Sympatric Chimpanzees (*Pan troglodytes troglodytes*) and Gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon: Dietary Composition, Seasonality, and Intersite Comparisons

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Abstract Dietary overlap of sympatric apes is complex and understudied, but its examination is essential to further our understanding of species distribution, abundance, and community ecology. Over 3 yr we studied food availability and dietary composition of central chimpanzees (*Pan troglodytes troglodytes*) and western gorillas (*Gorilla gorilla gorilla*) in Loango National Park, Gabon. We predicted that living in a habitat dominated by mature forest with sparse terrestrial herbaceous vegetation would lead to an increase in frugivory by gorillas, resulting in increased dietary overlap between the 2 ape species vs. other sites, but that chimpanzees would remain more frugivorous than gorillas. Through fecal analysis we measured overlap in fruit consumption between the 2 species on a bimonthly basis using the Renkonens method. Mean overlap was 27.5% but varied greatly seasonally, ranging between 0.3% and 69%, indicating that when examined on a finer scale, the degree of overlap appears much lower than at other study sites. In contrast to studies elsewhere, there was not a positive correlation between rainfall and fruit availability in Loango, and the long dry season was a period of high fruit production. As observed elsewhere, we found a positive correlation between fruit consumption and fruit availability for both chimpanzees and gorillas and we found that chimpanzees were more frugivorous than gorillas. A very low availability of herbs did not lead to increased frugivory by gorillas nor increased overlap between

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the 2 ape species vs. other field sites. We conclude that forest composition, fruit availability, and dietary variability of sympatric species can vary greatly between locations, and that chimpanzees and gorillas can adapt to primary forest with little undergrowth, where they concentrate their diet on fruit and leaves.

Introduction

Examining dietary overlap of sympatric species is useful for improving our understanding of species distribution and abundance, community ecology, and the processes of speciation and adaptive radiation. Most species that occur sympatrically and exploit similar foods are assumed to have evolved species-specific ecological adaptations that decrease interspecies competition and make coexistence possible (Begon *et al.* 2006; Dew 2005; Eccard and Ylönen 2003; Krebs and Davies 1993). Digestive flexibility is proposed as one mechanism that may allow the coexistence of sympatric species, as suggested for *Cercopithecus* species (Lambert 2002) and sympatric howlers (*Alouatta palliata*) and spider monkeys (*Atelese geoffroyi*: Milton 1993). In contrast, for sympatric primates with high dietary overlap, there is evidence that the presence of one species can potentially limit the presence of the other, as suggested for sympatric putty nose monkeys (*Cercopithecus nictitans stampflii*) and Diana monkeys (*Cercopithecus diana diana*: Eckardt and Zuberbühler 2004), and for sympatric mouse lemurs (*Microcebus berthae* and *M. murinus*: Dammhahn and Kappeler 2008). In nearly all environments where primates occur, ≥2 species live sympatrically, making them an interesting community of animals in which to consider dietary overlap, niche separation, and interspecific competition. However, many sympatric species may occupy a wide variety of ecological habitats, leading to variation in the degree of dietary overlap and niche separation (Chapman *et al.* 2002; Cords 1990; Eckardt and Zuberbühler 2004) such that caution should be taken when generalizing from a single study site to a broader area of sympatry.

Western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) live sympatrically in Central Africa, and researchers have described both species as generalized, opportunistic frugivores (Doran-Sheehy *et al.* 2009; Tutin *et al.* 1991). However, while chimpanzees are found in nearly all locations where gorillas occur, chimpanzees have a much wider distribution than gorillas in both eastern and western Africa (Kingdon 2004). Paradoxically, despite their ability to occupy a wider range of habitat types, chimpanzees are considered to be more specialized frugivores whereas gorillas are considered to be more generalist folivore-frugivores. It could be argued that gorillas exhibit more dietary special-isations than chimpanzees, such as having digestive tracts and dentition that enable them to consistently use vegetation as a fallback food when ripe fruit is scarce (Marshall and Wrangham 2007; Marshall *et al.* 2009; Remis *et al.* 2001; Yamagiwa and Basabose 2009), while the wider distribution of chimpanzees may result from a greater degree of flexibility in locomotion, grouping patterns and smaller body size

that enables them to survive in a more resource limited or seasonally variable environment, and allows them to continue in their pursuit of fruit resources even when availability is low (Basabose 2004; Boesch 1996; Constantino et al., 2009; Wrangham et al. 1998).

