

RESEARCH ARTICLE

Feeding Ecology of Bonobos Living in Forest-Savannah Mosaics: Diet Seasonal Variation and Importance of Fallback Foods

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Primates along with many other animal taxa are forced to cope with large shifts in basic ecological conditions because of rapid anthropogenically induced changes of their habitats. One of the coping strategies for primates is to adjust their diet to these changes, and several studies have demonstrated the importance of fallback resources for this. Bonobos, like chimpanzees, might be particularly vulnerable to habitat fragmentation because of their high dependence on fruit availability. Little is known, however, about bonobo feeding ecology in fragmented habitats and their use of fallback resources. In this study, we investigate diet seasonal variation and the exploitation of preferred and fallback foods in a bonobo population living in forest-savannah mosaics. Results show that bonobos have adapted to this fragmented habitat by feeding on only a few fruit species, including an important number of non-tree species (liana, herb and savannah shrub), in comparison to populations living in dense forests. These non-tree plants have been defined as fallback and non-preferred foods, which are most probably consumed to maintain high frugivory. Interestingly, we identified that preferred foods are all typical of mature forests while fallback resources are mainly found in forest edges or disturbed areas. This finding indicates that bonobos prefer to use mature forests when feeding, as they do for nesting, but extend their range use to forest areas in close proximity to humans when the availability of preferred fruits is low. Finally, we show that bonobo diet relies heavily on two abundant fallback fruits: *Musanga cecropioides* and *Marantochloa leucantha*. Other studies have demonstrated that the selection of abundant fallback resources enables primates to subsist at high densities and to maintain cohesive groups, as observed at this study site. Our findings suggest that bonobos living in forest-savannah mosaics can be considered as staple fallback food consumers. *Am. J. Primatol.* 77:948–962, 2015. © 2015 Wiley Periodicals, Inc.

Key words: feeding ecology; fragmented environment; fallback foods; bonobos

INTRODUCTION

In the current context of rapid anthropogenically induced landscape modification across primate habitat countries, improving our knowledge about the capacity of primates to adapt is crucial [Corlett, 2011]. As anthropogenic activities cause the proportion of secondary forests to increase at the expense of primary forests, primate habitats are facing structural and dynamic changes [Pan et al., 2011], which can affect forest composition and species abundance [Wright, 2005]. As a consequence, most primate species are forced to cope with large shifts in ecological conditions and associated food resources [Fahrig, 2003; Fischer & Lindenmayer, 2007; Marsh

et al., 2013]. An increasing number of studies are addressing the impact of habitat fragmentation on primates [reviewed in Marsh & Chapman, 2013], demonstrating, in feeding ecology, varying dietary

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adjustments such as reduced frugivory [*Cercopithecus cephus* and *nicitans*: Tutin, 1999], food diversification [*Ateles geoffroyi*: Chaves & Stoner, 2012], increased reliance on low-quality food items [*Eulemur collaris*: Donati et al., 2011], or on fallback resources [*Propithecus diadema*: Irwin 2008; Irwin et al., 2014; *Pan troglodytes*: Chancellor et al., 2012] and even incorporation of human cultivated items in the diet [*Pan troglodytes*: Chancellor et al., 2012; McLennan 2013]. Studying feeding ecology in fragments provides the opportunity to examine the plasticity of primate foraging behaviour [Boyle & Smith, 2010b; Chancellor et al., 2012] and to gain a better understanding of the resilience of primates living in these environments [Marsh & Chapman, 2013]. In addition, such studies are essential to formulate more species-specific conservation measures [Boyle & Smith, 2010a; Chapman et al., 2007; Marsh, 2003; Marsh & Chapman, 2013; Onderdonk & Chapman, 2000].

Bonobos, like chimpanzees, may be particularly vulnerable to fragmented environments and shifts in ecological conditions because of their high dependence on fruit availability. Indeed, both species are known to maintain their frugivorous habits even in periods of fruit scarcity [White & Lanjouw, 1992; Wrangham et al., 1998], through various adaptive responses such as: (i) flexibility in ranging and grouping patterns according to the spatio-temporal fluctuations of food patches [chimpanzee: Hashimoto et al., 2003; Itoh & Nishida, 2007; Lehmann et al., 2007; bonobos: Mulavwa et al., 2008], (ii) increase in the types of habitats used when fruit availability is low [chimpanzee: Basabose, 2005; Chancellor et al., 2012; bonobos: Mulavwa et al., 2010] and, (iii) for chimpanzees, a shift to consumption of fallback foods of lower quality, but which are more abundant [Conklin-Brittain et al., 1998; Watts et al., 2012; Wrangham et al., 1991]. Since habitat fragmentation may lead to even more pronounced periods of fruit scarcity, studying the effect of fragmentation on feeding ecology is essential but still limited for chimpanzees [Chancellor et al., 2012; McLennan, 2013; Tutin, 1999] and almost unknown for bonobos [but see Thompson, 1997]. The discovery of bonobos also inhabiting fragmented environments, i.e., in forest-savannah mosaics, was only made in the late 1990s. This particular bonobo habitat has still received very little attention [Serckx, 2014; Thompson, 1997, 2001] although it is a particularly interesting place in which to study bonobo dietary plasticity, given its large spatio-temporal variation in resource availability [Serckx et al., 2014].

Identifying the fallback foods (FBF) of primates living in fragmented environments is important because their exploitation may allow primates to subsist in higher densities than otherwise possible [Marshall et al., 2009]. In contrast to preferred foods that are consumed disproportionately relative to

their abundance in the habitat [Marshall & Wrangham, 2007], FBFs are defined as the resources consumed when the abundance of preferred foods decline [Harrison & Marshall, 2011; Marshall & Wrangham, 2007; Marshall et al., 2009]. FBFs are also typically lower in energy than preferred foods [Conklin-Brittain et al., 1998; Doran-Sheehy et al., 2009; Irwin et al., 2014; Wrangham et al., 1998]. Two major publications presented an overview of the topic of fallback foods. Authors pointed out that we should distinguish between “staple” and “filler” FBFs because their roles differ in the diet and they have distinct evolutionary effects [Lambert, 2007; Marshall & Wrangham, 2007]. Staple FBFs are available and consumed throughout the year, may seasonally constitute up to 100% of the diet at a given time and are typically low-quality foods. Filler FBFs never constitute 100% of the diet, may be completely avoided when preferred foods are available but are usually high-quality items. Chimpanzees typically use FBFs as filler foods [Harrison & Marshall, 2011; Lambert, 2007; Marshall & Wrangham, 2007], with variation in the types of the FBFs across sites [figs: Wrangham et al., 1993; insects: Yamagiwa & Basabose, 2009; bark cambium: Chancellor et al., 2012]. However, the classification of bonobos as staple or filler FBF consumers remains unclear because their FBFs have not yet been well identified [Harrison & Marshall, 2011; Marshall et al., 2009; Yamagiwa & Basabose, 2009]. Some studies have shown that bonobos switch to terrestrial herbaceous vegetation (THV) during times of fruit shortage [Conklin-Brittain et al., 2001], but bonobos consumed THV of high quality [Malenky & Wrangham, 1994], which makes their classification as FBFs ambiguous [Marshall et al., 2009]. Similarly, figs were reported to be more intensively consumed when the availability of other fruits decline [Hohmann et al., 2006], but it is still unclear whether figs represent FBFs for bonobos or not [Harrison & Marshall, 2011]. Harrison and Marshall [2011] concluded that bonobo consumption of FBFs is either very high or very low and that we need detailed comparisons of potential FBF use versus availability of preferred foods to define in which category of FBF consumers we should classify bonobos. Since studies have suggested that filler and staple FBFs have different effects on ape socio-ecology (i.e., the abundance of FBFs will influence primate carrying capacity in its habitat and thus the maximal group size as well as group cohesion, with cascading effects on social dynamics) [Marshall & Wrangham, 2007], identifying the bonobo fallback strategy might be important to improve our understanding of the differences in the evolution of socio-ecology within the African Apes.

