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2 **Mandrills (*Mandrillus sphinx*)**

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15 **Seasonal Change in Diet and Habitat Use in Wild Mandrills (*Mandrillus sphinx*)**

16 Short running title: Diet and Habitat Use in Mandrills

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40 **Abstract**

41 Primates show various behavioural responses to resource seasonality, including changes in diet
42 and habitat use. These responses may be particularly important for species living in large
43 groups, due to strong competition for resources. We investigated seasonality in diet and habitat
44 use in wild mandrills (*Mandrillus sphinx*), which form some of the largest primate groups, in
45 Moukalaba-Doudou National Park, Gabon. We used a fallen fruit census to measure fruit
46 availability and camera-trapping to measure visit frequency by mandrill groups on 11 line
47 transects from January 2012 to November 2013, and collected mandrill faeces for 25 months
48 in 2009–2013 to assess their diets. Fruit availability varied seasonally, with a peak in
49 December–February, and a scarce period in March–August. Relative volumes of fruit skin,
50 pulp and intact seeds in faecal remains varied with fruit availability, whereas faeces contained
51 as a large proportion of crushed seeds in the fruit scarce season as in the fruit-peak season. The
52 relative volumes of woody tissue (e.g., bark and roots) and the number of food types increased
53 in the fruit-scarce season compared to in the fruit-peak season. Camera-trapping revealed
54 seasonality in habitat use. In fruit-rich seasons, mandrill visits were highly biased towards
55 transects where fruit species that appeared in the majority of faeces in a group were abundant.
56 In contrast, in fruit-scarce seasons, visit frequencies were distributed more uniformly and the
57 relationship with fruit availability was unclear. Our results suggest that mandrill groups in the
58 study area respond to seasonal fruit scarcity by consuming seeds and woody tissue and by
59 ranging more widely than in fruit-rich seasons. These flexible dietary and ranging behaviours
60 may contribute to the maintenance of extremely large groups in mandrills.

61

62 **Keywords:** Behavioural flexibility; Camera-trapping; Faecal analysis; Fruiting phenology;
63 Moukalaba-Doudou

64

65 **Introduction**

66 Primates show a wide variety of diets and habitat use patterns between and within species.
67 While body size and morphology largely determine primate diet and habitat use (Fleagle 2013),
68 social organisation and environmental factors, including disturbance (Johns and Skorupa
69 1987), seasonal inundation (Terada et al. 2015) and topographic steepness (Etiendem et al.
70 2013), also affect habitat use patterns. Since food resources change seasonally in most of the
71 primate habitats (Hanya et al. 2013; van Schaik and Pfannes 2005), behavioural responses to
72 resource seasonality, including changes in diet and habitat use, are important adaptations for
73 most primates (Hemingway and Bynum 2005; Tsuji et al. 2013). For example, rhesus
74 macaques (*Macaca mulatta*) eat more mature leaves (Tang et al. 2016) and eastern lowland
75 gorillas (*Gorilla beringei*) eat more bark and leaves (Yamagiwa et al. 1994) when fruits
76 become scarce. Larger species except great apes (5–15 kg) tend to eat lower-quality foods,
77 such as mature leaves and other vegetative matter, than smaller species, which rely on higher-
78 quality exudate and nectar for alternative foods during fruit scarce seasons (Hemingway and
79 Bynum 2005). Some primates show seasonal differences in dietary diversity. For example,
80 Japanese macaques (*Macaca fuscata*: Nakagawa 1989) and black-and-white colobus (*Colobus*
81 *guereza*: Harris et al. 2010) have more diverse diets in seasons where their main foods are
82 scarce, whereas blue monkeys (*Cercopithecus mitis*: Kaplin et al. 1998) decrease dietary
83 diversity by eating a particular seed species frequently when fruits are scarce. Dietary
84 responses can also vary between populations of the same species (e.g., grey-cheeked
85 mangabeys, *Lophocebus albigena*: Hemingway and Bynum 2005). Changes in ranging
86 patterns include seasonal changes in habitat (e.g., common brown lemurs, *Eulemur fulvus*:
87 Sato 2013) and increased home range size (e.g., tufted capuchins, *Sapajus apella*: Di Bitetti
88 2001).

89 Biogeographic differences in phenology and environments affect primate

90 behavioural responses to food seasonality (Hemingway and Bynum 2005). For example, while
91 African primates often show increased dietary diversity during seasons of food scarcity but do
92 not change in home range size seasonally, New World monkeys, particularly Atelinae and
93 Cebinae species with relatively large home ranges, rarely increase diversity of their diets but
94 often expand their home range or change their habitats when foods are scarce. These regional
95 contrasts may be due to differences in phenology and forest structure: the interval between
96 peak leaf flush and peak fruiting is shorter in American than in African forests (van Schaik and
97 Pfannes 2005), and the Amazonian waterways cause high heterogeneity of habitat types in
98 American tropical forests (Hemingway and Bynum 2005).

99 Group size may also influence primate seasonal behaviours, and behavioural
100 responses may be particularly important for large groups, since larger groups experience
101 stronger scramble feeding competition (Janson 1988). For example, the dietary diversity of
102 red colobus (*Procolobus rufomitratus*) correlates positively with their group size (Gogarten et
103 al. 2014), and seasonal changes in habitat are confined to species with the largest group sizes
104 among the primate community at Uruku River, Brazil (Peres 1994).

105 Mandrills (*Mandrillus sphinx*) and drills (*M. leucophaeus*) live in coastal tropical
106 forests in central Africa where resource production varies seasonally (Newbery et al. 1998;
107 White 1994). They form among the largest wild primate groups of up to 845 (mandrills:
108 Abernethy et al. 2002) and 400 (drills: Wild et al. 2005) individuals. However, the dense
109 vegetation of their habitats make it difficult to observe them directly without habituation,
110 which is nearly impossible due to their large group sizes and large home ranges. Consequently,
111 no ecological studies of mandrills or drills based on direct behavioural observations of
112 identified animals have been achieved in the wild, and available data are limited to a
113 provisioned mandrill group established by releasing captive animals in Lékédi Park, Gabon
114 (Brockmeyer et al. 2015; Nsi Akoue et al. 2017).

115 Based on indirect data from faeces and food remnants, wild mandrills and drills are
116 omnivorous with a high preference for fruits (Astaras and Waltert 2010; Hoshino 1985; Lahm
117 1986; Rogers et al. 1996). Provisioned mandrills are also omnivorous with a clear frugivorous
118 tendency (Nsi Akoue et al. 2017). *Mandrillus* species, and closely-related *Cercocebus* species,
119 have enlarged premolars, which are adapted to processing hard nuts and seeds (Fleagle and
120 McGraw 2002), and monkeys of both genera eat seeds frequently (Astaras and Waltert 2010;
121 Hoshino 1985; McGrew et al. 2009). However, seasonal patterns in diets differ between the
122 genera: while *Mandrillus* species increase the diversity of food types by eating fallen seeds
123 and monocotyledonous herbs in fruit-scarce seasons (Astaras and Waltert 2010; Hoshino
124 1985; Tutin et al. 1997), *Cercocebus* species eat a lot of fruits and seeds year-round, and
125 changes in their diet do not always relate to fruiting seasonality (McGraw et al. 2014; Mitani
126 1989).

127 We know much less about ranging behaviours of wild mandrills and drills than about
128 their diets. A study in Lopé National Park, Gabon, estimated the home range of a wild mandrill
129 group of *ca.* 700 individuals at 182 km², including 89 km² of forested area (White et al. 2010),
130 whereas a provisioned mandrill group of 120 animals has much smaller home range of 8.7 km²
131 (Brockmeyer et al. 2015). Surveys report that mandrills prefer primary forests and avoid
132 savannah (Lahm 1986; Rogers et al. 1996), and drills occur from lowland to montane forests
133 at up to 2,000 m elevation (Wild et al. 2005). Their seasonality in habitat use is barely
134 understood. Researchers at Lopé (Rogers et al. 1996) observed groups in gallery forests more
135 frequently during dry seasons than rainy seasons, but a subsequent report at the same site
136 (White 2007) did not confirm this pattern because the core area of the group was in gallery
137 forests regardless of season. Conversely, *Cercocebus* mangabeys mainly inhabit riverine and
138 swamp forests with groups of 10–125 animals and much smaller home ranges of 1–3 km²
139 (Swedell 2011), and red-capped mangabeys (*C. torquatus*) show seasonal changes in habitat

140 (Mitani 1989).

141 In this study, we examined seasonal changes in the diet and habitat use of wild
142 mandrills in Moukalaba-Doudou National Park, Gabon. A previous study at the same site
143 (Hongo 2014) obtained three full counts of mandrill groups of 169, 350 and 442 individuals,
144 but we do not know how many groups there are in our study population. We obtained data on
145 diet from faecal samples, and used camera-traps to collect data on differential habitat use, both
146 for multiple unhabituated groups. Digestive efficiencies vary with food type (Litvaitis 2000),
147 so we used faecal analysis to examine seasonal differences in the consumption of each food
148 type, but did not compare the relative importance of food types.

149 We had three objectives. First, we assessed fruiting phenology in the study area to
150 define seasons based on fruit availability. Second, we examined seasonal changes in mandrill
151 diet by comparing the relative volumes of each food type and the number of food types in
152 faecal remains between seasons. Third, we examined seasonal changes in mandrill habitat use
153 based on the frequency of visits to camera-traps. We explored correlations between visit
154 frequency and the availability of important mandrill fruits, seasons, and habitat parameters,
155 and compared the spatial distribution of visits to camera traps between seasons to explore
156 seasonality in mandrill ranging patterns.