Despite several studies of either chimpanzees or gorillas, to date researchers have examined dietary overlap of western gorillas and chimpanzees in only 2 locations: Lopé, Gabon (Tutin et al. 1991, 1997) and Nouabalé-Ndoki, Republic of Congo (Kuroda 1992, 1996; Morgan and Sanz 2006). Both are characterized by seasonally available fruit and a relatively high density of constantly available terrestrial herbaceous vegetation. Gorillas and chimpanzees consume approximately the same number of fruit species, and dietary overlap of all fruit species eaten is between 50–84% (Kuroda 1992, 1996; Morgan and Sanz 2006; Tutin and Fernandez 1993; Tutin et al. 1991). Gorillas consume herbaceous vegetation more frequently and fruit less often than chimpanzees. More interestingly, these studies found greater niche separation in feeding behavior between chimpanzees and gorillas during months with low fruit availability (Kuroda et al. 1996; Tutin and Fernandez 1993), observing that gorillas show a more seasonal shift in the amount of fruit versus herbaceous vegetation in the diet (Remis 1997), whereas chimpanzees maintain a high intake of fruit year round. Further, gorillas tended to avoid lipid rich fruits that were exploited by chimpanzees (Remis et al. 2001; Rogers et al. 1990, 1992; Williamson et al. 1990).

Given the large area of the Congo Basin, variation in food availability for the African apes is expected. In particular, terrestrial herbaceous vegetation, an important food for gorillas (Rogers et al. 2004), has been found at a much lower density in some areas than in either Lopé or Nouabalé-Ndoki, and it has been suggested that a lower abundance of terrestrial herbs may result in a low density of gorillas (Furuichi et al. 1997; Morgan 2000; Rogers et al. 2004; Wrangham et al. 1993;) and an increased reliance on fruits (Kuroda et al. 1996). However, more recent studies using direct observations have placed more significance on tree leaves than terrestrial herbs as important foods for western gorillas (Doran-Sheehy et al. 2009; Masi et al. 2009). It is therefore useful to examine dietary overlap of chimpanzees and gorillas in a habitat with low availability of herbs.

Loango consists of a mosaic of habitat types including coastal forest, savannah, swamps, and primary forest. Previous researchers, based in a restricted area near the coast in this region, found the forest composition to be dramatically different from other locations where apes have been studied in Africa (Furuichi et al. 1997; Morgan 2000). In particular, the density of herbaceous vegetation was notably lower, with a correspondingly low density of gorillas (0.08 individuals/km² [Morgan 2000]) and 0.21 individuals/km² (Furuichi et al. [1997]). Therefore, because foods commonly consumed by one species are found in low abundance in Loango, it is a useful location to examine dietary overlap among chimpanzees and gorillas.

Our goals here are 3-fold: 1) We aim to provide a quantitative description of ape food availability in Loango to examine how it differs from other study sites in central Africa. In particular, we present results on density of herbaceous vegetation and seasonality in fruit availability. 2) We also test hypotheses about dietary overlap. Specifically, following results of other studies, we expect relatively high dietary overlap (between 50% and 80%) between the 2 ape species for all food types (fruits, tree leaves, herbaceous vegetation), but the degree of overlap will vary seasonally.

We predict that fruit consumption by gorillas will correlate with fruit availability and that during times of fruit scarcity they will shift to a more fibrous diet (Kuroda *et al.* 1996). Chimpanzees, on the other hand, would be expected to exploit fruit resources continuously, even when availability is low, but still show a correlation between their fruit consumption and fruit availability (Wrangham *et al.* 1998). We also expect that the lower density of terrestrial herbaceous vegetation in Loango may lead to greater dietary overlap between the gorillas and chimpanzees than at other study sites, and increased frugivory by gorillas (Kuroda *et al.* 1996). 3) Given forest composition is expected to vary between Loango and other central African forests where chimpanzees and gorillas have been studied, we also determine which foods are important in the diet of the apes in Loango and make comparisons with other ape study sites. We present results from the first 3 yr of the study, during which time the apes were not habituated and so we rely predominantly on indirect signs of diet (fecal analysis and feeding remains left on trails) but we include some direct observations from the most recent year of the study.

