composition (permutation test: F=1.04, df=2, P=0.37) (ESM Appendix S6).

351

Discussion

Dietary Composition and Diversity

354   This study reports the first detailed quantitative data on diet of LCNP

355 chimpanzees during the dry season. Overall, faecal samples were dominated by fruits

356 relative to foliage and flowers, and a total of 31 plant species representing 16 families

357 were identified. Many of these species were also documented as being consumed by

358 chimpanzees in other forest and dry sites (see Table I). Dry sites have low mean annual

359 rainfall (around 1000 mm), and are mostly composed of dry habitats characterized by

360 different vegetation types ranging from open grasslands to closed woodlands and small

361 areas of forested habitats such as gallery or riverine (see Hernandez-Aguilar 2009;

362 Hernandez-Aguilar *et al.* 2013). Although a similar pattern in terms of the proportional

363 representation of different food items was found for forest-dwelling chimpanzee

364 populations (McLennan 2013; Phillips and McGrew 2014; Tutin and Fernandez 1985;

365 Tutin and Fernandez 1993a), the number of plant species reported herein is likely to

366 represent an underestimate of the true dietary diversity at LCNP because only dry

367 season faecal samples were collected. Given that chimpanzee diet varies over time and

368 dietary richness tends to increase in long-term studies (Morgan and Sanz 2006; Nishida

369 and Shigeo 1983; Sugiyama and Koman 1992), more research is necessary to

370 complement our findings and to adequately describe the full dietary repertoire of LCNP

371 chimpanzees, specifically by including wet season faecal samples and direct feeding

372 observations.

373

374 Assessment of Food Availability

375   In LCNP, leaf flushing and flowering peaks were preceded by leaf shedding that

376 occurred during the dry season, as described for other seasonally dry forests (van Schaik

377 *et al.* 1993). Fruiting phenology was partially coincident with flowering phenology and

378 fruits were abundant during the dry season, in accordance with fruiting peaks

379 documented at forest-dwelling chimpanzee sites with a unimodal rainfall pattern

380 (Hockings *et al.* 2009) or a bimodal rainfall pattern (Anderson *et al.* 2005). In contrast,

381 other forested sites characterized by patterns of rainfall either unimodal (Basabose

382 2005; Tutin *et al.* 1991) or bimodal (Chapman *et al.* 1999; Moscovice *et al.* 2007)

383 showed fruiting peaks during the wet season, as also reported for a dry site with a

384 unimodal pattern of rainfall (Hernandez-Aguilar 2009). Despite this variation, our data

385 indicate that the peak in ripe fruit abundance at LCNP occurs when conditions for seed

germination are optimal, i.e. in the late dry season (Frankie *et al.* 1974). Long-term

surveys conducted elsewhere showed considerable interannual variation in fruit

production (Chapman *et al.* 2005; Chapman *et al.* 1999; Tutin and Fernandez 1993a;

van Schaik *et al.* 1993). Moreover, some plant species show synchronized fruiting while

others fruit asynchronously (Chapman *et al.* 1999). Given such variation documented in

long-term studies, it is important to consider our findings as preliminary due to the short

duration of this study.

Most wild and cultivated species monitored during phenology surveys were

selected based on local knowledge. Park guards and residents mentioned that

chimpanzees in the dry season come closer to agricultural fields and cashew plantations

than in the wet season. Consequently, our data on fruiting phenology may be more

representative of plant species consumed during the dry season as they all had fruits

during this season. We recommend that future studies collect phenological data within a

delineated area (i.e. plot) to get a clear picture of wild and cultivated fruit availability.

We therefore advocate the use of techniques such as Remote Sensing and Geographic

Information Systems to map agricultural areas in LCNP and to quantify fruit

availability, as well as site-specific management of wild and cultivated species (Panda

et al. 2010).

Fruit Consumption and Availability

Confirming our hypothesis, dry season faecal samples were dominated by fruit

items in periods of high fruit availability (Anderson *et al.* 2005; Duvall 2008; Hockings

et al. 2009). Similarly, during peaks of leaf flushing and flowering, foliage or flower

items were the most consumed (Chancellor *et al.* 2012; Tutin *et al.* 1997; Wrangham *et

al.* 1998). However, the latter pattern needs to be interpreted with caution. Firstly, the

411 peak in foliage and flower occurrence in faeces in the mid dry season (MDS) could be a

412 consequence of low sample size, as the fewest faeces were collected then. However,

413 faecal samples from the early dry season (EDS), which in terms of sampling effort is

414 well represented, suggest that fruit consumption decreases over the course of EDS, a

415 trend that probably extends into MDS. Secondly, macroscopic analysis of faeces is

416 more accurate for identifying fruit items than non-fruit items (Phillips and McGrew

417 2013). Finally, Phillips and McGrew (2014) showed that sieve mesh size influences the

418 detection of food items, and small items such as foliage and non-plant foods are better

419 detected in 0.5 mm sieves. As we used sieves of 1 mm mesh, consumption of foliage

420 and flower items may be higher than what we report herein. More dry season faecal

421 samples are needed to determine if this is an artefact of our data or a problem with the

422 methodology used to quantify non-fruit items.