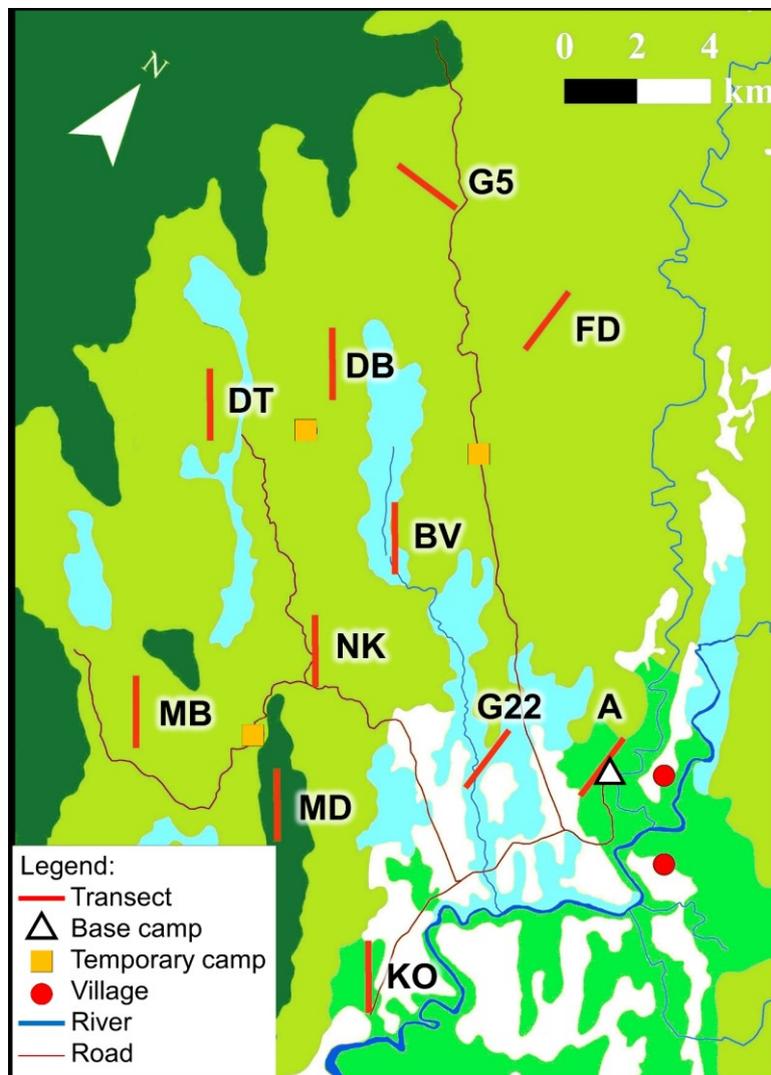
157

158 **Methods**

159 **Study Area**

160 Our study area encompassed about 400 km² in the eastern part of Moukalaba-Doudou National
161 Park, Gabon. Given that a home range of the mandrill group at Lopé includes 89 km² of
162 forested area (White et al. 2010), the study area is likely to cover the home ranges of several
163 groups. Our base camp was located at S2° 19' and E 10° 34'. The study area comprises different
164 habitat types, according to LandsatTM, radar and aerial imagery (Ministère des Eaux et Forêts

165 et du Reboisement, Tecslult International, Quebec, Canada; provided by WWF Gamba; Fig. 1).
166 Annual rainfall during 2002–2013 was 1,176–2,043 mm, and the mean monthly minimum and
167 maximum temperatures during 2006–2013 were 18.7–25.0°C and 26.7–34.3°C, respectively
168 (PROCOBHA research team, unpublished data). Typically, the dry season is from May to
169 September, and the rainy season is from October to April, but there is little rain from December
170 to February in some years (Takenoshita et al. 2008).
171



172

173 **Fig. 1** Map of the study area in Moukalaba-Doudou National Park, Gabon, with transects and
174 vegetation types. *Dark green* (transect MD) is mountainous primary forest; *olive green* (NK,

175 MB, DB, DT, FD, and G5) is lowland primary forest; *lime green* (A and KO) is disturbed
176 secondary forest; *light blue* (G22 and BV) is seasonally inundated riverine forest; *white* is
177 savannah.

178

179 **Fruiting Phenology and Definition of Seasons**

180 To monitor fruiting phenology in the study area, we conducted a monthly fallen-fruit census
181 (Furuichi et al. 2001) from January 2012 to January 2014. We established 11 line transects
182 separated by at least 2 km and covering all types of vegetation in the study area (Fig. 1). We
183 set the length of transects to 2 km to prevent transects from crossing different vegetation types.
184 We defined a ‘fruit cluster’ as one or more fresh fruits that had fallen on the ground from the
185 same tree. We noted and photographed fruit clusters of all species within 1 m of the centre of
186 the transects (total area censused = 4.4 ha). We also counted partially-eaten fruits as fruit
187 clusters if we found a fruiting tree of the same species above them. To avoid counting multiple
188 clusters from the same fruiting tree, we did not record clusters that fell within 10 m of the
189 previous cluster of the same species. When we found two fruit clusters of the same species
190 more than 10 m apart, we only counted the second cluster if we found a different fruiting tree
191 above them. Thus, the number of fruit clusters should match the number of fruiting trees near
192 the transects, although we may have failed to count tree species whose fruits seldom fall to the
193 ground or rarely remain for a long time due to consumption by animals (Furuichi et al. 2001).
194 Our measure is a rough indicator of fruit abundance as we did not quantify the numbers or the
195 mass of the fruits.

196 We attempted to classify the fruit clusters taxonomically using photographs and plant
197 lists for our study area (Takenoshita et al. 2007; Yumoto et al. 2015). We finished the
198 classification of the fruits found in mandrill faeces; the classification of other fruit species is
199 ongoing.

200 We used fruit census data from January 2012 to November 2013 for analysis. To
201 examine seasonal variation in fruit availability, we drew boxplots of the monthly numbers of
202 fruit clusters of all species, based on which we defined four seasons: ‘fruit-peak season’ from
203 December to February, ‘early fruit-scarce season’ from March to May, ‘late fruit-scarce season’
204 from June to August, and ‘fruit-increase season’ from September to November. We tested
205 whether numbers of fruit clusters are statistically different among the four seasons using pair-
206 wise Welch t-tests with the Holm’s p-value adjustment (Holm 1979).

207

208 **Faecal Sample Collection and Analysis**

209 We searched for mandrill groups with research assistants over the whole study area for 25
210 months between 2009 and 2013 (August–November 2009, January–June 2010, November
211 2011–March 2012, June–August 2012, October 2012–February 2013, and June–September
212 2013). When we found a group, we followed it and collected faecal samples ad libitum.

213 We conducted faecal analysis following a standardised protocol (McGrew et al.
214 2009). On the day of collection, we washed faecal samples in a 1-mm² sieve until the waste
215 water was clear and dried the samples in the shade. We then sorted faecal remains into nine
216 food types using a magnifying glass: fruit fibre (fruit skin, pulp, and intact seeds); crushed
217 seeds (including crushed seed coats); dicotyledonous leaves; monocotyledonous herbs (blades
218 and pith); woody tissue (bark, woody liana, roots and subterranean stems); flowers;
219 invertebrates; vertebrates (hairs and feathers); and other (including soil, stones, and dead
220 leaves). Unlike several previous studies of *Mandrillus* species, where intact seeds were
221 discarded and/or fruit fibre and seeds were both categorised as ‘fruits’ (Hoshino 1985; Owens
222 et al. 2015), we categorised intact and crushed seeds into ‘fruit fibre’ and ‘seeds’, respectively,
223 because fruit fibre and seeds are considerably different in terms of phenology and nutrition
224 intake. Since fruit skin and pulp rarely occurred in faeces, and the occurrence of intact seeds

225 means that mandrills receive nutrition from fruit skin and/or pulp not from seeds, excluding
226 intact seeds would substantially underestimate the dietary contribution of fruit fibre. We
227 estimated the relative volume of each food type in the faecal remains on a five-point scale at
228 25% intervals (i.e., 0%, 12.5%, 37.5%, 62.5%, and 87.5%).

229 We identified fruit items to the lowest possible taxonomic group based on their
230 morphological traits. We identified ‘important’ fruits for mandrills from the list of fruit items
231 found in their faeces. To find an objective threshold for importance, we calculated proportion
232 of occurrence by date and fruit item whenever we collected more than five faeces during a
233 group follow, and plotted a density curve. The curve showed a bimodal distribution with a
234 local minimum at 61.7%. We therefore defined important fruits as fruit items that occurred \geq
235 60% at least once.

236

237 **Camera-trapping and Capture Rate of Mandrill Groups**

238 From January 2012 to February 2014, we deployed 10 camera-traps (Bushnell® Trophy Cam
239 2010, Overland Park, MO) along each transect at 200-m intervals, as part of a comprehensive
240 study of mammalian ecology (Nakashima 2015). We strapped each camera to a tree 10 m from
241 the transect and adjusted it to be parallel to the ground at a height of 30 cm. We did not move
242 cameras during the study period. We configured the cameras to start in response to the passage
243 of animals and to record a video image of 30 s or 60 s at a minimum interval of 30 s (3 min
244 from January to July 2012). We checked the conditions of the cameras monthly and replaced
245 them as soon as possible when they broke.

246 We used camera-trap data from January 2012 to November 2013 for analysis,
247 because the number of deployed camera-traps decreased substantially in December 2013. To
248 count the number of mandrill group visits to transects, we first counted ‘camera visits’, where
249 a camera took videos at intervals of < 30 min (O'Brien et al. 2003). We regarded visits as group

250 visits only when two or more reproductive females, juveniles, or infants passed within 5 m of
251 a camera. Next, we calculated time intervals between consecutive group visits recorded by
252 cameras along the same transect and plotted a density curve. We used only intervals of less
253 than 3 days ($N = 157$) and excluded night-time (18:00–06:00h) from the intervals. The curve
254 showed an exponent function-like shape with a clear change in slope at 10 hours, so we pooled
255 camera-based group visits recorded within 10 hours (excluding night-time) by cameras along
256 the same transect. That is, we regarded group visits filmed in the same transect at an interval
257 of > 10 h or recorded in different transects, as independent. Finally, we counted independent
258 group visits for each transect and season, and calculated capture rates as the number of
259 independent group visits divided by the total number of days when cameras worked.

260

261 **Habitat Parameters**

262 We categorised habitat types of the transects in secondary forests as ‘disturbed’ and those in
263 riverine forests as ‘seasonally inundated’ habitats. We quantified the topographic steepness of
264 all transects by measuring the inclination of the ground in front of each camera-trap using a
265 laser range finder (Laser Technology TruPulse® 200, Centennial, CO). We used the mean of
266 the inclination angles as an indicator of the steepness of transects.