Methods

Study Area

We established the Loango Ape Project in February 2005 (Boesch *et al.* 2007, 2009), with the study site based in the northern sector of Loango National Park, Gabon (2°04′S and 9°33′E), covering 80 km² on a long strip of land bordered to the west by the Atlantic Ocean and to the east by a large lagoon. The diversity in habitat types includes coastal forests and savannah in the west, multiple lowland swamps fed by the lagoon in the east, and heterogeneous tropical rainforest throughout. Parts of the study area were selectively logged until the 1970s (Farmer 2000), but there is very little dense secondary forest, and the understorey is typically open in 57% of the study area (J. Head *unpubl. data*). Between June 2006 and May 2009, the mean annual rainfall was 2215 mm, and the mean minimum and maximum temperatures were 22.9°C and 27.2°C respectively. There is a long rainy season (October–April) that is often interrupted by a short dry season (December–January). The long dry season stretches from May to September (Fig. 1).
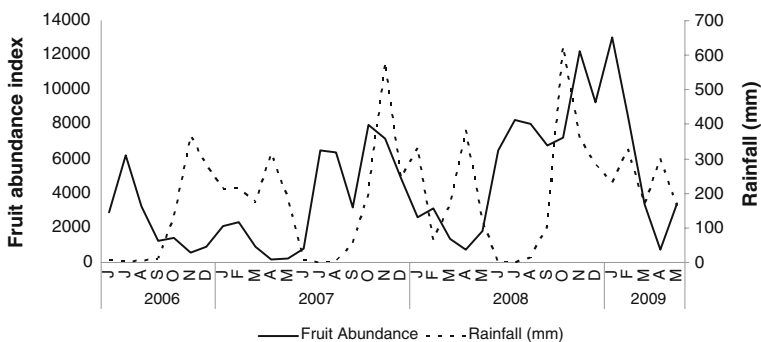

Fig. 1 Overall fruit availability and rainfall per month. Fruit abundance is 1000 times the values on the *y*-axis.

Measures of Food Availability

We estimated the density of tree species by recording all trees (diameter at breast height [DBH] >10 cm) in transects placed north–south within each 1-km² grid overlaid onto a map within the 80-km² study zone. Transects were 20 m wide and 240 m long, split into 12 20×20 m plots. We did not collect data when transects went through very deep swamps. We identified 9080 trees from 171 different species and 36 families, and the area covered by the 80 transects was 0.28 km².

We estimated herb densities in the same transects by placing 12 nested quadrats of 1×1 m (with intervals of 19 m) along each 240-m transect. Any plants <2 m high were considered as herbs, including seedlings and saplings (Nkurunungi *et al.* 2004). We identified herbs only when they were known to be consumed by apes; we counted any other herb as a nonfood plant. We provide both the density of all herbs and the density of herbs consumed by apes (as done by Doran *et al.* 2002) to allow comparisons with other sites. In 872 herb plots we counted 7131 individual herbs, of which 202 were known to be foods consumed by apes (from 10 plant species), and the area covered by the transects was 0.0009 km².

On a monthly basis, we monitored phenological changes in 750 trees (all with DBH of >10 cm) from 57 species known to be consumed by chimpanzees or gorillas, over a distance of 35 km along a trail system. Initially we monitored 46 different species, but as our knowledge of which fruits were eaten by the apes increased, we added another 8 species in May 2007 and a further 4 species in March 2008. We monitored a minimum of 10 individual trees per species where possible (max=28), but when trees were rare the number was smaller (n=4 species, n=3–8 trees). We collected data on the presence of fruits, flowers, and young leaves. When fruits were present we counted the number of fruits on a 1-m length of 3 terminal branches, and then used a score for each branch ranging from 1 to 5 (1 = 0 fruits, 2 = 1–10 fruits, 3 = 11–50 fruits, 4 = 51–100 fruits, 5 = >100 fruits). We also scored fruits for degree of ripeness (1 = no fruits, 2 = immature, 3 = unripe, 4 = ripe, 5 = decaying), and we used only fruits with ripe scores in this analysis.