423   Furthermore, dietary richness of fruit species in EDS was higher than in the late

424 dry season (LDS), but more wild and cultivated species fruited in LDS when more ripe

425 fruits were available. Contrary to our hypothesis and previous findings from other

426 studies (Basabose 2002; Tutin *et al.* 1997; Watts *et al.* 2012; Wrangham *et al.* 1998),

427 dietary richness increased with ripe fruit availability. This indicates that LCNP

428 chimpanzees over the course of the dry season expand the number of ripe fruit species

429 selected. Nevertheless, in line with our hypothesis, chimpanzees chose certain fruits

430 disproportionately to their overall availability, and some wild species such as *A.*

431 *toxicaria*, *Ficus* spp., *P. excelsa*, *S. mombin* and *U. chamae* were selected over others.

432 These species are also reported to be preferred species consumed by chimpanzees

433 elsewhere (Table I). Fig fruits are important components of the diet of chimpanzees

434 throughout their range (Table I), providing food when other resources are scarce, similar

435 to other primates (Lambert and Garber 1998; Tutin *et al.* 1997). *Ficus polita* is one of

the most abundant species in open forest at LCNP, but the majority of *Ficus* spp. occur

at lower abundances (Carvalho *et al.* 2015). *Ficus* spp. were selectively consumed even

when other species were available, suggesting that they are not exclusively a fallback

food, as also documented for a dry site (Hernandez-Aguilar 2009) as well as several

forest sites (Chancellor *et al.* 2012; Morgan and Sanz 2006; Tutin *et al.* 1997).

The two liana species *L. heudelotii* and *S. senegalensis*, the cultivated species *M. paradisiaca*, and the oil-palm *E. guineensis* were available year-round. They constitute

fallback foods for chimpanzees elsewhere (Table I). Hockings and McLennan (2012)

conducted a systematic review about cultivar feeding by comparing chimpanzees in dry

and forest sites. Despite some selectivity in the choice of cultivated species among sites,

M. paradisiaca consistently was the most consumed (Hockings and McLennan 2012).

Two cultivated species consumed by LCNP chimpanzees were not reported elsewhere

(Hockings and McLennan 2012): *Pennisetum glaucum* (pearl millet) and *Hibiscus sabdariffa* (roselle). Humle and Matsuzawa (2004) found greater consumption of oil-palm items during the wet season in Bossou (Guinea) than in Yealé (Ivory Coast),

whereas in Seringbara (Guinea) chimpanzees never included oil-palm in their diet.

Although oil-palms in Bossou occur at greater densities than in Yealé and Seringbara,

differences in their use as food resource among sites were not supported by clear

differences in environmental variables, suggesting that these differences are cultural.

Oil-palm density at LCNP is lower than for Seringbara (0.03-0.12 individuals /km^2

(Carvalho *et al.* 2015) *vs* 1.0 individuals /km^2 (Humle and Matsuzawa 2004)), and

LCNP chimpanzees use this species both for feeding and nesting (Carvalho *et al.* 2015).

However, as our study covered only the dry season and Humle and Matsuzawa (2004)

studied feeding patterns during the rainy season, comparisons are difficult.

Spatial Variation in Dietary Composition

461

462   Home range sizes for chimpanzees average 12 km^2 (range 5-400; Oates *et al.*

463   2008) and they daily travel between 2 and 4 km (Herbinger *et al.* 2001). Given this and

464   a mean gut retention time of 31.5 hours ($\pm$ 12.1 standard deviation, Lambert 2002) it

465   seems unlikely that a chimpanzee traverses its entire home range before defecating.

466   Therefore, and because of the large spatial scale over which samples were collected, a

467   faecal sample should mostly reflect consumption within a relatively small area.

468   However, contrary to expectations, dietary composition was not correlated with

469   distances among faeces, suggesting that chimpanzees fed on roughly the same set of

470   plant species over the entire area sampled. Moreover, the lack of an influence of

471   settlements or roads as proxies for the presence of cultivated areas on dietary

472   composition indicates that even though they live in a highly human-modified landscape

473   their proximity to humans does not seem to influence patterns of preferred food

474   consumption.

475   In LCNP, agricultural areas could provide food supplement, but chimpanzees

476   always included wild plant foods in their diet (Duvall 2008; Hockings *et al.* 2009;

477   McLennan 2013; Nishida and Shigeo 1983; Sabater-Pí 1979; Sousa *et al.* 2013; Tutin

478   and Fernandez 1985). Cultivated species were harder to identify in faecal samples than

479   in feeding remains because the consumption of most cultivated species often results in

480   seedless fruit pulp (e.g. extracting juice from the cashew fruits). Thus, feeding

481   observations are necessary for a more accurate knowledge of the repertoire of cultivated

482   foods in the diet of LCNP chimpanzees.