267

268 **Statistical Analysis**

269 We performed all statistical analyses using R version 3.3.3 (R Core Team 2017). All statistical
270 tests were performed as two-tailed tests, and we considered $P < 0.05$ as significant.

271

272 *Diet Seasonality*

273 We examined seasonal variation in the relative volume of each food type in faecal samples,
274 except for flower, vertebrate and other, which rarely occurred in faecal samples. Since the

275 relative volumes are non-binomial, we logit-transformed them using the following equation
276 based on a previous study (Warton and Hui 2011): $z = \log([y+0.05]/[1-y+0.05])$, where y is a
277 relative volume. We added 0.05 to both the numerator and denominator of the logit function,
278 because the simple logit function does not accept 0. We then constructed linear mixed models
279 (LMMs) using the *lmer* function in the *lme4* package (Bates et al. 2015). The full model
280 contained the response variable *logit-transformed relative volume* (z), a fixed effect of *season*
281 (four-level categorical variable with fruit-peak season as a control level), and a random effect
282 of *date of group follow* (random intercept). We included the date of group follows as a random
283 effect because we collected multiple faecal samples in each group follow. We did not include
284 the number of fruit clusters as a fixed effect in the model, because we did not conduct the fruit
285 census before 2012 and we collected faecal samples both along the transects and elsewhere in
286 the study area.

287 To explore the statistical differences in the relative volumes among seasons, we used
288 the ‘grouping model comparison’ (Mori et al. 2009). We generated 15 candidate models,
289 including a full model where all four seasons were different levels, 13 possible ‘group’ models
290 where two or more seasons were grouped as identical levels, and a null model where all the
291 seasons were regarded as a single level. We conducted model selection based on AIC values
292 (Akaike 1974) and probabilities that a given model has the smallest AIC among the candidate
293 models (model selection frequencies, Burnham and Anderson 2002) from a non-parametric
294 bootstrap of 1,000 replicates. We considered models with a model selection frequency of $\geq 5\%$
295 as confident models (Shimodaira 1998) and used them to interpret the results. We checked the
296 residual plots and normal Q-Q plots of both the full model and the smallest-AIC model for
297 diagnostics and confirmed model stability.

298 To examine seasonality in the number of food types, we constructed a generalised
299 linear mixed model (GLMM) with a binomial error distribution and a logit link function using

300 the *glmer* function in the *lme4* package. We used the number of food types (except ‘flowers’,
301 ‘vertebrates’ and ‘others’) in a faecal sample as the response variable (integer variable of 1–6).
302 The full model also contained a fixed effect of *season* and a random effect of *date of group*
303 *follow*. We evaluated differences across seasons using the grouping model comparison,
304 followed by model selection and diagnostics similar to those described above.

305

306 *Habitat Use Seasonality*

307 To examine the influence of fruit availability and other environmental factors on the capture
308 rates, we constructed a GLMM with a Poisson error distribution and a log link function, using
309 the *glmer* function. We created a data set by counting the number of independent group visits
310 for each transect and season. The full model contained a response variable of *the number of*
311 *group visits* (integer variable) corrected by an offset of *log(camera-days)*, fixed effects of *mean*
312 *number of the ‘important’ fruit clusters* (continuous variable), *season*, the *interaction between*
313 *mean number of the ‘important’ fruit clusters and season*, and three habitat parameters
314 (*steepness* (continuous variable), *seasonally inundated habitat* and *disturbed habitat* (binary
315 variables of Yes or No)), and a random effect of *transect* (random intercept). We standardised
316 all the continuous variables. We included an interaction between the number of fruits and
317 season because the effect of fruit availability on habitat preference may differ between seasons.
318 We generated 40 candidate models using all possible combinations of the fixed effects and
319 conducted model selection and diagnostics as for the analysis of diet seasonality.

320 To test for seasonality in ranging patterns, we calculated variances in capture rates
321 across transects for each season and compared them among the four seasons using a Levene’s
322 test (Levene 1960). If the result of the Levene’s test was significant, we then tested the
323 differences in variance for all pairwise comparisons using F tests with a Holm’s p-value
324 adjustment. Large variances of capture rates indicated seasonally intensive use of particular

325 transects, whereas small variances meant an even distribution of habitat use.

326

327 **Ethical Note**

328 This study complied with the IPS Code of Best Practices for Field Primatology and the laws
329 of the Gabonese Republic and was conducted with approval from the Centre National de la
330 Recherche Scientifique et Technologique
331 (N° AR0031/11/MENESRSIC/CENAREST/CG/CST/CSAR) and the Agence Nationale des
332 Parcs Nationaux (N° 000017/PR/ANPN/SE/CS/AEPN,
333 N° 000022/PR/ANPN/SE/CS/AEPN).

334

335 **Data Availability**

336 The datasets during and/or analysed during the current study are available from the
337 corresponding author on reasonable request.

338

339 **Results**

340 **Fruiting Phenology**

341 We conducted the monthly fallen fruit census in 240 transect-months from January 2012 to
342 November 2013. We could not census in the other 13 transect-months (Fig. 2), because it was
343 impossible to access to the transects due to logistic problems. This lack of data may mean that
344 we underestimate variance in the number of fruit clusters across transects, and underestimate
345 the mean for February 2013. The number of fruit clusters of all species showed a seasonal
346 pattern: numbers were largest in December–February, decreased substantially in March–May,
347 reached their lowest numbers in June–August, and increased again in September–November
348 (Table 1, Fig. 2). The differences among the four seasons were all statistically significant
349 (Table 1).

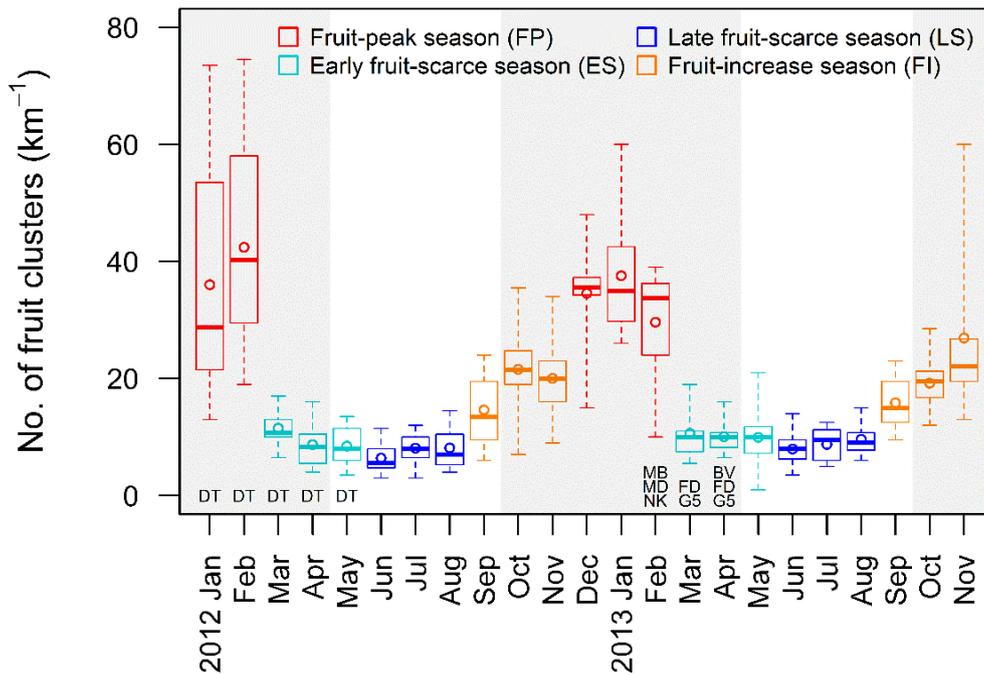
350 **Table 1** Seasonal comparisons of the numbers of fallen fruit clusters on transects in
 351 Moukalaba-Doudou National Park, Gabon, January 2012–November 2013.

Season	Number of transect-months	Number of all fruit clusters per km (Mean ± SD)	Welch t-test with the Holm's p-value adjustment		
			vs. early fruit- scarce	vs. late fruit- scarce	vs. fruit- increase
Fruit-peak (Dec.–Feb.)	50	36.3 ± 13.9	t = 13.0 <i>P</i> < 0.001	t = 14.0 <i>P</i> < 0.001	t = 7.4 <i>P</i> < 0.001
Early fruit-scarce (Mar.–May)	58	9.9 ± 3.9	-	t = 2.7 <i>P</i> = 0.009	t = -8.4 <i>P</i> < 0.001
Late fruit-scarce (Jun.–Jul.)	66	8.2 ± 3.0	-	-	t = -13.8 <i>P</i> < 0.001
Fruit-increase (Sep.–Nov.)	66	19.7 ± 8.6	-	-	-

352

353

354



355

356 **Fig. 2** Seasonality in the number of fallen fruit clusters on transects in Moukalaba-Doudou

357 National Park, Gabon (January 2012–November 2013). *Circles* show monthly means,

358 *horizontal lines in boxes* show monthly medians, *boxes* show inter-quartile ranges, and

359 *whiskers* show ranges. *Characters below boxes* indicate transect IDs where the census was

360 not conducted (see also Fig. 1). *White* and *shaded area* indicate the dry and rainy seasons,

361 respectively.

362

363 Seasonality in Diet

364 We sought mandrill groups on 432 days and located them on 49 days, during which

365 we followed groups for a mean of 4.1 hours per day (range: 0.2–10.1 h) and collected a mean

366 of 12.3 faeces (range: 2–52). We analysed 417 faecal samples and distinguished 54 fruit items:

367 we identified 31 items to species and 12 items to genus (Table 2); the remaining 11 items were

368 unclassified. We classified 22 fruit items (17 species and five genera) as ‘important’ fruits for

369 mandrill groups (Table 2).