A variety of methods have been employed to describe productivity and fruit availability, which makes comparison between sites difficult (Chapman and Wrangham 1994). We used a commonly used measure to estimate fruit availability (Anderson *et al.* 2005; Masi 2008; Nkurunungi *et al.* 2004; Yamagiwa and Basabose 2006), the monthly fruit abundance index (A_m):

$$A_m = \sum_{k=1}^{n} D_k B_k P_{km}$$

where D_k = density of species k per km², B_k = mean basal diameter of species k, and P_{km} = percentage of trees of species k showing ripe fruits in a month m. We calculated the fruit abundance index for all fruits consumed by either ape, and each ape species separately, including only fruits each consumed and, because it was based on fecal analysis, on whose seeds they swallowed. For the analysis of trail signs we also included abundance of fruits consumed with seeds too large to swallow.

Indirect Measures of Diet

Fecal Analysis We opportunistically collected 644 (monthly mean=17, range=3–62) fresh dung samples from gorillas and 390 (monthly mean=11, range=3–29) from chimpanzees between June 2006 and May 2009. We collected ≤2 samples/d per group/community to ensure the independence of sampling. We collected feces on fresh ape trails, at nest sites <1 d old and after direct observations. We collected feces only when they could be reliably assigned to either ape species. Genetic analysis of fecal samples showed that we were able to distinguish correctly between chimpanzee and gorilla feces with 96% accuracy (Arandjelovic *et al.* 2010). We weighed all feces and then dissociated through a 1-mm mesh sieve with water. We examined the remains macroscopically, identified the species of seed found, and counted the number of seeds. For seeds of both *Ficus* sp. and *Nauclea didderichii*, we estimated the quantity, as seeds were too small to be reliably counted. For any seeds that were unknown, we photographed and gave a code for later identification. In cases where genera had >1 species whose seeds were indistinguishable from one another in the feces (*Uvaria* sp., *Ficus* sp., and *Landolphia* sp.), we recorded only the genus and hence combined species.

To estimate the relative frugivory of chimpanzees and gorillas, we calculated a fruit:dung ratio (FDR) for each bimonthly period. The denominator of that ratio equaled the cumulative weight of dung that we collected from either primate during a bimonthly period. The numerator equaled the estimated amount of fruit consumption (FC) that had contributed to the dung that was collected:

$$FC = \sum_{i=1}^{n} FW_i * SD_i / SF_i$$

where FW_i equals the weight of 1 fruit of each species *i*, SD_i equals the number of seeds of species *i* in the dung collected during the bimonthly period, and SF_i equals the average number of seeds in 1 fruit of species *i*.

We collected 30 specimens from 57 fruit species consumed by either ape. We weighed fruits whole, and then for species where the apes did not consume the skin, we weighed the fruit again after its removal. Finally, we removed the seeds and weighed them singularly or in groups. We did not include the weight of seeds in the average weight of each fruit (FW_i) or the weight of the collected dung.

Both gorillas and chimpanzees eat several fruits that have seeds that are too large to swallow (*n*=9 species). In addition, chimpanzees sometimes wadge fruits (fruit juices are sucked out and swallowed and then pulp/seeds spat out; *n*=4 species). We included only fruit species whose seeds showed up in fecal remains in the analysis. Even if fruit skin was clearly recognizable in the feces and could be reliably assigned to a particular species, we did not include it because it is impossible to measure indirectly what proportion of a large fleshy fruit has been consumed when the seeds are not ingested.