483

Methodological Considerations

484

485   In areas with poorly habituated ape populations, using local knowledge with

486   regard to which plant species chimpanzees feed on is an alternative that can help to

487   improve scientific information (Sousa *et al.* 2013). For instance, local knowledge seems

488   to integrate scientific knowledge and vice versa (Ericksen *et al.* 2005). We relied on

489   local knowledge in our study when implementing the phenological surveys, and about

490   half of the species matched with those species identified in faecal samples.

491   Consequently, our data on ripe fruit availability represent underestimates. For a more

492   reliable evaluation of the relationship between dietary diversity and composition and

493   fruit availability we recommend the collection of pilot data, i.e. preliminary analysis of

494   faecal samples, cross-checking of this information with that provided by locals, and

495   subsequent monitoring of the plant species identified by these two sources of

496   information. Besides, for populations like ours for which foreknowledge of diet was

497   limited, it would have been more accurate to monitor all trees and lianas over a certain

498   dbh along phenology trails for calculating food availability indices (Marshall and Wich

499   2013).

500   On the other hand, the fact that we relied on macroscopic analysis of faeces

501   could also have biased the relationship between dietary diversity and composition and

502   ripe fruit availability. Faecal samples can neither fully reveal dietary composition nor

503   allow an accurate measure of each food item or species eaten because some items are

504   more easily detected than others (e.g. seeds *vs* leaves), the consumption of fruit items

505   can be overestimated, and interspecific differences in seed size can underestimate or

506   overestimate the real consumption of the respective species. In spite of these limitations,

507   macroscopic analysis of faeces can be used as a rough proxy of the time spent feeding

508   on different items, as the percentage volume of food items in faeces gives similar results

509   to feeding observations (Phillips and McGrew 2014). Additionally, studies relying on

510 macroscopic analysis provide important information on the fruits eaten because

511 identification is often possible to the species level as many swallowed seeds remain

512 intact following gut passage (McGrew *et al.* 1988; Tutin and Fernandez 1993b). In the

513 case of chimpanzees, most of the fruits are swallowed unharmed (e.g. 82%, Lambert

514 and Garber 1998). However, foliage or non-plant foods are hard to identify and mostly

515 underrepresented (Phillips and McGrew 2013). Microscopic inspection such as

516 phytolith analyses of faecal samples (Phillips and Lancelotti 2014) or DNA-based

517 techniques (Quéméré *et al.* 2013) are recommended to overcome these problems.

518   Supplementing faecal analysis with the analysis of feeding remains is important,

519 as shown here, because it confirmed the consumption of cultivated species, which

520 would have been very hard to detect in faeces. Combining macroscopic inspection of

521 faeces with feeding observations is also a useful procedure to estimate gut passage rates

522 either for captive chimpanzees (Lambert 2002) or wild populations (Phillips and

523 McGrew 2013). We are aware that chimpanzees also consume non-plant items such as

524 mammals, birds, insects, reptiles, among others (Anderson *et al.* 1983; Hladik 1977;

525 Nishida and Shigeo 1983; Tutin *et al.* 1997). Long-term data on dietary composition are

526 necessary (McGrew *et al.* 2009; Phillips and McGrew 2014) for a better understanding

527 of the importance of non-plant items in the diet of LCNP chimpanzees. Finally, data on

528 tool-use could provide additional insights since it has played an important role in

529 broadening chimpanzee diet (Anderson *et al.* 1983; Boesch and Boesch 1983; Humle

530 and Matsuzawa 2004).

531

Acknowledgments

546

547 Supporting Information (Appendix S1-S6) is available online.

548

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TABLES

Table I List of the plant species monitored and eaten by chimpanzees, with the corresponding fruit availability index (F_m) by season and mean occurrence (%) of the plant species found in faeces.