370

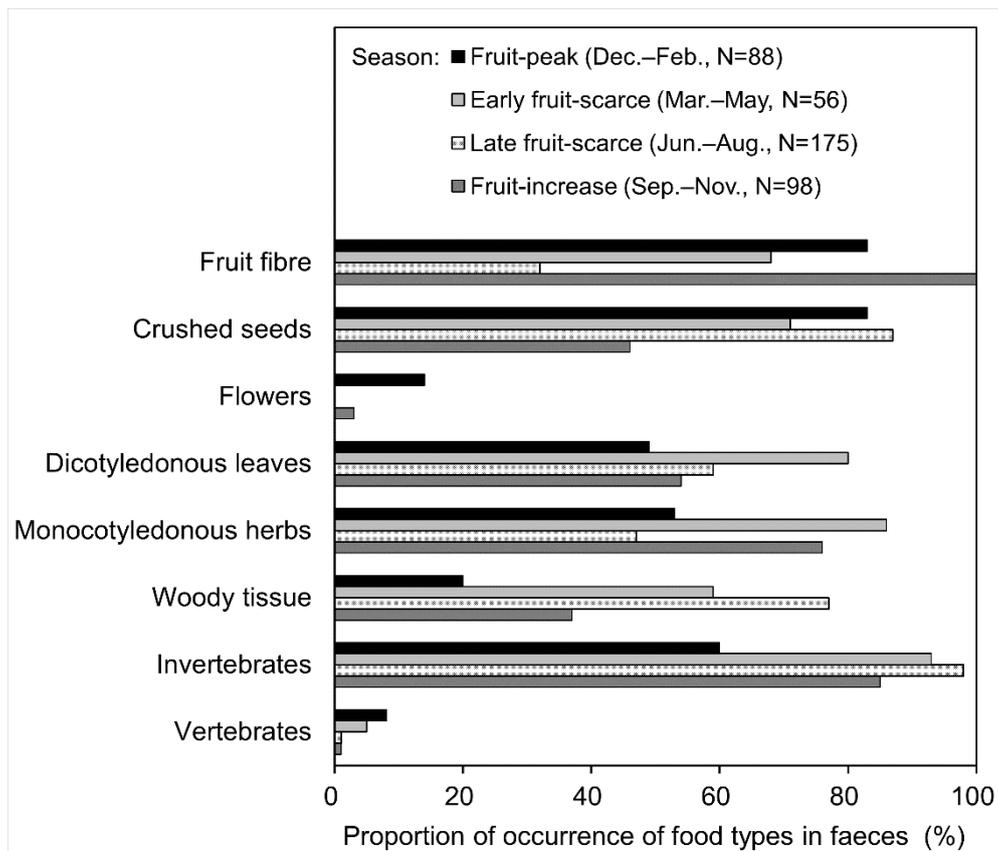
Table 2 Fruit items identified in mandrill faecal samples in Moukalaba-Doudou National Park, Gabon, August 2009–September 2013.

Fruit item	Family	Food type	Season			
			Fruit-peak (Dec.–Feb.)	Early fruit- scarce (Mar.–May)	Late fruit- scarce (Jun.–Aug.)	Fruit- increase (Sep.–Nov.)
<i>Aframomum</i> spp.	Zingiberaceae	F	●	●	○	○
<i>Anthocleista vogelii</i>	Gentianaceae	F	○			
<i>Anthonotha</i> sp.	Fabaceae	S				○
<i>Bombax chevalieri</i>	Bombacaceae	S			○	
<i>Caloncoba welwitschii</i>	Flacourtiaceae	F	●			
<i>Ceiba pentandra</i>	Bombacaceae	S	○			
<i>Cissus dinklagei</i>	Vitaceae	F				○
<i>Cola</i> spp.	Sterculiaceae	F, S	●			
<i>Coula edulis</i>	Olacaceae	S	●	●	○	
<i>Daniellia klainei</i>	Fabaceae	S		●		
<i>Desplatsia</i> sp.	Tiliaceae	F	○			○
<i>Dialium</i> sp.	Fabaceae	F, S	○			○
<i>Diogoia zenkeri</i>	Olacaceae	S				○
<i>Diospyros</i> spp.	Ebenaceae	S	●	○	○	
<i>Discoglyprena caloneura</i>	Euphorbiaceae	S	●	●		
<i>Drypetes</i> sp.	Putranjivaceae	F	○			
<i>Duboscia macrocarpa</i>	Tiliaceae	F, S	○			○
<i>Ficus</i> spp.	Moraceae	F	●	●	○	●
<i>Gambeya africana</i>	Sapotaceae	F				●
<i>Grewia coriacea</i>	Tiliaceae	F				○
<i>Hexalobus crispiflorus</i>	Annonaceae	F	○			
<i>Irvingia gabonensis</i>	Irvingiaceae	F	●			
<i>Klainedoxa gabonensis</i>	Irvingiaceae	F, S	○		○	●
<i>Laccosperma</i> sp.	Arecaceae	F		●		
<i>Landolphia</i> spp.	Apocynaceae	F, S	○			
<i>Meiocarpidium lepidotum</i>	Annonaceae	F, S				○
<i>Mimusops zeyheri</i>	Sapotaceae	F			○	
<i>Musanga cecropioides</i>	Cecropiaceae	F	○	●		○
<i>Myrianthus arboreus</i>	Cecropiaceae	F				○
<i>Pentaclethra macrophylla</i>	Fabaceae	S			●	
<i>Polyalthia suaveolens</i>	Annonaceae	S			●	
<i>Porterandia cladantha</i>	Rubiaceae	F				●
<i>Pseudospondias longifolia</i>	Anacardiaceae	F			○	
<i>Sacoglottis gabonensis</i>	Humiriaceae	F, S			●	●
<i>Salacia</i> spp.	Celastraceae	F	○			
<i>Santiria trimera</i>	Burseraceae	F	●	○		●
<i>Staudtia gabonensis</i>	Myristicaceae	F			●	
<i>Synsepalum dulcificum</i>	Sapotaceae	F				●

<i>Tabernanthe iboga</i>	Apocynaceae	F, S	○	
<i>Treculia africana</i>	Moraceae	F	○	
<i>Uapaca guineensis</i>	Phyllanthaceae	F, S		● ○
<i>Uvaria</i> sp.	Annonaceae	F		○
<i>Uvariastrum pierreanum</i>	Annonaceae	F	●	

373 Food type: F = fruit fibre, S = crushed seeds. Season: ○, items found during the given seasons; ●, items identified
374 as 'important' fruits (see Methods).
375

376 Fruit fibre and crushed seeds both occurred in a large proportion of the faecal remains,
377 but their seasonal patterns differed. Fruit fibre occurrence was high during the fruit-peak and
378 fruit-increase seasons, and decreased substantially in the late fruit-scarce season (Fig. 3). The
379 results of LMMs and AIC model selection identified two confident models which showed that
380 relative volumes in the fruit-peak and fruit-increase seasons (mean relative volume = 45.0%)
381 were much larger than in the early and late fruit-scarce seasons (9.3%) (Table 3 (i), Fig. 4a).
382 In contrast, the occurrence of crushed seeds was high from the fruit-peak to the late fruit-scarce
383 season (Fig. 3). Four confident models (Table 3 (ii)) showed that relative volumes were largest
384 in the fruit-peak and late fruit-scarce seasons (mean relative volume = 42.6%), smallest in the
385 fruit-increase season (9.3%), and intermediate in early the fruit-scarce season (22.8%) (Fig.
386 4b). Most of the seeds found in faeces of fruit-scarce seasons were finely crushed and
387 unidentifiable, but we identified *Coula edulis* nuts and *Sacoglottis gabonensis* seeds as
388 ‘important’ foods in fruit-scarce seasons, when these species do not produce many fruits
389 (Table 2).



390

391 **Fig. 3** Seasonality in the occurrence of food types in mandrill faeces (number of faeces
 392 containing a food type divided by the total number of faeces) in Moukalaba-Doudou National
 393 Park, Gabon (August 2009–September 2013).