Trail Signs From March 2005 to June 2009 we recorded all food items found on ape trails of either species. We defined trail signs as all feeding remains from gorillas and chimpanzees found while walking in the forest or at fresh nest sites, and we recorded

all signs (Tutin and Fernandez, 1993). To be included in the diet of either ape, a new food item had to be observed as feeding remains on trails on 3 separate occasions. We then used the data to create a list of food items that were present or absent in the diet of either species (Table I). We assigned feeding remains to an ape species as a result of the species-specific characteristic manner in which they had been processed (Doran-Sheehy *et al.* 2006) and by accompanying hand or foot imprints or fecal remains that we distinguished from those of other animals (Ganas *et al.* 2008; Morgan and Sanz 2006).

Between May 2008 and June 2009 we systematically followed 1 group of gorillas and 1 community of chimpanzees, so we were able to document presence or absence of food items on a near daily basis for each group (daily trail signs) to give us a measure of how frequently different food items were consumed. We included in the analysis only months during which the trail was followed on >15 d (n=15–30 d during 12 mo for gorillas, n=15–28 d during 13 mo for chimpanzees). We split food types into 3 categories: fruit, fiber (herbs, tree leaves, stems, and bark) and other (flowers, insects, sap, honey, and meat), and we calculated the frequency as the number of trail signs per category per month, divided by the total number of trail signs counted in that month. Although this indirect method provides no measure of intake of each food item, it does measure the regularity with which it was consumed, and we assume that increased frequency in consumption of one food type corresponds to increased biomass consumed of that food type.

Direct Observations During 52 mo between March 2005 and June 2009, we directly observed gorillas and chimpanzees during 1065 and 1169 contacts for a total observation time of 185 and 173.2 h respectively. We defined a contact as any visual observation of an ape, and multiple contacts on the same day were separated either by time (15 min) or distance (100 m). During each observation we recorded all food items and species that were consumed by the apes. When visibility was poor or the individual fled immediately, we approached after the individual's departure and attempted to identify what had been eaten from remains left on the ground. We used this information in conjunction with trail signs to compile a list of food items consumed by one or both apes (Table I).

Measuring Overlap and Frugivory with Fecal Analysis

Researchers typically have measured dietary overlap of chimpanzees and gorillas as a simple presence or absence in the diets of both species in the same month or

Table I Shared and exclusive food items for chimpanzees and gorillas from trail signs, fecal analysis, and direct observations

	Fruits	Leaves	Stem pith	Seeds	Bark	Flowers	Insects	Other
Shared food item	60	12	5	6	0	2	2	1
Exclusive chimpanzee food item	37	12	1	3	0	3	2	3
Exclusive gorilla food item	22	48	15	5	14	2	4	5

regardless of month from fecal analysis (Kuroda *et al.* 1996; Tutin and Fernandez 1993; Tutin *et al.* 1991), but this can exaggerate the level of overlap because it does not take into account the importance of each item in the diet of either species. For comparative reasons we used the method employed by Tutin, but we also measured dietary overlap between chimpanzees and gorillas (via fecal analysis) with the Renkonen method, which is more widely used in ecological studies (Eckardt and Zuberbühler 2004):

$$P_{jk} = \left[\sum_{i=1}^{n} \left(\min p_{ij}, p_{ik} \right) \right] 100$$

where P_{jk} is the percentage overlap between species j and species k, p_{ij} is the proportion resource i is of the total resources used by species j, p_{ik} is the proportion resource i is of the total number of resources used by species k, and n is the total number of resource states. Because we did not have a direct measure of intake data, we used estimated volume of fruit in feces from the fecal analysis (fruit content). For some months we had few (<6) fecal samples analyzed for diet (chimpanzee=6 mo, gorilla=4 mo), so for this analysis we combined the data into 2-mo periods (bimonths). We used the same bimonth method for calculating fruit content of fecal samples and mean number of species (based on seeds) per feces. We performed all other analysis on a monthly basis.