The objective of this study is to improve our understanding of bonobo feeding ecology in a fragmented environment, the forest-savannah mosaic of

northwestern Democratic Republic of Congo (DRC). Based on fecal analysis, we investigate seasonal dietary variation, associated foods in the diet and the exploitation of preferred and fallback foods.

METHODS

Study Site

The study site is located in a forest-savannah mosaic in northwestern DRC, close to the WWF Malebo research station [170 km² made up 102 km² of forest patches, 16.41–16.56°E, 2.45–2.66°S, Fig. 1; for a detailed description of the study site, see Serckx et al., 2014]. Forest patches were mostly located on *terra firma* soils and were characterized by various habitat types, i.e., re-colonizing *Uapaca* sp., old

secondary, mixed mature, old growth mono-dominant, riverine gallery and Marantaceae forests [Inogwabini et al., 2008]. Zones of slash-and-burn agriculture were also present inside the forests. Surrounding savannahs were mainly grassland. Since 2007, two bonobo communities living in the forest patches close to Nkala and Mpelu villages were the subject of habituation and conservation efforts by WWF-DRC [Inogwabini et al., 2008].

Data Collection

Diet identification

Between May 2011 and June 2013, we collected feces every morning at nesting sites (one sample below each fresh nest, $n = 2,252$, 270 days) in the

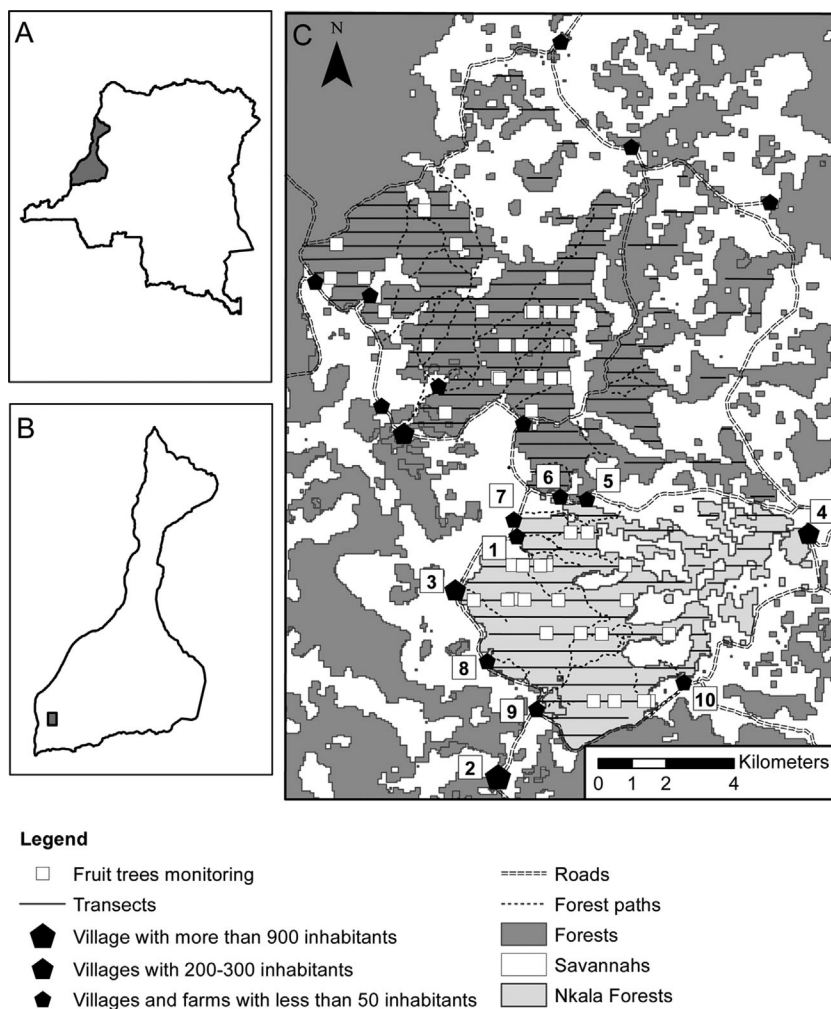


Fig. 1. Map of the study site. (A) Lake Tumba landscape in Democratic Republic of Congo. (B) The study site inside the Lake Tumba landscape. (C) Study site details. Forests are indicated in grey and savannahs in white [the map is based on a non-supervised classification—RED and IR on a Landsat7 (2007)]. The Nkala Forest in which lived the study bonobo community, is shaded pale grey. Villages are depicted as black pentagons. Numbers 1 to 3 represent villages: (1) Nkoo, (2) Lebomo, (3) Nkala and number 4 to 10 indicate farms: (4) Nkoo clinic, (5) Moza, (6) Mbou-Mon-Tour, (7) Mayi Monene, (8) Motsuemontoro, (9) Bosieli, and (10) Lensiana. Parallel dashed lines indicate the roads surrounding the study site, whereas dotted lines indicate the main forest paths. Vertical solid lines depict the 114 line transects (179.1 km) travelled in 2011, 2012, and 2013, and white squares indicate the plots of our fruit tree-monitoring project (see Appendix 1).

home range of the southern bonobo community, the 32.45 km² Nkala Forest (Fig. 1). WWF trackers who daily followed the bonobos for the purpose of habituation located nesting sites. After collection, we stored the feces in plastic bags for examination within 48 hr. We weighed each sample and washed it through 1-mm mesh sieves. We recorded fecal contents per food category: (i) fruits with large seeds, i.e., seeds larger than 2 mm which may be easily counted in the fecal remains (including seeds, skin and pulp remains), (ii) fruits with small and uncountable seeds (smaller than 2 mm), such as *Ficus sp.* or *Musanga cecropioides* (seeds, skin and pulp remains), (iii) foliage (fiber, digested fragments of leaves and flowers), (iv) fragments of insects or other animal matter and (v) other items (soil, small branches, mushrooms or undefined items). We visually estimated the percentage of each category within 5% intervals, based on its volume in the fecal material [Basabose, 2002]. We identified cleaned fruit seeds to the species level and counted large seeds. Non-fruit plant items were identified and described as accurately as possible.