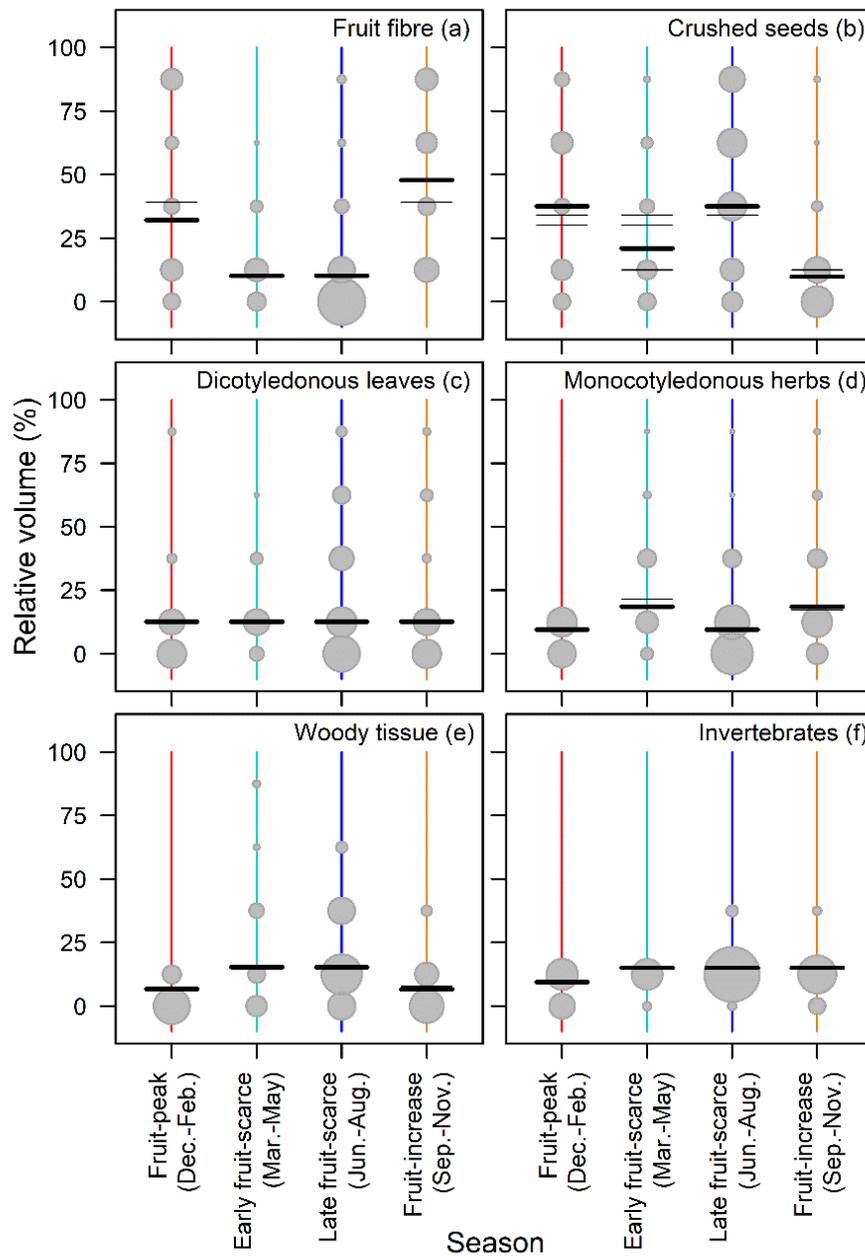
394

395 Non-fruit vegetable foods (dicotyledonous leaves, monocotyledonous herbs, and
 396 woody tissue) in faeces showed different seasonal patterns. Relative volumes of
 397 dicotyledonous leaves showed no seasonal pattern (mean relative volume = 15.6%)
 398 (Table 3 (iii), Fig. 4c). Mandrills fed on the pith of *Aframomum* spp. (Zingiberaceae),
 399 *Marantochloa* spp. (Marantaceae), and on *Palisota hirsuta* (Commelinaceae), and blades of
 400 forest grasses (Poaceae) in various seasons. Relative volumes of monocotyledonous herbs
 401 were larger in the early fruit-scarce and fruit-increase seasons (mean relative volume = 20.0%)
 402 than in the fruit-peak and late fruit-scarce seasons (8.4%) (Table 3 (iv), Fig. 4d). Conversely,

403 woody tissue showed a clear seasonal pattern. Proportions of occurrence in the early and late
404 fruit-scarce seasons were twice as high as those in the other seasons (Fig. 3), and relative
405 volumes in the early and late fruit-scarce seasons (mean relative volume = 17.5%) were much
406 larger than those in the fruit-peak and fruit-increase seasons (4.4%) (Table 3 (v), Fig. 4e).

407 Invertebrates, mainly ants (Formicidae) and grasshoppers (Acrididae), occurred
408 frequently in faeces (Fig. 3) but at consistently low relative volumes (Fig. 4f). The relative
409 volumes were stable from early fruit-scarce to fruit-increase seasons (mean relative volume =
410 12.5%), and decreased in the fruit-peak seasons (7.5%) (Table 3 (vi)).

411 The number of food types in faeces varied seasonally. Numbers were smallest in the
412 fruit-peak season (mean number of food types = 3.5), largest in the early fruit-scarce season
413 (4.5), and intermediate in the late fruit-scarce and fruit-increase seasons (4.0) (Table 3 (vii)).



414

415 **Fig. 4** Seasonality in relative volumes of fruit fibre, crushed seeds, dicotyledonous leaves,
 416 monocotyledonous herbs, woody tissue, and invertebrates in mandrill faecal samples from
 417 Moukalaba-Doudou National Park, Gabon (August 2009–September 2013). *Areas of grey*
 418 *circles* are proportional to the number of faecal samples. *Bold horizontal lines* and *fine*
 419 *horizontal lines* show estimates of the smallest-AIC models and those of the other confident
 420 models, respectively.

421 **Table 3** Models of mandrill diet seasonality in Moukalaba-National Park, Gabon (August 2009–September 2013, N = 417). Model rank is based on
 422 AIC, and the table includes only the ‘confident models’, with model selection frequencies of ≥ 0.05 .

Rank	Model ^a	AIC	Model selection frequency	Fixed effect (estimate \pm SE)				Random effect (estimate)
				Season				SD of follow date
				Fruit-peak (Dec.–Feb.) [a]	Early fruit-scarce (Mar.–May) [b]	Late fruit-scarce (Jun.–Aug.) [c]	Fruit-increase (Sep.–Nov.) [d]	
(i) Relative volume of fruit fibre (logit-transformed LMM)								
1	[a][bc][d]	1278.1	0.729	-0.75 \pm 0.26	-2.18 \pm 0.24	(identical to [b])	-0.08 \pm 0.28	0.97
2	[ad][bc]	1279.0	0.268	-0.44 \pm 0.19	-2.18 \pm 0.25	(identical to [b])	(identical to [a])	1.00
(ii) Relative volume of crushed seeds (logit-transformed LMM)								
1	[ac][b][d]	1289.9	0.804	-0.51 \pm 0.21	-1.33 \pm 0.46	(identical to [a])	-2.22 \pm 0.30	1.07
2	[abc][d]	1290.9	0.068	-0.66 \pm 0.20	(identical to [a])	(identical to [a])	-2.22 \pm 0.31	1.10
3	[ac][bd]	1291.1	0.055	-0.51 \pm 0.22	-1.94 \pm 0.26	(identical to [a])	(identical to [b])	1.09
5	[ab][c][d]	1291.3	0.068	-0.84 \pm 0.24	(identical to [a])	-0.32 \pm 0.33	-2.22 \pm 0.31	1.09
(iii) Relative volume of dicotyledonous leaves (logit-transformed LMM)								
1	[abcd]	1209.9	0.949	-1.93 \pm 0.13	(identical to [a])	(identical to [a])	(identical to [a])	0.86
(iv) Relative volume of monocotyledonous herbs (logit-transformed LMM)								
1	[ac][bd]	1109.7	0.923	-2.25 \pm 0.11	-1.48 \pm 0.13	(identical to [a])	(identical to [b])	0.49
2	[ac][b][d]	1111.4	0.076	-2.25 \pm 0.11	-1.29 \pm 0.23	(identical to [a])	-1.57 \pm 0.16	0.49
(v) Relative volume of woody tissue (logit-transformed LMM)								
1	[ad][bc]	1043.7	0.893	-2.64 \pm 0.11	-1.71 \pm 0.13	(identical to [b])	(identical to [a])	0.50
2	[a][bc][d]	1044.9	0.097	-2.78 \pm 0.15	-1.71 \pm 0.13	(identical to [b])	-2.48 \pm 0.15	0.50
(vi) Relative volume of invertebrates (logit-transformed LMM)								
1	[a][bcd]	570.3	0.982	-2.26 \pm 0.07	-1.73 \pm 0.05	(identical to [b])	(identical to [b])	0.00
(vii) Number of food types (binomial GLMM)								
1	[a][b][cd]	334.8	0.898	0.33 \pm 0.09	1.16 \pm 0.13	0.70 \pm 0.07	(identical to [c])	0.10

423 a. “Model” column shows grouping patterns of seasons: for example, the smallest-AIC model for relative volume of fruit fibre (i.e., [a][bc][d]) indicates that relative
 424 volumes in the early and late fruit-scarce seasons were estimated to be identical, and that the other combinations were estimated to be different each other.

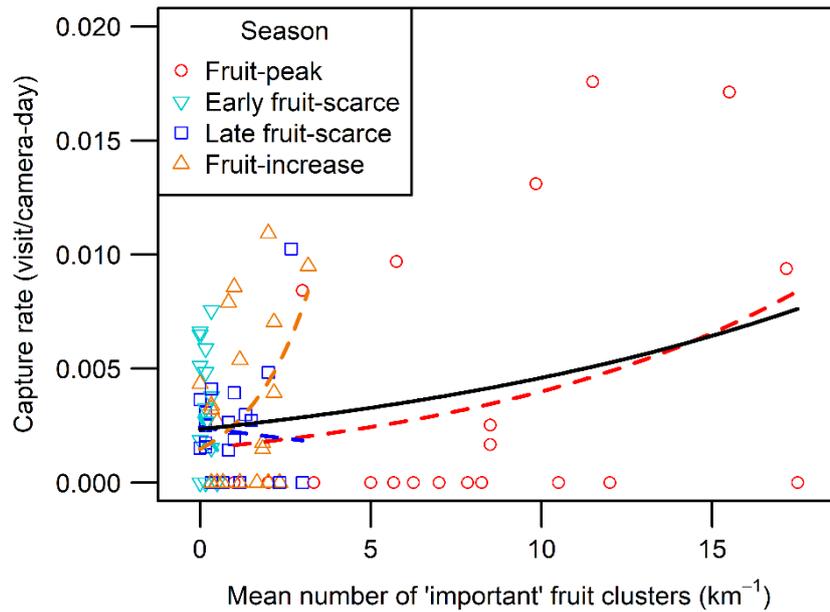
425 **Seasonality in Habitat Use**

426 We calculated capture rates in 87 transect-seasons from January 2012 to November 2013 (total
427 camera-days = 54,541). We identified 155 independent group visits on 169 days (overall
428 capture rate = 0.0028 visit/camera-day). Groups visited two different transects on 14 days but
429 never three or more transects on any given day. Given that the estimated mean ranging speed
430 of groups in the study area is 0.9 km/h (Hongo 2016), all but one case of these visits to two
431 different transects were too distant for a group to arrive within the time intervals of the visits,
432 suggesting that they were unlikely to be two consecutive visits by the same group.

433 We identified seven confident models showing that the mean number of ‘important’
434 fruit clusters affected the capture rates positively, and that habitat disturbance had a negative
435 effect on capture rates (Table 4). Four of these models also included the interaction term
436 between important fruits and season. According to the second smallest-AIC model, which had
437 the highest model selection frequency, the mean number of important fruit clusters correlated
438 positively with capture rates in the fruit-peak and fruit-increase seasons, but correlations in the
439 early and late fruit-scarce seasons were not reliable, as the standard errors of the interaction
440 term were large (Fig. 5, Table 4). Although some models included other habitat parameters,
441 the effects were unclear because their standard errors were large (Table 4).