Scientific name (abbreviation)	Family	Life form	F_m		Item eaten			Occurrence (%)
Wild Species			Dry	Wet	Foliage	Flower	Fruit	
Adansonia digitata [1,2,4,5] (A.digi)	Bombacaceae	tree	2.51	-	-	-	-	-
Aframomum sp.[4] (Afram.spp)	Zingiberaceae	herb	-	-	-	-	F	2.30
Afzelia africana [1] (A.afri)	Legum./Caesalp.	tree	33.13	6.95	F	F	F,R	2.96
Allophylus africanus (Al.afri)	Sapindaceae	tree	-	-	-	-	F	0.58
Antiaris toxicaria [4] (A.toxi)	Moraceae	tree	20.79	20.79	F	-	F,R	11.15
Antisdesma membranaceum (A.memb)	Euphorbiaceae	tree	-	-	-	-	F	2.09
Borassus aethiopum [4] (B.aeth)	Palmae	tree	6.78	0.35	-	-	-	-
Ceiba pentandra [1,5] (C.pent)	Bombacaceae	tree	46.53	-	-	-	-	-
Cola cordifolia [1,2,5] (C.cord)	Sterculiaceae	tree	0.16	1.89	-	-	-	-
Daniellia oliveri [2,5] (D.oliv)	Legum./Caesalp.	tree	52.27	-	-	-	-	-
Detarium senegalense (D.sene)	Legum./Caesalp.	tree	49.94	3.57	-	-	-	-
Dialium guineense [4] (D.guin)	Legum./Caesalp.	tree	254.81	57.54	F,R	-	F,R	11.37
Elaeis guineensis [3,4,7] (E.guin)	Palmae	tree	58.60	12.98	F,R	F,R	F,R	7.74
Euphorbia schimperiana (E.schi)	Euphorbiaceae	herb	-	-	-	-	F	1.66
Ficus spp. [1-9] (Ficus.spp)	Moraceae	tree	6.38	-	F	-	F,R	14.42
Landolphia heudelotii [1,5] (L.heud)	Apocynaceae	liana	0.79	0.42	-	-	F	0.50
Mezoneuron benthamianum (M.bent)	Legum./Caesalp.	liana	-	-	-	-	F	0.33
Mucuna sp. (Mucuna.spp)	Legum./Papil.	liana	-	-	F	-	-	0.83
Neocarya macrophylla [4] (N.macr)	Chrysobalanaceae	tree	2.08	-	-	-	F,R	0.61
Parinari excelsa [3,4,6,8] (P.exce)	Chrysobalanaceae	tree	40.99	-	-	-	F,R	6.24
Parkia biglobosa [1,2,4,5] (P.bigl)	Legum./Mimos.	tree	5.28	5.28	F	-	R	0.24
Paullinia pinnata (P.pinn)	Sapindaceae	liana	-	-	F	-	F	0.20
Piliostigma thonningi [2,5] (P.thon)	Legum./Caesalp.	tree	-	-	-	-	F	0.08
Prosopis africana (P.afri)	Legum./Mimos.	tree	50.34	-	F	-	F	2.18
Pterocarpus erinaceus [2,5] (P.erin)	Legum./Papil.	tree	88.90	4.68	-	-	-	-
Ricinus communis (R.comm)	Euphorbiaceae	tree	-	-	F	-	-	0.73
Saba senegalensis [1,2,4,5] (S.sene)	Apocynaceae	liana	0.28	0.20	-	-	-	-
Spondias mombin [1-5] (S.momb)	Anacardiaceae	tree	1.92	19.66	-	-	F	4.16
Uapaca togoensis (U.togo)	Euphorbiaceae	tree	-	-	-	-	F	0.28
Uvaria chamae [4] (U.cham)	Annonaceae	shrub	1.06	-	-	-	F,R	9.30
Vitex sp. [1,2,4] (Vitex.spp)	Labiatae	tree	-	-	-	-	F	1.61
Voacanga africana (V.afri)	Apocynaceae	tree	-	-	-	-	F	0.30
Xylopia aethiopica (X.aeth)	Annonaceae	tree	-	-	F	-	F	0.66
Cultivated Species								
Anacardium occidentale [4] (A.occi)	Anacardiaceae	tree	78.71	7.16	-	-	R	-
Carica papaya [4] (C.papa)	Caricaceae	tree	0.15	0.05	-	-	-	-

Species	Family	Habit						
Citrus sinensis [4] (C.sine)	Rutaceae	tree	1.46	-	-	-	-	-
Hibiscus sabdariffa [4] (H.sabd)	Malvaceae	herb	-	-	F,R	-	-	0.25
Mangifera indica [4] (M.indi)	Anacardiaceae	tree	14.07	5.21	-	-	-	-
Musa paradisiaca [3,4,9] (M.para)	Musaceae	herb	1.83	0.28	F	-	-	0.55
Pennisetum glaucum (P.glau)	Gramineae	herb	-	-	F,R	-	-	0.08
Saccharum officinarum [4] (S.offi)	Gramineae	herb	-	-	R	-	-	-
Sorghum bicolor (S.bico)	Gramineae	herb	-	-	R	-	-	-
Unidentified Species								
Unidentified 6 (unid6)*	-	-	-	-	-	-	F	0.71
Unidentified 39 (unid39)*	-	-	-	-	F	-	F	0.33
Foliage unidentified (Foliage.unid) [4]	-	-	-	-	F	-		11.62
Flower unidentified (Flower.unid)	-	-	-	-	-	F	-	1.26
Fruit unidentified (Fruit.unid)	-	-	-	-	-	-	F	2.79

Type of data: F- Faecal sample, R- Feeding remains.