In order to complete our description of the diet, we identified food remains found in the forest ($N = 311$) and, for each sample, we identified the species, the plant part eaten and counted the number of each item along 179.1 km of transects sampled in 2011, 2012, and 2013 [114 transects running from west to east, spaced 500 m and of variable lengths, Fig. 1; for details on transect design, see Serckx et al., 2014].

Fruit availability in the forest

To relate the contents of the feces to fruit availability in the forest, we recorded data on the abundance of fruiting trees. Over a period of 26 months, from May 2011 to June 2013, we monitored all trees with a diameter at breast height (DBH) greater than 10 cm within 14 plots randomly located in the Nkala Forest (each plot measuring 0.04 ha, 0.56 ha in total). This represented a total of 346 trees belonging to 77 species. In May 2012, we added 8 additional plots (five 1 ha plots and three 0.25 ha plots, 5.75 ha in total) to improve our representation of fruiting trees. Our sample size increased by 2239 trees representing 32 additional species (14 monitored months). Every two weeks, we visited each of the plots and recorded which trees were fruiting by inspecting their crowns and counting the fruits on the ground [Basabose & Yamagiwa, 2002]. We then calculated an index of fruit availability (FAI). Fruit species considered for this index were derived by selecting tree species (i) eaten by bonobos (this study, Kano and Mulavwa 1992 Beaune et al., 2013) or (ii) producing fleshy fruits [Tailfer, 1989; Wilks & Issembe, 2000; Djoufack et al., 2007] (Supplementary Appendix 1, Table I). We used each tree basal area to estimate the canopy volume (Strier, 1989 cited in Basabose, 2002) and calculated

the monthly fruit availability index (FAI) as: $FAI_m = \sum_{phi} p_{phi} \times ba_k$ where p is the proportion of trees of species k bearing fruits during the plot visit i and ba is the basal area (in square meters per hectare) of species k in the forest. We assigned for each date of fecal sampling collection the closest recorded FAI.

Analytical Methods

Diet description

We calculated the occurrence of food species in each fecal sample ($n = 2,252$ samples), for all feces sampled per day ($n = 270$ days) and for food remains sampled along transects ($n = 311$ samples). Based on fecal samples, we defined important fruits as those present in more than 50% of fecal samples for at least 1 month [McLennan, 2013; Rogers et al., 2004; Wrangham et al., 1991]. We considered as “important species” the fruit species occurring in more than 10% of sampled days to represent fruit eaten regularly even if not intensively [Moscovice et al., 2007; McLennan, 2013]. For fecal samples, we made sure that the analysis covered a long enough period of time to detect all species consumed by the bonobos (cumulative distribution of species through time, Basabose, 2002). We analysed whether the variation in food categories were correlated with each other and whether the two fruit categories and the daily number of consumed fruit species were correlated with the fruit availability index (approximate test of Spearman correlations, derived using a self-written function in R).

We investigated whether the daily number of consumed fruit species varied over time. We used a generalized linear model with a negative binomial error structure and log link function. To model the number of species consumed daily and to account for differences in daily sampling efforts, we incorporated the sum of all species observed per feces each day as the response and we included an offset term to control for the variation of sampled feces (the daily number of feces log transformed). We included the sine and cosine of the date, converted to a circular variable, to estimate seasonal patterns. We introduced a temporal autocorrelation term to account for the difference in sample size collection according to time. For this, we used the average of the residuals of all other sampled days derived from the full model and weighted by distance as an additional predictor. The weight function had the shape of a Gaussian distribution with a mean of zero (maximal weight at distance equals zero) and a standard deviation chosen such that the likelihood of the full model with the derived variable (autocorrelation term) included was maximized [Fürtbauer et al., 2011]. After running the model, we checked various model diagnostics [Field, 2005; Quinn & Keough, 2002]. Dfbetas and variance inflation factors did not reveal any issues (Supplementary Appendix 1, Table II and Table III). As the data showed some potentially

influential cases of leverage, we used a subset of the data for the analysis ($n = 254$). To check the overall effect of seasonality on the number of fruit species consumed daily, we compared the deviance of the full model with the deviance of a null model comprising only the autocorrelation and the offset terms, using a likelihood ratio test.

Diet seasonality

To test if the consumption of the important fruit species followed a seasonal pattern, we performed for each species a generalized linear model with binomial error structure and logit link function. We used the presence/absence of each species in feces ($n = 2,252$) as the response. We incorporated the sine and cosine of the date, converted to a circular variable, to estimate seasonal patterns. To account for temporal autocorrelation, we used the average of residuals of all other fecal samples derived from the full model and weighted (with the same function as for the previous model) by temporal distance as an additional predictor. After running the models, we checked various model diagnostics [Field, 2005; Quinn & Keough, 2002]: $dfbetas$ and variance inflation factors did not reveal any issues, and we removed potentially influential cases of leverage (Supplementary Appendix 2, Table I and Table II). To check the overall effect of seasonality on species consumption, we compared the deviance of the full model with that of a null model comprising only the autocorrelation term, using a likelihood ratio test. We used the R^2 coefficient of determination [Nagelkerke, 1991] to come up with a comparable value between species.

Association of food species in diet

We investigated whether important fruit species presented association patterns in the diet using cluster analysis. We calculated the matrix of Ochiai similarity based on species daily occurrence (presence/absence) in feces [Legendre & Legendre, 1998]. We clustered species using the Ward's Minimum Variance method [Borcard et al., 2011]. The adequate number of groups of species association was defined by comparing the original distance matrix to binary matrices computed for the dendrogram cut at various levels and by choosing the level where the matrix Mantel correlation between the two was the highest [Borcard et al., 2011]. Matrix Mantel correlations were realized using Spearman correlations, which maximizes highlighting of ecological structure [Legendre & Legendre, 1998]. We checked for clustering stability using the Complete Linkage Agglomerative Method [Borcard et al., 2011] and by inspecting both clustering methods in a matrix with Jaccard or Sorenson similarities. Species association remained similar in all cases.

Preferred and Fallback foods

Preferred foods are commonly defined as species consumed disproportionately relative to their abundance in the habitat [Marshall & Wrangham, 2007]. We used a food preference index (FPI) that measured relative use of species over their relative availability. Since we did not collect fruit availability for lianas and herbs, we estimated the food preference index only for important fruits of tree species. We calculated FPI using the following equation: $FPI = F_c/F_a$ where F_c represents the number of days the food was consumed and F_a represents the number of days we scored the food as available [Chancellor et al., 2012; Doran-Sheehy et al., 2009]. If the score was larger than 1, we considered the food preferred, and if the score was smaller than 1, we considered the food non-preferred.