442 Variance in capture rates was significantly different among seasons (Levene’s test:
443 $F = 13.9, P = 2.1 \times 10^{-7}$). Post hoc pairwise comparisons showed that the variance in the fruit-
444 peak season was significantly higher than in the other seasons (Table 5). In fruit-peak seasons,
445 cameras in more than half of the transects recorded no mandrill groups, and capture rates of
446 transects DB and DT were particularly high (Fig. 6 (a, e)). In contrast, in most of the other
447 seasons, cameras in most transects recorded groups at relatively lower rates (Fig. 6).

448



449

450 **Fig. 5** The influence of the number of ‘important’ fruit clusters and season on camera-trap
 451 capture rates of mandrill groups in Moukalaba-Doudou National Park, Gabon (January 2012–
 452 November 2013). Data points represent values for individual transect-seasons. *Solid black line*
 453 shows the regression curve of the smallest-AIC model, whereas *dashed lines* show those of
 454 the second smallest-AIC model, which had the highest model selection frequency.

455

456

457 **Table 4** Models of seasonality in habitat use by mandrill groups in Moukalaba-National Park, Gabon (January 2012–November 2013, N = 87).

458 Model rank is based on AIC, and the table includes only ‘confident models’, with model selection frequencies of ≥ 0.05 .

Rank	1	2	3	5	6	7	9
Model	β_1, β_4	$\beta_1, \beta_2, \beta_1 \times \beta_2, \beta_4$	$\beta_1, \beta_2, \beta_4$	$\beta_1, \beta_2, \beta_1 \times \beta_2, \beta_4, \beta_5$	$\beta_1, \beta_2, \beta_1 \times \beta_2, \beta_3, \beta_4$	$\beta_1, \beta_2, \beta_4, \beta_5$	$\beta_1, \beta_2, \beta_1 \times \beta_2, \beta_3, \beta_4, \beta_5$
AIC	170.5	170.7	171.6	171.6	172.1	172.2	172.5
Model selection frequency	0.136	0.300	0.117	0.109	0.073	0.056	0.082
Fixed effect (estimate \pm SE)							
Intercept	-5.88 ± 0.22	-6.25 ± 0.42	-6.40 ± 0.41	-6.17 ± 0.42	-6.22 ± 0.42	-6.32 ± 0.41	-6.12 ± 0.41
Mean number of ‘important’ fruit clusters [β_1]	0.27 ± 0.07	0.39 ± 0.17	0.49 ± 0.16	0.42 ± 0.17	0.39 ± 0.17	0.52 ± 0.17	0.42 ± 0.17
Season [β_2]							
Early fruit-scarce	–	-3.46 ± 3.83	0.65 ± 0.49	-3.14 ± 3.83	-3.41 ± 3.81	0.72 ± 0.50	-2.94 ± 3.81
Late fruit-scarce	–	-0.01 ± 0.54	0.48 ± 0.45	0.07 ± 0.55	-0.03 ± 0.54	0.54 ± 0.45	0.06 ± 0.55
Fruit-increase	–	1.18 ± 0.45	0.82 ± 0.43	1.23 ± 0.46	1.20 ± 0.45	0.88 ± 0.44	1.28 ± 0.46
Interaction between number of ‘important’ fruit clusters and season [$\beta_1 \times \beta_2$]							
Early fruit-scarce	–	-6.27 ± 6.03	–	-5.86 ± 6.02	-6.18 ± 6.01	–	-5.55 ± 5.99
Late fruit-scarce	–	-0.77 ± 0.84	–	-0.72 ± 0.84	-0.78 ± 0.84	–	-0.73 ± 0.84
Fruit-increase	–	1.80 ± 0.80	–	1.77 ± 0.79	1.91 ± 0.81	–	1.92 ± 0.81
Steepness [β_3]	–	–	–	–	-0.17 ± 0.22	–	-0.21 ± 0.20
Disturbed habitats [β_4]	-1.97 ± 0.66	-2.02 ± 0.70	-1.94 ± 0.66	-2.12 ± 0.67	-2.16 ± 0.71	-2.04 ± 0.63	-2.29 ± 0.67
Seasonally inundated habitats [β_5]	–	–	–	-0.58 ± 0.53	–	-0.59 ± 0.49	-0.67 ± 0.51
Random effect (estimate)							
SD of transect	0.58	0.63	0.58	0.57	0.61	0.51	0.53

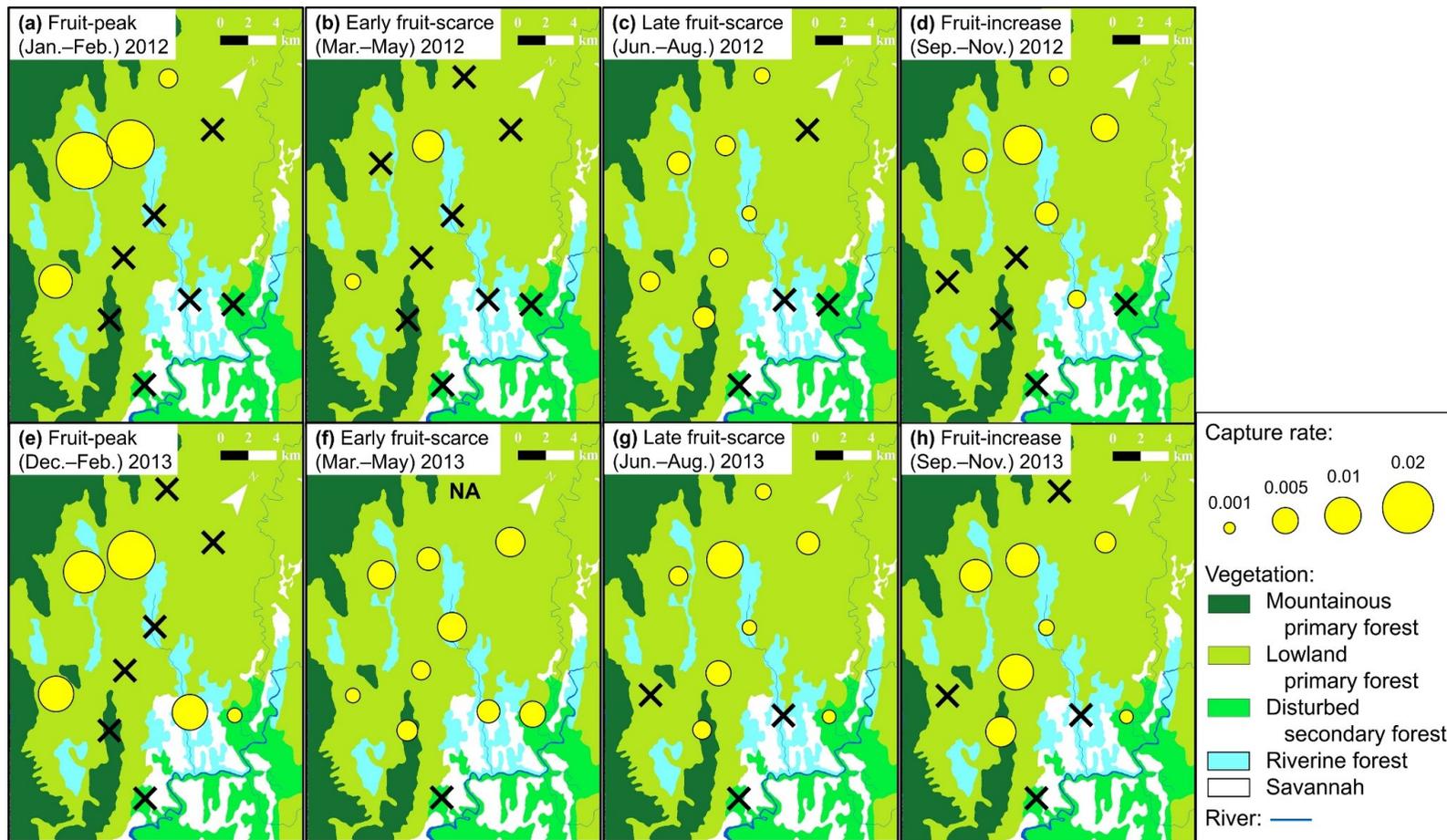
459

460 **Table 5** Seasonal comparisons of variance in camera-trap capture rates of mandrill groups in
 461 Moukalaba-Doudou National Park, Gabon (January 2012–November 2013).

Season	Total number of transects	Variance in capture rates across transects (camera-days ⁻²)	F test with Holm's p-value adjustment		
			vs. Early fruit-scarce	vs. Late fruit-scarce	vs. Fruit- increase
Fruit-peak	22	5.0×10^{-5}	F = 7.1 <i>P</i> < 0.001	F = 9.4 <i>P</i> < 0.001	F = 4.1 <i>P</i> = 0.008
Early fruit- scarce	21*	7.0×10^{-6}	-	F = 1.3 <i>P</i> = 0.54	F = 0.58 <i>P</i> = 0.44
Late fruit- scarce	22	5.4×10^{-6}	-	-	F = 0.44 <i>P</i> = 0.19
Fruit- increase	22	1.2×10^{-5}	-	-	-

462 * No camera-trap worked in transect G5 in the early fruit-scarce season in 2013.

463



464

465 **Fig. 6** Camera-trap capture rates for mandrill groups in each season in Moukalaba-Doudou National Park, Gabon (January 2012–November 2013).

466 *X* indicates no mandrill groups were filmed. *NA* in (f) means no camera worked during the season.

467

468 **Discussion**

469 We found seasonal changes in diet and habitat use patterns in wild mandrill groups. In fruit-
470 rich seasons, mandrill faeces contained a high proportion of fruit fibre, and groups visited
471 transects where fruit production was high intensively. In contrast, in fruit-scarce seasons,
472 crushed seeds made up a large volume of the faecal samples, the proportion of woody tissue
473 and the number of food types increased. Groups also visited larger numbers of transects, and
474 their visit frequencies were distributed more uniformly in fruit-scarce seasons.