Also reported in [1]Assirik (Senegal) (McGrew *et al.* 1988), [2]Bafing (Mali) (Duvall 2008), [3]Bossou (Guinea) (Hockings *et al.* 2009; Humle and Matsuzawa 2004; Sugiyama and Koman 1992), [4]Cantanhez (Guinea-Bissau) (Sousa *et al.* 2013), [5]Fongoli (Senegal) (Bertolani and Pruetz 2011), [6]Kahuzi (DR Congo) (Basabose 2002), [7]Lopé (Gabon) (Tutin *et al.* 1997), [8]Ngogo (Uganda) (Watts *et al.* 2012; Wrangham *et al.* 1998), [9]Okoróbiko (Equatorial Guinea) (Sabater-Pí 1979).

*These species were previously described by Carvalho et al. (2015).

Tree (sub) family: Legum. – Leguminosae, Caesalp. – Caesalpinioideae, Mimos. – Mimosoideae, Papil. – Papilionoideae.

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FIGURE LEGENDS

Fig. 1 Sampling locations of the phenological surveys and chimpanzee faeces collected

in the protected area Lagoas de Cufada Natural Park, Guinea-Bissau.

Fig. 2 The percentage volume of fruits, foliage, and flowers, in dry season faecal

samples. The number of faecal samples collected in each month is also provided. No

data were recorded in January.

Fig. 3 Mean (± SE) of ripe fruit availability (F_m index) for all fruit species ($F_{m\ All\ species}$),

wild fruit species ($F_{m\ Wild\ species}$) and cultivated fruit species ($F_{m\ Cultivated\ species}$).

Fig. 4 Comparison of ripe fruit availability (F_m index) and the percentage of occurrence

of fruit species in chimpanzee faeces during the dry season. For some species, such as

Afzelia africana, *Antiaris toxicaria*, *Ficus* spp., *Landolphia heudelotii*, *Neocarya*

macrophylla, *Prosopis africana*, *Parinari excelsa*, *Spondias mombin*, and *Uvaria*

chamae, fruit consumption exceeded its estimated availability during some periods of

the dry season. Note that the scale of y-axis differs among species. Fruit occurrence in

faeces for January represents the mean of fruit occurrence recorded for December and

February. See Table I for species abbreviations.

Fig. 5 Expected proportions based on random sampling with replacement (1000x) of

fruit species consumption if the selection by chimpanzees was random (p_{RS}), as a

function of observed proportions of fruit species consumed (p_{CS}). Results for *Dialium*

guineense, which was much less frequently consumed than expected based on its

798   availability, are not shown here for better visualization of the results for the other

799   species. See Table I for species abbreviations.
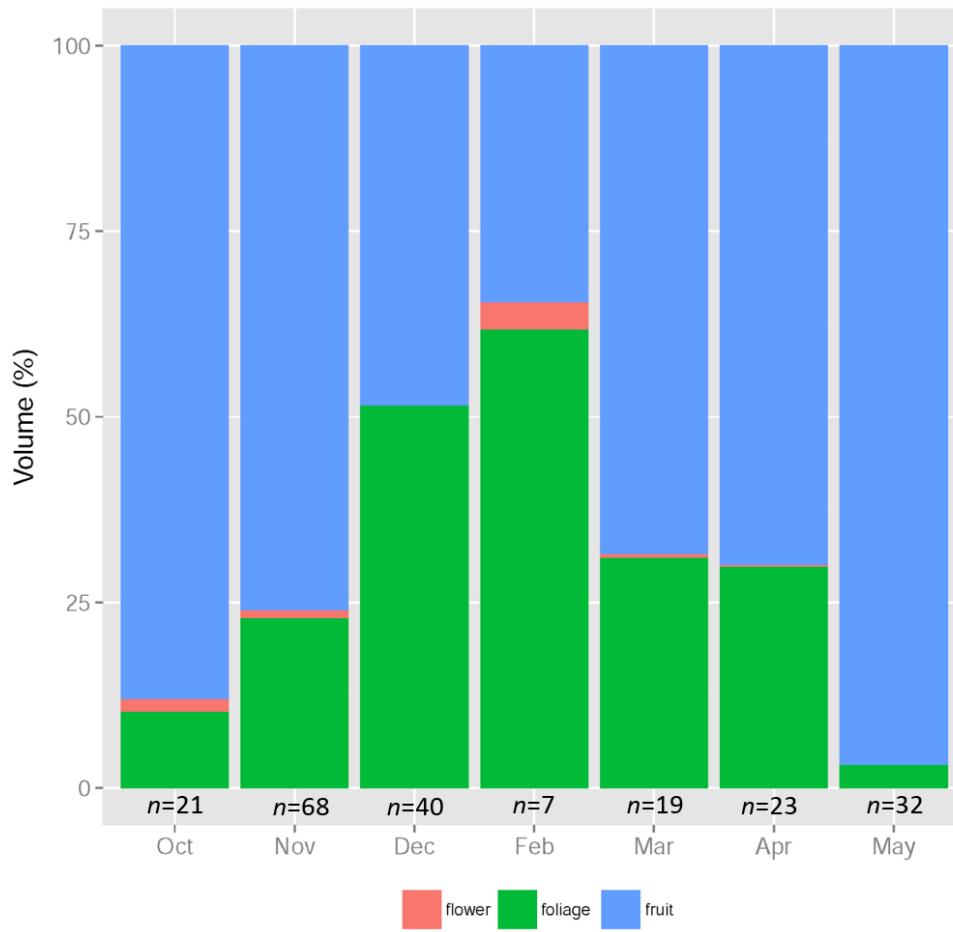
800   **Figure 1**