Fallback foods (FBFs) are, in contrast, species increasingly consumed when the availability of preferred foods decline [Marshall & Wrangham, 2007; Marshall et al., 2009]. We tested whether non-preferred fruits of tree species, important herb and liana species and unidentified fibers (i.e., residuals of THV and Marantaceae) should be considered as FBFs, by performing, for each species, a generalized linear model (GLM). We used GLMs with a negative binomial error structure and log link function for species present in more than one quarter of fecal samples. Because these models became unstable for less-consumed species, we used GLMs with binomial error structure and logit link function for the other important species. Only the response ($n = 2,230$) changed depending on GLM types. For negative binomial models, we used, for important fruit species, the seed abundance in feces as the response. We calculated seed abundance as the total number of seeds of the given species divided by the wet weight of the fecal sample and multiplied by 100 to obtain a standardized measure of the relative amount of seeds consumed per fruit species per fecal sample [Moscovice et al., 2007]. For unidentified fibers and small-seed species, we used the volume proportion in the feces as the response. For binomial models, we used the presence/absence of the species as the response. To test whether the consumption of the given species was related to the consumption of preferred foods, we incorporated as predictors the seed abundance of preferred foods. Since FBFs are consumed when availability of preferred species declines, we included FAI of preferred foods as a predictor. We also incorporated the global FAI as a predictor to test the influence of fruit tree availability on important fruit consumption. To account for temporal autocorrelation, we used the average of residuals of all other fecal samples derived from the full model and weighted (with the same function as for the previous models) by temporal distance as an additional predictor. Prior to running the models, we checked that correlations between predictors were not

an issue with a Spearman test and that all predictors had a symmetrical distribution. Predictors of seed abundance were log-transformed and FAI of preferred foods was square-root transformed. All predictors were z-transformed to a mean of zero and a standard deviation of one to achieve more easily interpretable coefficients [Schielzeth, 2010]. After running the models, we checked various model diagnostics [Field, 2005; Quinn & Keough, 2002]. Dfbetas did not reveal any issues. Since the VIFs were too high for FAI of preferred foods and *Dialium sp.* abundance because of their high correlation (Spearman, $r_s = 0.56$), we decided to remove *Dialium sp.* from the model. VIFs did not reveal any issues in the new models, and we removed potentially influential cases of leverage (Supplementary Appendix 3, Tables I and II). To check the overall effect of preferred food consumption and availability, we compared the deviance of the full model with that of a null model comprising only the autocorrelation term, using a likelihood ratio test. We further tested the effect of preferred food consumption by comparing the deviance of the full model with that of a reduced model comprising only the FAIs and the autocorrelation term, using likelihood ratio tests. We considered the species was a FBF when we found significant negative correlations (i) between its consumption and preferred food consumption (i.e., the comparison between the full and reduced model is significant and predictor estimates are negative) and (ii) between its consumption and FAI of preferred foods (i.e., the estimate of FAI of preferred foods is significantly negative).

All analyses were conducted using R [R Core Team, 2013] and the additional packages car [Fox & Weisberg, 2011], MASS [Venables & Ripley, 2002], cluster [Maechler et al., 2013] and exactRankTests [Hothorn & Hornik, 2013].

Research Ethics

This non-invasive research is part of a PhD project which was conducted using only indirect signs of bonobo presence (nests, feces and food remains) under the WWF-DRC research permit (RM441976, granted by the Minister of Foreign Affairs and International Cooperation of Democratic Republic of Congo). Research complies with the Animal care and ethic committee of the Biology Department of the Unikin (University of Kinshasa), American Society of Primatologists Principles for Ethical Treatment of Nonhuman Primates and RDC Wildlife Authority regulations.

RESULTS

Diet Description

We identified 51 fruit species (out of 77 species present) in the 2,252 fecal samples and 10 foliage

species as food remains on the trails. Unidentified fruit species were all occurring less than 10% of sampled days (Table IV in Supplementary Appendix 1). Sixteen fruit species were classified as important (Table I). The data collection period was sufficient to identify all the important species but probably not all the consumed species (Fig. 2A). Fruits constituted the majority of species identified in fecal samples (100% of presence in fecal samples; feces mean volume: 95.2%; Table V in Supplementary Appendix 1); of these, one species, *Musanga cecropioides* was particularly frequent (55% of all feces). Foliage was much less common in the feces (31% of feces; feces mean volume: 4.1%), but one species, *Haumania liebrechtsiana*, was particularly common on trails (55% of food remain samples). Animal matter and other items were rarely found (0.1% and 7.5% of feces, respectively). The presence of fruits of *M. cecropioides* in feces was negatively correlated with the presence of other fruit species (Spearman, $r_s = -0.92$, $P < 0.0001$; Table V in Supplementary Appendix 1). The FAI was slightly positively correlated with the proportion of fruits in feces (Spearman, $r_s = 0.28$, $P < 0.0001$) and slightly negatively correlated with the proportion of *Musanga cecropioides* fruits (Spearman, $r_s = -0.24$, $P < 0.0001$, Fig. 2B). FAI was also slightly positively correlated with the number of daily consumed fruit species (Spearman, $r_s = -0.14$, $P < 0.0001$). We found a daily mean of $2.8 \pm \text{SD } 1.2$ fruit species in fecal samples, showing significant seasonal variation (comparison between full and null model, $X^2 = 17.65$, $df = 2$, $P < 0.001$), with a peak between January and March (Fig. 2C).

Diet Seasonality

The presence in feces of 12 of the 16 important fruit species followed a seasonal pattern (likelihood ratio test, Table I) and the effect of seasonality was generally stronger for fruits of liana and herb species (i.e., *Aframomum sp.*, *Cissus dinklagei*, *Landolphia sp1.* and *Landolphia sp2.*, R^2 in Table I, Fig. 3) than for those of tree species. Two of the most highly-consumed fruit species, *M. cecropioides* and *Marantochloa leucantha*, showed small seasonal variation in amplitude (and small R^2), reflecting that they were eaten throughout the year.

Association of Food Species in Diet

Within the important fruit species, we found six groups of foods regularly consumed together (Fig. 4). This association pattern was likely related to the seasonality of species consumption (Fig. 3): species of group-2 species were essentially consumed between August and December while species of group-6 peaked between March and August. Group-4 contained species with a significant seasonal pattern (consumption between February and August) but of

TABLE I. Important Fruit Species Found in Bonobo Feces

Scientific name	Family	No. feces (%)	No. days (%)	Seasonality			Group	FPI	Preferred foods	FBF foods	Tree guild
				X ²	P-value	R ²					
<i>Musanga cecropioides</i>	Urticaceae	1251 (55)	180 (67)	6.16	*	0.05	6	1.60	No ^b	Yes ^b	P
<i>Aframomum</i> sp.	Zingiberaceae	855 (38)	167 (62)	120.35	***	0.54	6	—	—	No	—
<i>Marantochloa leucantha</i>	Marantaceae	560 (25)	133 (49)	19.85	***	0.10	6	—	—	Yes	—
<i>Uapaca</i> sp.	Euphorbiaceae	386 (17)	79 (29)	48.50	***	0.29	2	0.85	No	Yes	NPLD
<i>Cissus dinklagei</i>	Vitaceae	342 (15)	76 (28)	120.15	***	0.61	2	—	—	No	—
<i>Landolphia</i> sp3.	Apocynaceae	238 (10)	65 (24)	0.49	N.S.	—	4	—	—	No	—
<i>Piptostigma fasciculatum</i>	Annonaceae	236 (10)	57 (21)	7.63	*	0.05	4	1.02	Yes	—	SB
<i>Dialium</i> sp.	Fabaceae (caesalpinoideae)	372 (16)	55 (20)	8.35	*	0.08	4	1.67	Yes	—	SB
<i>Landolphia</i> sp2.	Apocynaceae	225 (10)	51 (19)	48.84	***	0.44	5	—	—	Yes	—
<i>Landolphia</i> sp1.	Apocynaceae	336 (15)	48 (18)	92.45	***	0.66	6	—	—	Yes	—
<i>Polyalthia suaveolens</i>	Annonaceae	193 (8)	46 (17)	69.28	***	0.52	2	1.02	Yes	—	SB
NID_local.name: Lenkala	NID	182 (8)	44 (16)	25.88	***	0.20	4	—	—	No	—
<i>Pycnanthus angolensis</i>	Myristicaceae	108 (5)	43 (16)	54.74	***	0.38	2	0.39	No	No	NPLD
<i>Cordia platythyrsa</i>	Boraginaceae	136 (6)	37 (14)	1.60	N.S.	—	5	^a	Yes ^a	—	NA
<i>Pancovia laurentii</i>	Sapindaceae	141 (6)	35 (13)	1.15	N.S.	—	3	^a	Yes ^a	—	SB
<i>Annona senegalensis</i>	Annonaceae	57 (3)	18 (7)	0.23	N.S.	—	1	—	—	—	Sav.