475 The relative volume of fruit fibre in faeces varied with fruit availability, and the
476 number of food types was smallest in the fruit-peak season, although faeces contained multiple
477 food types year-round. These results suggest that mandrills at Moukalaba-Doudou are
478 omnivorous year-round but become more frugivorous when fruits are available. The relative
479 volume of crushed seeds was high even in fruit-scarce seasons, and seeds of several species
480 that do not produce many fruits in these seasons appeared in faeces frequently, suggesting that
481 mandrills in the study area respond to seasonal fruit scarcity by foraging on buried seeds. These
482 dietary patterns are in common with mandrills at other sites (Rogers et al. 1996; Tutin et al.
483 1997; White 2007) and drills in lowland forests (Astaras and Waltert 2010). Increased dietary
484 diversity during food scarcity is also a common strategy for other African primates
485 (Hemingway and Bynum 2005).

486 The relative volume of woody tissue increased in fruit-scarce seasons, but that of
487 monocotyledonous herbs did not show a seasonal pattern according to fruiting phenology.
488 These results differ from previous findings, where mandrills increase their herb consumption
489 when fruits are scarce (Hoshino 1985; Tutin et al. 1997), and may imply within-species
490 variation in feeding strategy, as observed in drills on Bioko Island (Owens et al. 2015). Herbs
491 and woody tissue are both low-quality foods, which are common alternative foods for large-
492 sized monkeys (Hemingway and Bynum 2005). Mandrills have powerful fore limb flexion

493 (Fleagle and McGraw 2002), which may enable them to excavate roots and subterranean stems
494 buried in leaf litter.

495 Camera-trap capture rates of mandrill groups showed positive correlations with
496 availability of ‘important’ fruits in fruit-rich seasons. Moreover, group visits in fruit-peak
497 seasons were highly biased toward two or three transects, whereas those in the other seasons
498 were more uniformly distributed across most of the transects. These results suggest seasonal
499 changes in mandrill habitat use. In fruit-rich seasons, mandrill groups in our study area may
500 show a high selectivity for habitats where fruits are highly available, to forage on fresh fruits.
501 In contrast, during fruit-scarce seasons, when mandrills consume more uniformly-distributed
502 seeds and woody tissue, they may become less selective in fruit availability and range over a
503 much wider area. Our findings on seasonal habitat use differ from those for a mandrill group
504 at Lopé, which used gallery forests intensively regardless of season (White 2007). This
505 difference may reflect differences in habitat. At Lopé, human-introduced *Elaeis guineensis*
506 trees are abundant in gallery forests (Ukizintambara et al. 2007). Their fruits are available year-
507 round, and mandrills consume them frequently (White 2007). This all-year-round available
508 food may retain the group in gallery forests. At Moukalaba-Doudou, no fruit species was
509 available year-round, and therefore mandrills may need change both diets and ranging patterns
510 seasonally.

511 Habitat disturbance affected the capture rates negatively, suggesting that mandrill
512 groups avoid disturbed forests. Mandrills are large-sized, frugivorous primates and this result
513 is consistent with a general pattern where the negative effect of disturbance on habitat
514 suitability increases with body weight and degree of frugivory (Johns and Skorupa 1987). The
515 effects of seasonal inundation and steepness on the capture rates were unclear. These habitat
516 parameters may not affect mandrill habitat use: in central Gabon, mandrills are observed in
517 forests close to streams frequently (Lahm 1986), and drills range in montane forests with steep

518 altitudinal gradients (Owens et al. 2015; Wild et al. 2005).

519 There is so far no clear evidence for seasonal range expansion in African primates,
520 but this is observed frequently in New World primates, particularly species with large home
521 ranges (Hemingway and Bynum 2005; Terborgh 1983). The unusually large range of mandrills
522 and heterogeneous vegetation distribution in the study area may allow them to show this
523 flexible ranging behaviour. Moreover, our findings highlight intergeneric differences between
524 *Mandrillus* and *Cercocebus* in adaptations to food seasonality. Although these genera share
525 morphology adapted to hard-object eating and terrestrial foraging (Fleagle and McGraw 2002),
526 *Cercocebus* species do not exhibit clear dietary seasonality (McGraw et al. 2014; Mitani 1989).
527 This gap may come from considerable difference in group size between the genera (Swedell
528 2011). Seasonal change in diet and seasonal range expansion may be both important for
529 *Mandrillus* species to maintain their large groups year-round, whereas changing habitat may
530 be sufficient for *Cercocebus* species of small group size to keep their diets stable year-round.
531 To clarify the effect of group size on behavioural flexibility in African primates, future studies
532 should compare both dietary and ranging responses to food seasonality between closely-
533 related sympatric species with different group sizes, as conducted in New World forests (Peres
534 1994). Mandrills and red-capped mangabeys may be good candidates for the comparison of
535 this kind.

536 Our study has two limitations. First, we conducted the fruit census for two years,
537 which covered only part of the periods when we collected faecal samples. Although fruiting
538 phenology showed a regular pattern, it may vary between years. We need longer-term studies
539 to confirm our findings. Second, we investigated seasonality in habitat use of mandrills at a
540 population level, but did not examine seasonality in group ranging behaviours *per se*. Field
541 studies of the ranging patterns of identified groups are needed to understand the ranging
542 seasonality of wild mandrills at a finer level.

543

544 **Conclusion and Perspectives**

545 Mandrills in the study area changed their diets from highly frugivorous to more omnivorous
546 when fruit availability decreased. Groups also reduced their habitat selectivity and used
547 different habitats more evenly when fruit availability decreased. These flexible feeding
548 behaviours may allow mandrills to maintain their extremely large groups. Using different
549 habitats evenly in fruit-scarce seasons may also benefit mandrill reproduction. The mandrill
550 mating season coincides with the fruit-scarce season (Hongo et al. 2016), and large groups
551 which travel widely and contain many sexually receptive females, may favour influxes by
552 many solitary males. Receptive females may be able to mate with multiple males, including
553 subordinate males (Setchell et al. 2005), and choose among males (Setchell 2005). Future
554 studies should examine the relationships between the ranging patterns of groups and solitary
555 males.

556

557 **Conflict of Interest**

558 The authors declare that they have no conflict of interest.

559

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577

578 **References**

- 579 Abernethy, K. A., White, L. J. T., & Wickings, E. J. (2002). Hordes of mandrills (*Mandrillus*
580 *sphinx*): extreme group size and seasonal male presence. *Journal of Zoology*, 258(1), 131–
581 137.
- 582 Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on*
583 *Automatic Control*, 19(6), 716–723.
- 584 Astaras, C., & Waltert, M. (2010). What does seed handling by the drill tell us about the
585 ecological services of terrestrial cercopithecines in African forests? *Animal Conservation*,
586 13(6), 568–578.
- 587 Bates, D., Mächler, M., Bolker, B. M., & Walker, S. C. (2015). Fitting linear mixed-effects
588 models using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- 589 Brockmeyer, T., Kappeler, P. M., Willaume, E., Benoit, L., Mboumba, S., & Charpentier, M.
590 J. (2015). Social organization and space use of a wild mandrill (*Mandrillus sphinx*) group.
591 *American Journal of Primatology*, 77(10), 1036–1048.
- 592 Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: a*

- 593 *practical information-theoretic approach*. New York, USA: Springer.
- 594 Di Bitetti, M. S. (2001). Home-range use by the tufted capuchin monkey (*Cebus apella*
595 *nigritus*) in a subtropical rainforest of Argentina. *Journal of Zoology*, 253(1), 33–45.
- 596 Etiendem, D. N., Funwi-Gabga, N., Tagg, N., Hens, L., & Indah, E. K. (2013). The Cross
597 River gorillas (*Gorilla gorilla diehli*) at Mawambi Hills, South-West Cameroon: habitat
598 suitability and vulnerability to anthropogenic disturbance. *Folia Primatologica*, 84(1), 18–
599 31.
- 600 Fleagle, J. G., & McGraw, W. S. (2002). Skeletal and dental morphology of African papionins:
601 unmasking a cryptic clade. *Journal of Human Evolution*, 42(3), 267–292.
- 602 Fleagle, J. G. (2013). Primate adaptation and evolution (3 ed.). San Diego, USA: Academic
603 Press.
- 604 Furuichi, T., Hashimoto, C., & Tashiro, Y. (2001). Fruit availability and habitat use by
605 chimpanzees in the Kalinzu Forest, Uganda: examination of fallback foods. *International*
606 *Journal of Primatology*, 22(6), 929–945.
- 607 Gogarten, J. F., Bonnell, T. R., Brown, L. M., Campenni, M., Wasserman, M. D., & Chapman,
608 C. A. (2014). Increasing group size alters behavior of a folivorous primate. *International*
609 *Journal of Primatology*, 35(2), 590–608.
- 610 Hanya, G., Tsuji, Y., & Grueter, C. C. (2013). Fruiting and flushing phenology in Asian tropical
611 and temperate forests: implications for primate ecology. *Primates*, 54(2), 101–110.
- 612 Harris, T. R., Chapman, C. A., & Monfort, S. L. (2010). Small folivorous primate groups
613 exhibit behavioral and physiological effects of food scarcity. *Behavioral Ecology*, 21(1),
614 46–56.
- 615 Hemingway, C. A., & Bynum, N. (2005). The influence of seasonality on primate diet and
616 ranging. In D. K. Brockman & C. P. van Schaik (Eds.), *Seasonality in Primates: Studies*
617 *of Living and Extinct Human and Non-human Primates* (pp. 57–104). New York, USA:

618 Cambridge University Press.

619 Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian*
620 *Journal of Statistics*, 6(2), 65–70.

621 Hongo, S. (2014). New evidence from observations of progressions of mandrills (*Mandrillus*
622 *sphinx*): a multilevel or non-nested society? *Primates*, 55(4), 473–481.

623 Hongo, S. (2016). Socioecology of mandrills (*Mandrillus sphinx*): mating and feeding tactics
624 in a primate with extremely large group. Kyoto University, Kyoto, Japan.

625 Hongo, S., Nakashima, Y., Akomo-Okoue, E. F., & Mindonga-Nguelet, F. L. (2016). Female
626 reproductive seasonality and male influxes in wild mandrills (*Mandrillus sphinx*).
627 *International Journal of Primatology*, 37(3), 416–437.