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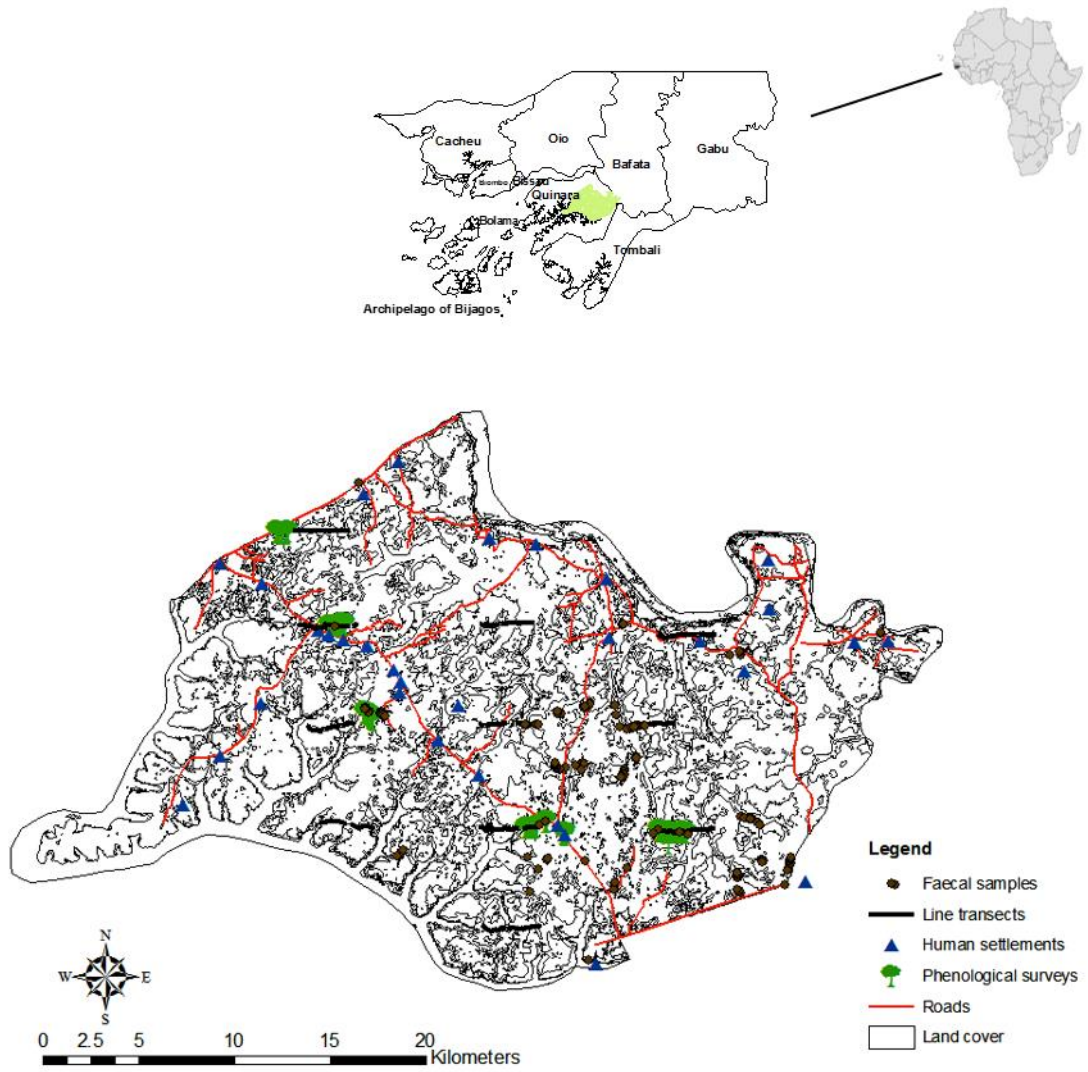
Figure 2