NID = not identified by Latin name. Following NID, the local name is given if identifiable by local assistants. Seasonality *P*-values indicate the significance of the chi-squared test comparing the fit of the full model and the null model (*****P* < 0.0001, ****P* < 0.001, ***P* < 0.05, N.S.: not significant). Seasonality (R²) indicates the coefficient of determination, i.e. the proportion of variance explained by the regression model. 'Group' indicates the result of the cluster analysis (Fig. 4). FPI is the food preference index, calculated for tree fruits by dividing the number of days the species was observed in feces with the number of days the species was fruiting in the forests.

^aindicates two tree species never observed fruiting in the forests, the FPI was then not calculable but their presence as important fruit species in bonobo diet makes us suggest they should be considered as preferred fruits. Preferred foods are defined based on the FPI values and fallback foods based on the model results (Table II).

^bFor *M. cecropioides*, we were not confident in its classification as a preferred food (FPI > 1) because we probably largely underestimated their fruit availability. We thus tested whether the species should rather not be considered as a FBF. Model results (Table II) clearly indicate its role as a FBF. Tree guild is categorized as shade-bearer (SB), pioneer (P), non-pioneer light demanding (NPLD), or information not available in the literature (NA) [Hawthorne, 1995].

small amplitude (small R²). Groups 1, 3, and 5 only included one or two species, with no seasonal pattern of consumption (with the exception of *Landolphia* sp2). Seasonal associations became even clearer when we looked at subgroups: e.g. the agglomerates between *Aframomum* sp. and *M. cecropioides*, as well as between *C. dinklagei* and *Uapaca* sp. depicted their seasonal synchrony. The three most highly-consumed fruit species, *M. cecropioides*, *Aframomum* sp. and *M. leucantha*, were the most strongly associated with one another (with the largest similarity coefficients), indicating that those species are commonly eaten together, reflecting their long fruiting periods.

Preferred and Fallback Foods

We evaluated fruit preferences only for important tree species (the food preference index is calculated

based on fruit availability, which was not recorded for herbs and lianas). Four of the eight important tree species (*M. cecropioides*, *Dialium* sp., *Polyalthia suaveolens*, and *Piptostigma fasciculatum*) were identified as preferred fruits (Table I). We decided to consider *Cordia platythyrsa* and *Pancovia laurentii* as preferred foods too. Indeed, these two species were never observed bearing fruits during our phenology surveys. In addition, the tree abundance survey conducted at the study site [Serckx et al., 2014] indicates that *Cordia platythyrsa* is rare in the forest (Table I in Supplementary Appendix 1). *Pancovia laurentii* was more common but mainly present at small DBH size (mean DBH: 16.35 cm), i.e., trees being probably too young to bear fruits. Since bonobos consume both species regularly, this suggests a high preference for these species despite their low fruit availability. In the case of *M. cecropioides*, we were not confident in its classification as a preferred food

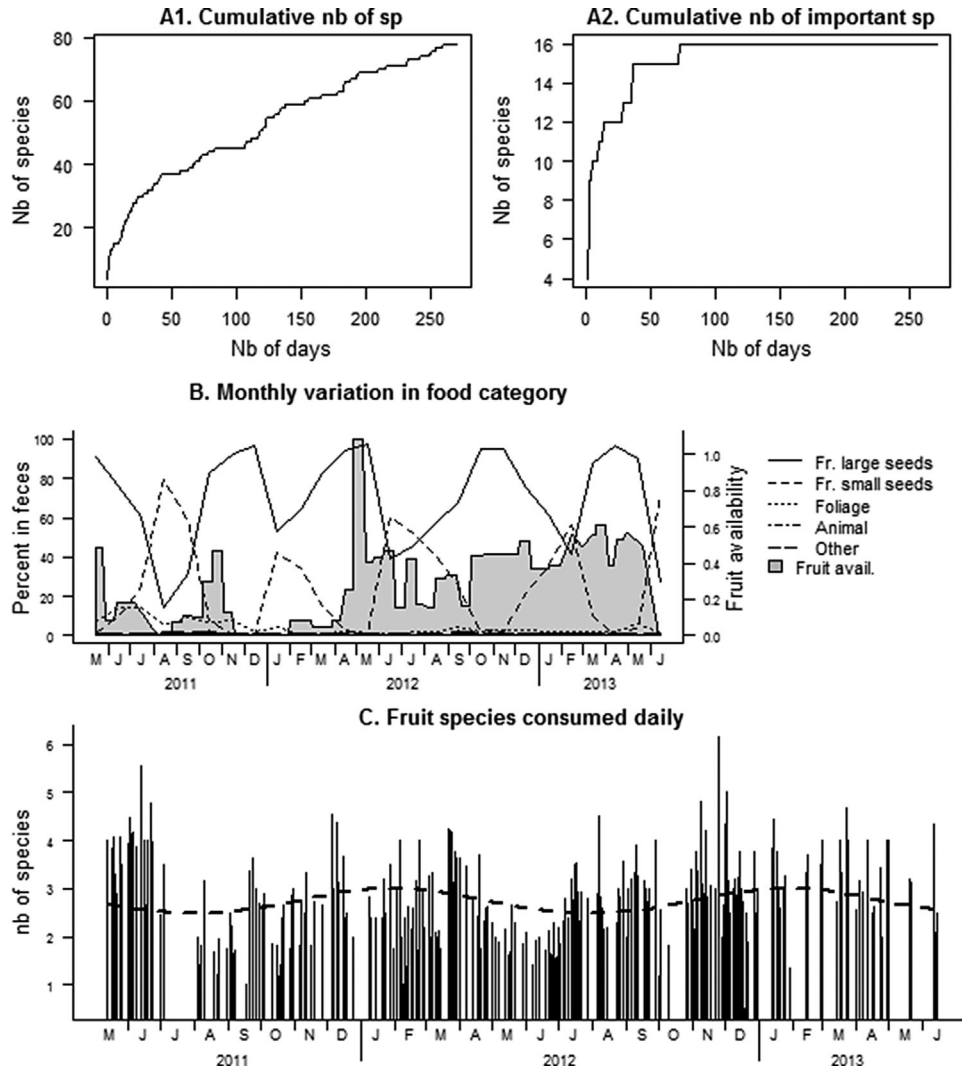


Fig. 2. Diet description **A1** and **A2** present the cumulative number of all consumed species and important species observed in feces over time. **(B)** shows the variation of the different food categories (percent of fecal volume) observed during fecal analyses (fruit with large seeds, fruit with small seeds, foliage, animal matter, and other items). The index of fruit availability calculated from fruit tree monitoring data is superimposed on the figure with its scale on a second y-axis. **(C)** shows the number of fruit species consumed daily and the fitted model is indicated by dashed line.