628 Hoshino, J. (1985). Feeding ecology of mandrills (*Mandrillus sphinx*) in Campo Animal
629 Reserve, Cameroon. *Primates*, 26(3), 248–273.

630 Janson, C. H. (1988). Food competition in brown capuchin monkeys (*Cebus apella*):
631 quantitative effects of group size and tree productivity. *Behaviour*, 105(1), 53–76.

632 Johns, A. D., & Skorupa, J. P. (1987). Responses of rain-forest primates to habitat disturbance:
633 a review. *International Journal of Primatology*, 8(2), 157–191.

634 Kaplin, B. A., Munyaligoga, V., & Moermond, T. C. (1998). The Influence of temporal
635 changes in fruit availability on diet composition and seed handling in blue monkeys
636 (*Cercopithecus mitis doggetti*). *Biotropica*, 30(1), 56–71.

637 Lahm, S. A. (1986). Diet and habitat preference of *Mandrillus sphinx* in Gabon: implications
638 of foraging strategy. *American Journal of Primatology*, 11(1), 9–26.

639 Levene, H. (1960). Robust tests for equality of variances. In I. Olkin, S. G. Ghurye, W.
640 Hoeffding, W. G. Madow & H. B. Mann (Eds.), *Contributions to Probability and*
641 *Statistics: Essays in Honor of Harold Hotelling* (pp. 278–292). Stanford, USA: Stanford
642 University Press.

- 643 Litvaitis, J. A. (2000). Investigating food habits of terrestrial vertebrates. In M. C. Pearl (Ed.),
644 *Research Techniques in Animal Ecology* (pp. 165–190). New York, USA: Columbia
645 University Press.
- 646 McGraw, W. S., Vick, A. E., & Daegling, D. J. (2014). Dietary variation and food hardness in
647 sooty mangabeys (*Cercocebus atys*): implications for fallback foods and dental adaptation.
648 *American Journal of Physical Anthropology*, 154(3), 413–423.
- 649 McGrew, W. C., Marchant, L. F., & Phillips, C. A. (2009). Standardised protocol for primate
650 faecal analysis. *Primates*, 50(4), 363–366.
- 651 Mitani, M. (1989). *Cercocebus torquatus*: adaptive feeding and ranging behaviors related to
652 seasonal fluctuations of food resources in the tropical rain forest of south-western
653 Cameroon. *Primates*, 30(3), 307–323.
- 654 Mori, Y., Nagamitsu, T., & Kubo, T. (2009). Clonal growth and its effects on male and female
655 reproductive success in *Prunus ssiiori* (Rosaceae). *Population Ecology*, 51(1), 175–186.
- 656 Nakagawa, N. (1989). Bioenergetics of Japanese monkeys (*Macaca fuscata*) on Kinkazan
657 Island during winter. *Primates*, 30(4), 441–460.
- 658 Nakashima, Y. (2015). Inventorying medium- and large-sized mammals in the African
659 lowland rainforest using camera trapping. *Tropics*, 23(4), 151–164.
- 660 Newbery, D. M., Songwe, N. C., & Chuyong, G. B. (1998). Phenology and dynamics of an
661 African rainforest at Korup, Cameroon. In D. M. Newbery, H. H. T. Prins & N. D. Brown
662 (Eds.), *Dynamics of tropical communities: 37th Symposium of the British Ecological*
663 *Society* (pp. 267–308). Oxford, UK: Blackwell Science.
- 664 Nsi Akoue, G., Mbading-Mbading, W., Willaume, E., Souza, A., Mbatchi, B., Charpentier, M.
665 J. E., et al. (2017). Seasonal and individual predictors of diet in a free-ranging population
666 of mandrills. *Ethology*, 123(9), 600–613.
- 667 O'Brien, T. G., Kinnaird, M. F., & Wibisono, H. T. (2003). Crouching tigers, hidden prey:

- 668 Sumatran tiger and prey populations in a tropical forest landscape. *Animal Conservation*,
669 6(2), 131–139.
- 670 Owens, J. R., Honarvar, S., Nessel, M., & Hearn, G. W. (2015). From frugivore to folivore:
671 altitudinal variations in the diet and feeding ecology of the Bioko Island drill (*Mandrillus*
672 *leucophaeus poensis*). *American Journal of Primatology*, 77(12), 1263–1275.
- 673 Peres, C. A. (1994). Primate responses to phenological changes in an Amazonian terra firme
674 forest. *Biotropica*, 26(1), 98–112.
- 675 R Core Team. (2017). R: a language and environment for statistical computing. R Foundation
676 for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- 677 Rogers, M. E., Abernethy, K. A., Fontaine, B., Wickings, E. J., White, L. J. T., & Tutin, C. E.
678 G. (1996). Ten days in the life of a mandrill horde in the Lopé Reserve, Gabon. *American*
679 *Journal of Primatology*, 40(4), 297–313.
- 680 Sato, H. (2013). Habitat shifting by the common brown lemur (*Eulemur fulvus fulvus*): a
681 response to food scarcity. *Primates*, 54(3), 229–235.
- 682 Setchell, J. M. (2005). Do female mandrills prefer brightly colored males? *International*
683 *Journal of Primatology*, 26(4), 715–735.
- 684 Setchell, J. M., Charpentier, M., & Wickings, E. J. (2005). Mate guarding and paternity in
685 mandrills: factors influencing alpha male monopoly. *Animal Behaviour*, 70(5), 1105–1120.
- 686 Shimodaira, H. (1998). An application of multiple comparison techniques to model selection.
687 *Annals of the Institute of Statistical Mathematics*, 50(1), 1–13.
- 688 Swedell, L. (2011). African papionins: diversity of social organization and ecological
689 flexibility. In C. J. Campbell, A. Fuentes, K. C. MacKinnon, Simon K. Bearder & R. M.
690 Stumpf (Eds.), *Primates in Perspective* (2 ed., pp. 241–277). New York, USA: Oxford
691 University Press.
- 692 Takenoshita, Y., Ando, C., Iwata, Y., Okayasu, N., Tashiro, Y., Yumoto, T., et al. (2007). Liste

693 d'espèces de plantes vasculaire dans la partie nord du Parc National de la Moukalaba-
694 Doudou, Gabon. In J. Projet en Primatologie de l'Université de Kyoto (Ed.), *Rapport de*
695 *Recherches Effectuées au Parc National de Moukalaba-Doudou, Gabon: Mars 2006 -*
696 *Février 2007* (pp. 41–50). Kyoto, Japan.

697 Takenoshita, Y., Ando, C., Iwata, Y., & Yamagiwa, J. (2008). Fruit phenology of the great ape
698 habitat in the Moukalaba-Doudou National Park, Gabon. *African Study Monographs,*
699 *Suppl. 39, 23–39.*

700 Tang, C., Huang, L., Huang, Z., Krzton, A., Lu, C., & Zhou, Q. (2016). Forest seasonality
701 shapes diet of limestone-living rhesus macaques at Nonggang, China. *Primates, 57*(1),
702 83–92.

703 Terada, S., Nackoney, J., Sakamaki, T., Mulavwa, M. N., Yumoto, T., & Furuichi, T. (2015).
704 Habitat use of bonobos (*Pan paniscus*) at Wamba: selection of vegetation types for ranging,
705 feeding, and night-sleeping. *American Journal of Primatology, 77*(6), 701–713.

706 Terborgh, J. (1983). *Five New World primates: a study in comparative ecology*. Princeton,
707 USA: Princeton University Press.

708 Tsuji, Y., Hanya, G., & Grueter, C. C. (2013). Feeding strategies of primates in temperate and
709 alpine forests: comparison of Asian macaques and colobines. *Primates, 54*(3), 201–215.

710 Tutin, C. E. G., Ham, R. M., White, L. J. T., & Harrison, M. J. S. (1997). The primate
711 community of the Lopé reserve, Gabon: diets, responses to fruit scarcity, and effects on
712 biomass. *American Journal of Primatology, 42*(1), 1–24.

713 Ukizintambara, T., White, L., Abernethy, K., & Thébaud, C. (2007). Gallery forests versus
714 bosquets: conservation of natural fragments at Lopé National Park in central Gabon.
715 *African Journal of Ecology, 45*(4), 476–482.

716 van Schaik, C. P., & Pfannes, K. R. (2005). Tropical climates and phenology: a primate
717 perspective. In D. K. Brockman & C. P. van Schaik (Eds.), *Seasonality in Primates:*

- 718 *Studies of Living and Extinct Human and Non-human Primates* (pp. 23–54). New York,
719 USA: Cambridge University Press.
- 720 Warton, D. I., & Hui, F. K. C. (2011). The arcsine is asinine: the analysis of proportions in
721 ecology. *Ecology*, *92*(1), 3–10.
- 722 White, E. C. (2007). Ecology of *Mandrillus sphinx*: ranging, diet and social structure of a
723 mandrill horde in Lopé National Park, Gabon. University of Exeter, Cornwall, UK.
- 724 White, E. C., Dikangadissi, J.-T., Dimoto, E., Karesh, W. B., Kock, M. D., Abiaga, N. O., et
725 al. (2010). Home-range use by a large horde of wild *Mandrillus sphinx*. *International*
726 *Journal of Primatology*, *31*(4), 627–645.
- 727 White, L. J. T. (1994). Patterns of fruit-fall phenology in the Lopé Reserve, Gabon. *Journal of*
728 *Tropical Ecology*, *10*(03), 289–312.
- 729 Wild, C., Morgan, B. J., & Dixon, A. (2005). Conservation of Drill Populations in
730 Bakossiland, Cameroon: Historical Trends and Current Status. *International Journal of*
731 *Primatology*, *26*(4), 759–773.
- 732 Yamagiwa, J., Mwanza, N., Yumoto, T., & Maruhashi, T. (1994). Seasonal change in the
733 composition of the diet of eastern lowland gorillas. *Primates*, *35*(1), 1–14.
- 734 Yumoto, T., Terakawa, M., Terada, S., Boupoya, A., & Nzabi, T. (2015). Species composition
735 of a middle altitude forest in Moukalaba-Doudou National Park, Gabon. *Tropics*, *23*(4),
736 205–213.