808   **Figure 3**
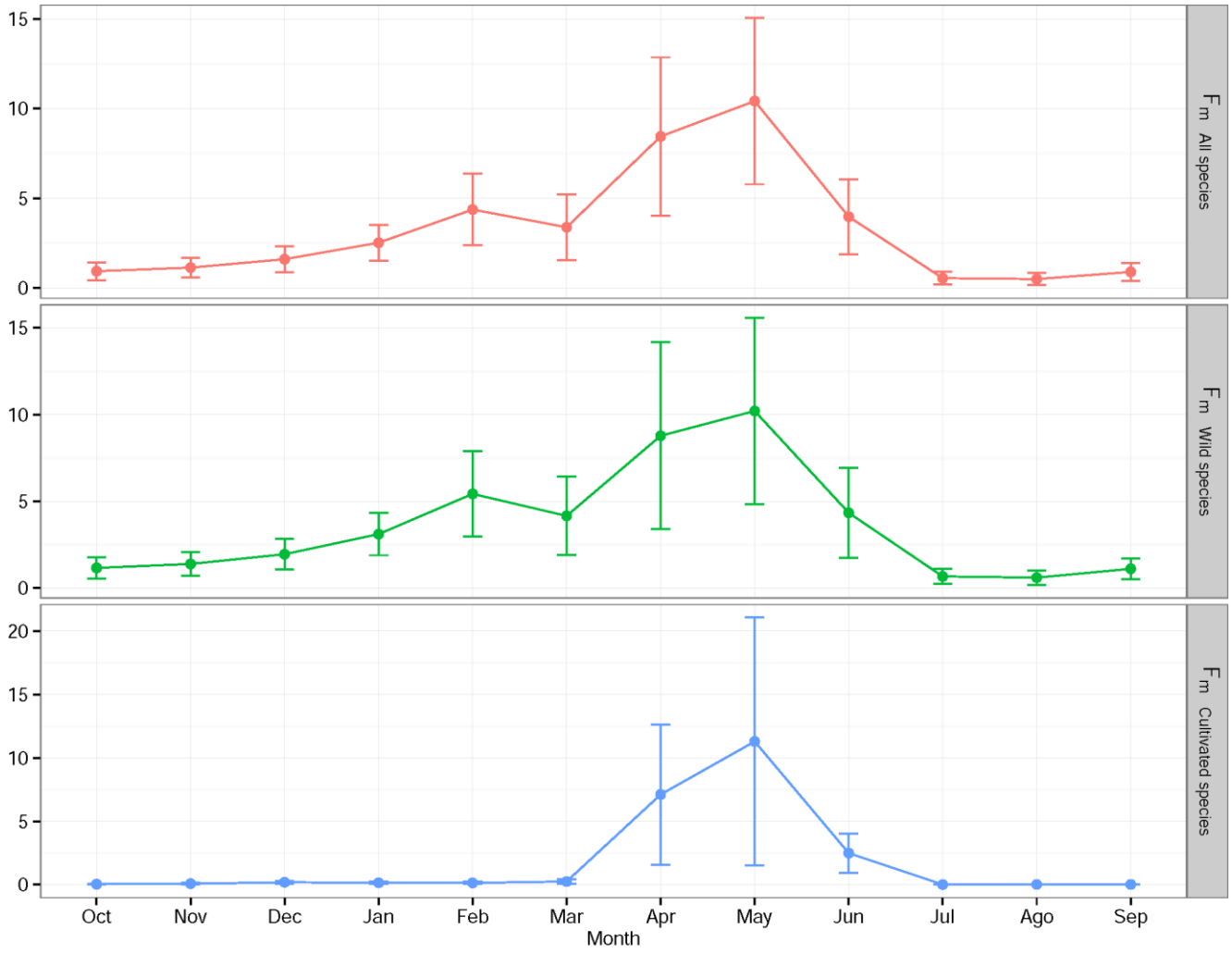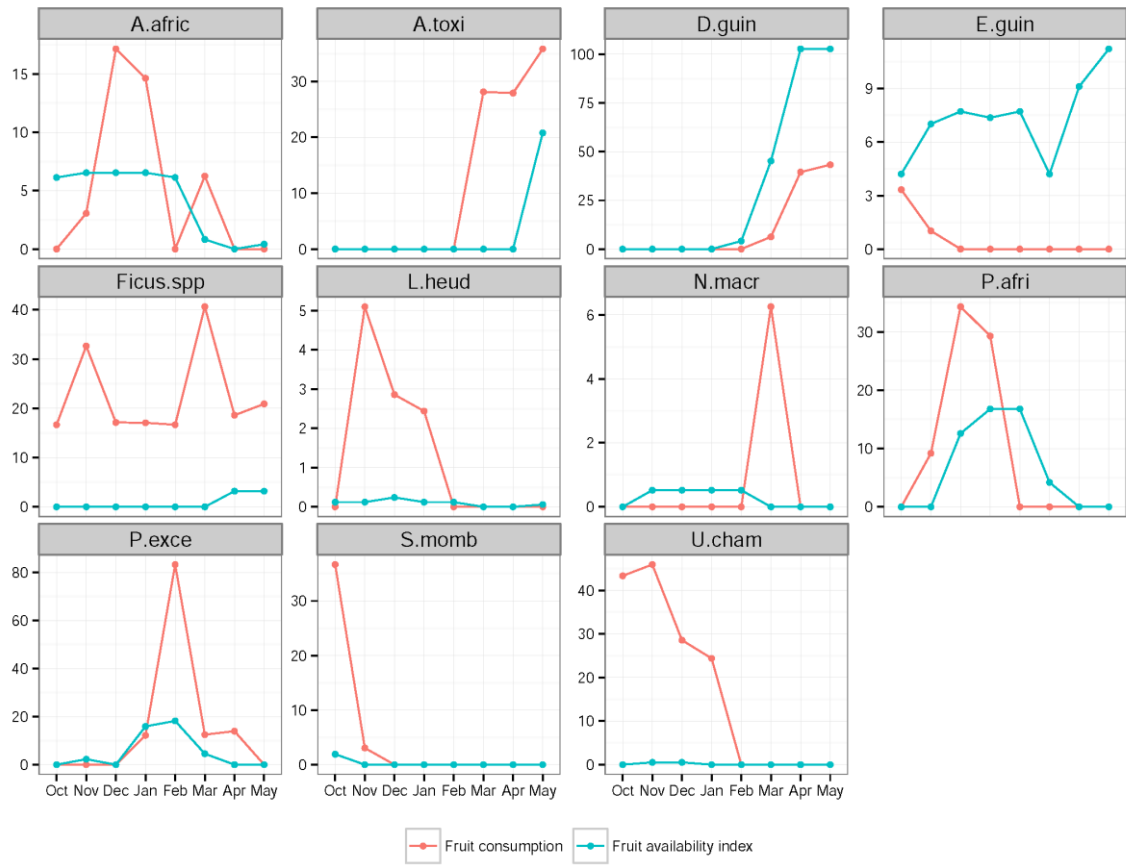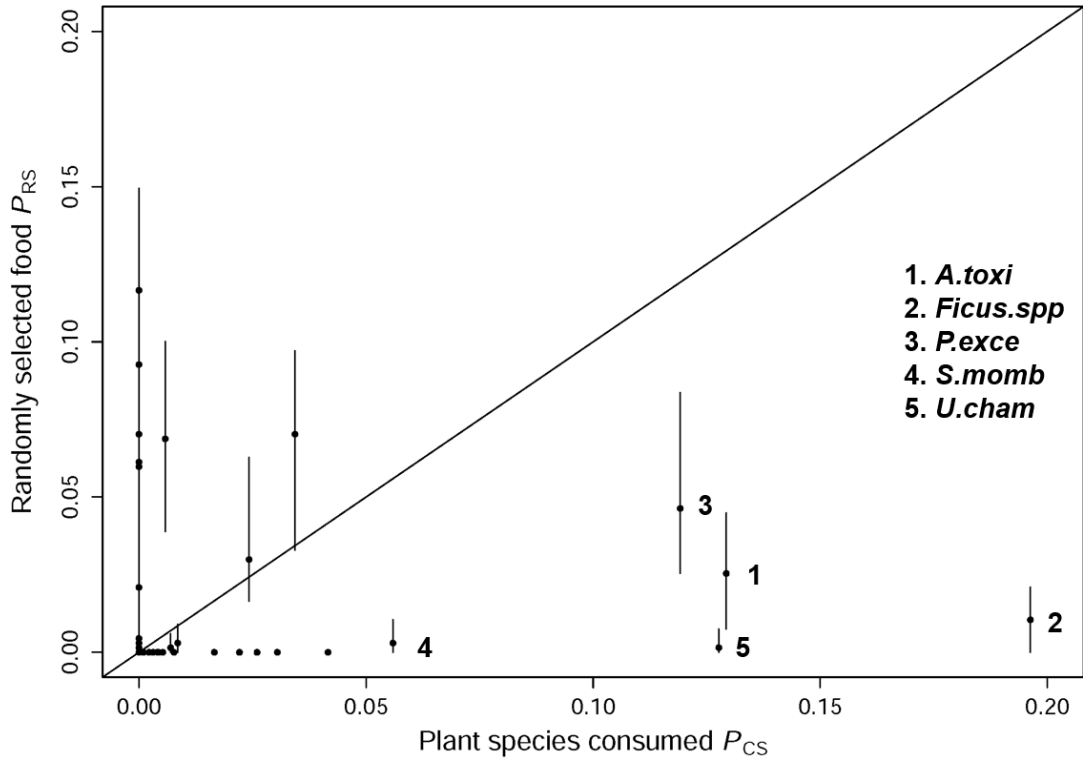
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812   **Figure 4**

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816   **Figure 5**

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