because we probably largely underestimated their fruit availability, due to the fact that the forest plots we used for phenology surveys were never situated in edge forests or disturbed areas, while the species is essentially observed in these habitat types. Consequently, we probably did not follow the appropriate trees to estimate species fruit availability. We thus decided to test whether the species should rather not be considered as a FBF. We found that *M. cecropioides* fruit consumption was clearly negatively correlated to fruit availability and abundance of other preferred fruits (Table II), indicating its role as a FBF. We further investigated the role of non-preferred tree species, liana and herb fruit species. Four other fruit species came out as FBFs: *Uapaca* sp, the

Marantaceae *M. leucantha* and two liana species: *Landolphia* sp1 and *Landolphia* sp2 (Table II, Fig. 5).

DISCUSSION

The primary aim of this study was to explore bonobos' feeding ecology in forest-savannah mosaics to gain a better understanding of their dietary adjustments in a fragmented environment. Based on fecal samples collected over a two-year period, we found that bonobos inhabiting forest-savannah mosaics consumed a number of fruit species ($n = 78$) similar in number to those living in tropical dense forests ($n = 93$, at Wamba: Kano, 1992; $n = 91$, at Lui-Kotale: Beaune et al., 2013). Of these, sixteen

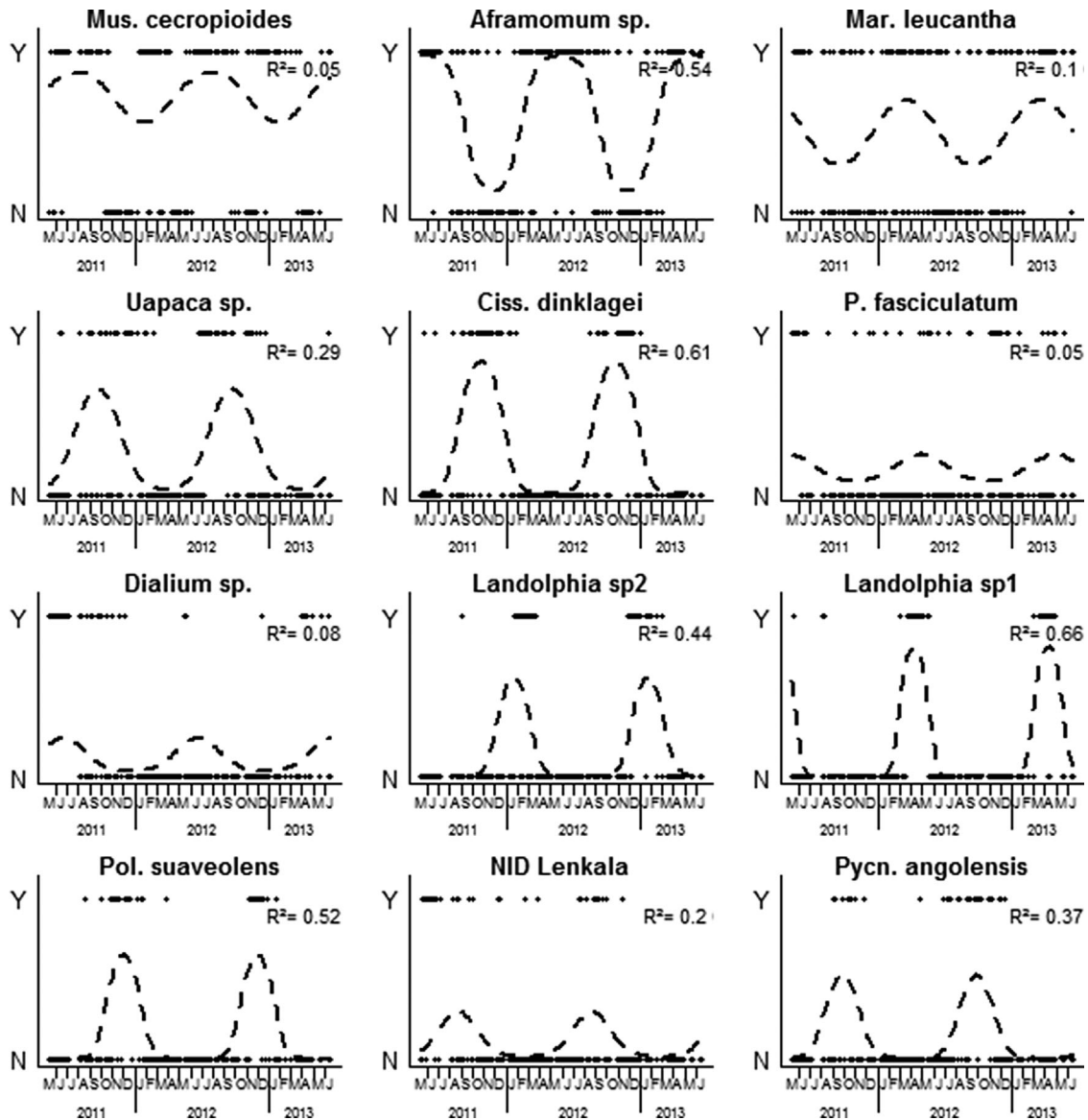


Fig. 3. Seasonality in the consumption of important fruit species. Only the fruit species for which a significant pattern of seasonality is found are presented. Fruit species are indicated as present (Y) or absent (N) for each day sampled and the fitted models are indicated by dashed lines. R^2 are the R-squared coefficients of determination, enabling comparisons of the seasonality effect between species.

fruit species were predominantly consumed (called important fruits). Fecal analyses suggested that bonobos were highly frugivorous (95% of feces volume was fruits), but we may have underestimated fiber consumption due to an artefact of our methodology (mesh sieve size of 1 mm). Our investigations revealed a seasonal pattern of consumption for 12 out of the 16 most important fruit species. Four species were identified as preferred fruits, and five species as FBFs (Table I). The consumption of the fruits of *M. cecropioides* and *M. leucantha* was especially important and we suggest that their role as FBFs may help

explain the bonobo foraging strategy and perhaps also its cohesiveness in such a forest-savannah ecosystem.

Our results highlight that, while bonobo diet in this habitat was largely composed on fruits from trees (34 of 51 identified fruit species), fruits classified as important include the same number of tree species (8) as of other life-form plants (5 lianas, 3 herbs, and 1 grassland shrub; Table I). Thompson [1997] already identified the importance of non-tree species in another bonobo population living in forest-savannah mosaics, where diet was composed of only

TABLE II. Fallback Food Species

Scientific name	Life form	GLM type	Overall effect (X ²)	Effect of pref. foods (X ²)	Intercept	<i>P. suaveolens</i>	<i>P. fasciculatum</i>	<i>C. platythyrsa</i>	<i>P. laurentii</i>	FAI global	FAI pref. fruits	Ac. term
<i>M. cecropioides</i>	tree	neg.bin	276.2***	94.1***	1.70***	-0.38***	-0.10*	0.03	-0.32***	-0.47***	-0.16**	1.71***
<i>M. leucantha</i>	herb	neg.bin	64.2***	16.1*	0.72***	-0.17	0.21*	-0.15	-0.30*	0.36***	-0.51***	1.79***
<i>Aframomum</i> sp.	herb	neg.bin	39.2***	37.8***	2.10***	-0.46***	-0.36***	-0.35*	0.04	-0.09	0.19	1.65***
Unidentified fibers	herb	neg.bin	97.7***	24.5***	0.50***	0.25*	-0.31*	-0.47*	0.02	0.00	1.00***	0.78***
<i>Uapaca</i> sp.	tree	bin	44.2***	22.6**	-3.12***	-0.17	-0.80*	-0.15	-0.57*	-0.38**	-0.41*	2.02***
<i>P. angolensis</i>	tree	bin	9.1	7.1	-6.52	-0.23	0.16	-9.67	-0.13	0.13	-0.14	1.27***
<i>A. senegalensis</i>	shrub	bin	31.7***	12.3*	-8.09	-0.19	-0.10	0.76***	-10.16	-0.20	1.74***	1.04***
<i>C. dinklagei</i>	liana	bin	29.0***	23.1**	-6.59	0.17	-0.52*	-11.16	-1.54*	-0.25*	0.06	1.90***
<i>Landolphia</i> sp2.	liana	bin	35.4***	9.3*	-4.93***	-0.51	-0.57	-1.01	-0.32	0.21	-1.98*	1.75***
<i>Landolphia</i> sp1.	liana	bin	74.1***	23.1**	-8.37	-8.57	0.10	-6.96	-0.80	0.82***	-1.37*	2.55***
<i>Landolphia</i> sp3.	liana	bin	29.2***	16.3*	-6.15	0.02	0.13	-0.16	-11.66	-0.12	0.38	1.32***
NID_Lenkala	liana	bin	71.8***	16.6*	-7.60	-1.20	-0.05	-7.43	-8.08	-0.04	0.98	1.00***

NID = not identified, NID is followed by the local name if identified by the local assistants. GLM type indicates the model we used depending on the frequency of the species in fecal samples (neg.bin: negative binomial; bin: binomial). The column "Overall effect" shows the χ^2 value when comparing the fit of the full model and the null model, "effect of pref. foods" the χ^2 value when comparing the fit of the full model with a model comprising only fruit availability and the ac. term. Last columns are the value of the different predictors. For χ^2 and predictors, *P*-values are indicated as ****P* < 0.0001, ***P* < 0.001, **P* < 0.05. Species defined as fallback foods are indicated in bold.

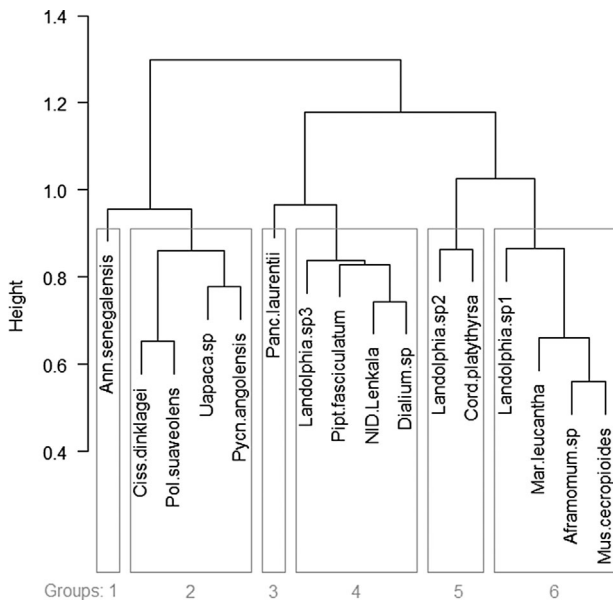


Fig. 4. Association between fruit species in bonobo diet Results from the cluster analysis. The height-axis represents the axis of the squared distances (distance = 1 - coefficient of similarity) between groups or species. The nodes between groups/species indicate the squared distances at which groups/species have been agglomerated within the same sub-group. Gray rectangles show the six groups adequately representing the associations between fruit species in the bonobo diet.

53% of forest fruit trees, but of numerous herb species and 3 savannah species. Unfortunately, we did not collect fruit availability data for these types of plants, preventing us from investigating their role as preferred foods in the bonobo diet. Our results showed, however, that 3 of the 8 species might be considered as FBFs (2 lianas: *Landolphia sp1*, *Landolphia sp2*, and 1 Marantaceae: *M. leucantha*). In addition, savannah fruit species have been found to be poor-sugar species compared to fruits from trees [Thompson, 2003] while the importance of sugars in food selection by great apes has already been widely demonstrated [Hohmann et al., 2006, 2010; Reynolds et al., 1998; Remis, 2002; Rothman et al., 2011]. Both points suggest that these species are most probably FBFs or non-preferred foods, but their consumption may enable bonobos to remain highly frugivorous in forest-savannah mosaics.

Interestingly, when analysing the selection of preferred and fallback foods, we found that all preferred fruits belong to tree species typical of mature forests (shade-bearer trees [Hawthorne, 1995], Table I) while fallback fruits are mainly found in edge forests or disturbed areas (*M. cecropioides* being a pioneer species observed in edge forests or close to cultivated fields; *Uapaca sp.*, a non-pioneer light demanding species observed in edge and young-colonizing forests [Hawthorne, 1995]; *M. leucantha*, a Marantaceae typical of various habitat types, notably road and savannah edges [Dhetchuvi,

1996]). This finding suggests that bonobos prefer to remain in mature forests, as already observed for nesting site preference [Serckx et al., 2014], but need to extend their range of forest use to other habitat types in periods of fruit scarcity. This pattern has already been observed in the Kalinzu forest (Uganda), where chimpanzees favour *Musanga*-dominated secondary forest when fruit availability in mixed mature forest decreases [Furuichi et al., 2001] or in Wamba (DRC), where bonobos increase their swamp forest use when the abundance of specific fruits typical in this habitat increases [Mulavwa et al., 2010]. Chancellor [2012] even observed that chimpanzees living in forest fragments of Rwanda increasingly use forest edges when fruit availability declines, to be close to maize fields for crop-raiding. We never found cultivated items in fecal samples. However, this does not mean bonobos never consume crops, as local populations mainly cultivate non-fruit species within forest fields (Serckx, data not shown), of which remains are difficult to observe in fecal samples. In fact, local people already complain that bonobos periodically degrade sugar cane fields. Even if crop-raiding does not seem to be a current problem in the region, as observed in some chimpanzee populations [Chancellor et al., 2012; Humle & Matsuzawa, 2004; McLennan, 2013], the regular use of disturbed habitats may lead to future human-bonobo conflicts, increasing the risk of poaching and injuries from snares for bonobos and also favouring zoonotic disease transmission [Köndgen et al., 2008; Leendertz et al., 2006].

The intense consumption of the fruits of *M. cecropioides* and *M. leucantha* (55 and 25% of fecal samples, respectively) was an interesting result of this study. While the role of *Musanga spp.* as FBF was already identified in various chimpanzee populations [Furuichi et al., 2001; Yamakoshi, 1998] and for other primates of Central Africa [Thomas, 1991], it was never the case, to our knowledge, for fruits of *M. leucantha*. An increasing number of studies have shown that abundant FBFs may be a key factor determining primate carrying capacity [Chancellor et al., 2012; Furuichi et al., 2001; Hanya & Chapman, 2013; Marshall et al., 2009; Oates et al., 1990; Thomas, 1991]. For example, the consumption of *Dombeya torrida* allows chimpanzee densities to remain high in forest fragments of Rwanda despite their small and degraded habitats [Chancellor et al., 2012]. *Musanga spp.* abundance has been suggested to play a role in chimpanzee density of Kalinzu forest [Furuichi et al., 2001] and in *Cercopithecus* biomass in the Ituri forest (DRC) [Thomas, 1991]. It is thus possible that the importance of *M. cecropioides* and *M. leucantha* in bonobo diet partially explains the similar density we found between forest-savannah mosaics and dense forest populations [Serckx et al., 2014]. Further studies comparing bonobo density in

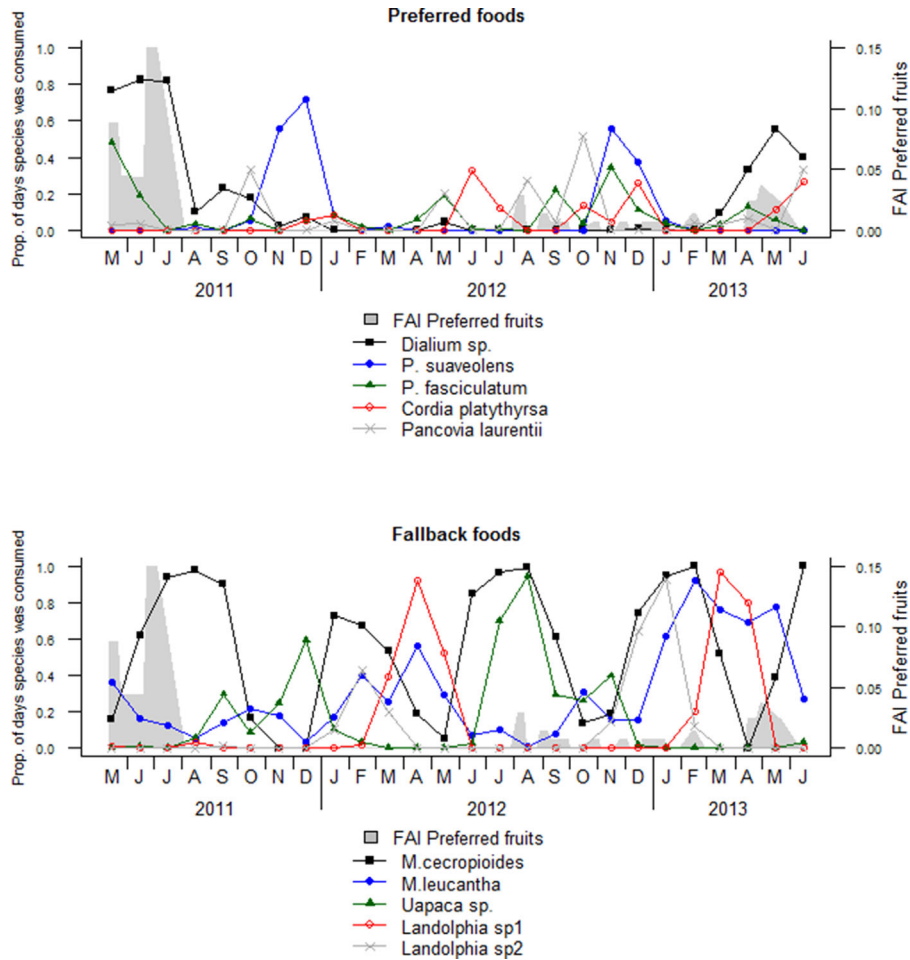


Fig. 5. Monthly proportion of preferred and fallback fruits in fecal samples Preferred and fallback foods are presented as the monthly proportion of fecal samples in which we observed the species (y-axis). Species are indicated in different colors. The index of fruit availability calculated from preferred fruits is superimposed on the figure with its scale on a second y-axis. The peak of fruit availability in July 2011 (FAI = 0.30 m²/ha) has been truncated to a value of 0.15 m²/ha to improve graphical representation.

different forest fragments according to *M. cecropioides* and *M. leucantha* abundance are needed however to confirm this hypothesis.

Finally, Marshall and Wrangham [2007] have suggested that the distinction between staple and filler FBFs enables us to explain differences in socioecology of primate species: staple FBF consumers are more constrained by the availability of staple foods but experience reduced feeding competition and form more stable groups, while filler FBF consumers are more constrained by the availability of preferred foods. Applying these concepts, it has been shown that gorillas can be considered as staple FBF consumers and chimpanzees as filler FBF consumers, but the classification of bonobos remains unclear [Harrison & Marshall, 2011; Marshall et al., 2009; Yamagiwa & Basabose, 2009]. Studies have demonstrated that gorillas usually form cohesive groups irrespective of fruit abundance but that frugivory and patchy distribution of fruits force them to extend

their daily path length [Yamagiwa & Basabose, 2009]. Interestingly, we found a similar pattern for bonobos. First, bonobo cohesiveness at night was independent of fruit availability [Serckx et al., 2014]. Second, WWF trackers have reported that bonobos frequently cross their entire home range in one day to reach particular food trees (pers. comm. Paulin Ebabu). Direct observations are needed to confirm these observations. However, such behaviours, combined with the importance of abundant FBFs in their diet, suggest that bonobos, or at least the populations living in forest-savannah mosaics, might be considered as staple FBF consumers.

In conclusion, our study offers new insights into bonobo dietary flexibility and especially into the importance of FBFs for their subsistence in fragmented environments. Identifying fallback resources is essential to develop appropriate conservation measures in environments where wildlife and humans share habitats [Marshall et al., 2009].

In addition, we found that bonobos are highly dependent on non-tree species for feeding while numerous potentially consumed tree species are available within their home range. We also observed that the important fruits could be separated into six groups of associated foods in their diet. Both these results deserve further investigation to gain a better understanding of bonobo food species selection in forest-savannah mosaics. In particular, additional studies on bonobo nutritional ecology [Felton et al., 2009; Irwin et al., 2014; Raubenheimer et al., 2009] will help to address such questions and may also be helpful in the development of targeted conservation strategies [Chapman et al., 2004; Felton et al., 2010].

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article.