Results

Forest Composition and Ape Diet in Loango

Overall herb density including seedlings and saplings in Loango was $9.3/m^2$ (range=0–132; median=7) but density of herbs consumed by gorillas was $0.26/m^2$ (range=0–11), and density of monocotyledons lower, only $0.04/m^2$. Tree stem density was 323/ha, and we identified 171 different tree species from 36 families. Twenty of the 30 most common tree species in the study area provided fruit for gorillas (n=16) or chimpanzees (n=16; Table II). Gorillas and chimpanzees consumed leaves from 12 and 4 of these species, and exploited 38 and 23 different food items from these 30 species respectively. Based on trail signs, fruits from 11 and 13 of the 30 most common tree species were consumed by gorillas and chimpanzees respectively in >10% of all months studied. We found fruits from the 19th most common tree species (*Staudtia gabonensis*) in 25.9% of chimpanzee feces, but never in gorilla feces. Gorillas consumed herbs from 16 different terrestrial species, whereas chimpanzees consumed only 1.

Fruit Availability and Seasonality

Fruit availability and rainfall fluctuated substantially on both a seasonal and interannual basis, with a peak in fruit availability for all 3 yr between July and November (Fig. 1). The end of the rainy season, around April, corresponded with the lowest values of fruit productivity in all 3 yr. We found no relationship between

Table II Most common tree species ranked by tree stem density, and their importance in the diet of chimpanzees and gorillas in Loango

Rank	Genus	Family	Average DBH (cm)	Stems /km²	Fruit	Leaves	Other	Frequency in fecal samples (fruit only), %[a]		Frequency on trails (fruit only), %[b]	
								Chimpanzee	Gorilla	Chimpanzee	Gorilla
1	*Diogoa zenkeri*	Olacaceae	23.1	3246							
2	*Diospyros* spp.	Ebenaceae	17.1	2403	C/G	G		1.5	0.28	12	12
3	*Onthostema aubrianum*	Euphorbiaceae	29.9	2343	C					2	2
4	*Garcinia* sp.	Guttifiere	14.6	2025	C/G			0.5	0.14	18	2
5	*Dichostemma* sp.	Euphorbiaceae	18.6	1711			G				
6	*Diospyros dendo*	Ebenaceae	17.3	1346	C/G			1.6	0.7	24	27
7	*Gilbertiodendron* sp.	Caesalpinioideae	26.3	1278		G	C/G				
8	*Strombosia glaucesens*	Olacaceae	28	1178	C/G	G		0.9	3.7	16	18
9	*Irvingia gabonensis*	Irvingaceae	29.1	1175	C/G	G			0.1	16	8
10	*Strombosiopsi tetandra*	Olacaceae	26.1	1111		G	G				
11	*Cola* sp.	Sterculiaceae	31.6	1043	G	C/G	C/G			16	16
12	*Uvariastrum pierreanum*	Annonaceae	14.9	654	C/G	G		1.4	4.2	14	18
13	*Chitranthus* sp.	Sapindaceae	13	607	C/G	C		0.5	4.9	8	12
14	*Coula edulis*	Olacaceae	32.2	607	G		C/G		0.7		20
15	*Mitragyna ciliata(Hallea)*	Rubiaceae	30.7	596		G	G				
16	*Scottellia coriaceae*	Flacourtiaceae	27.7	507	C			4.5		16	
17	*Calypocalyx* sp.	Caesalpinaceae	79	482	C/G		G	0.9		37	2
18	*Saccoglottis gabonensis*	Humiriaceae	66.9	471	C/G				0.4	29	12
19	*Staudtia gabonensis*	Myristicaceae	43.8	414	C	G	G	25.9		59	
20	*Syzigium guineense*	Myrtaceae	35.5	371	C/G			0.2	4.5	22	31
21	*Baphia* sp.	Papilionaceae	27	336		G	G				

Table II (continued)

Rank	Genus	Family	Average DBH (cm)	Stems /km^2	Fruit	Leaves	Other	Frequency in fecal samples (fruit only), %[a]		Frequency on trails (fruit only), %[b]	
								Chimpanzee	Gorilla	Chimpanzee	Gorilla
22	*Monodora myristicaceae*	Annonaceae	22.5	329	C/G			8.2	0.4	29	10
23	*Maprounea membranacea*	Euphorbiaceae	23.5	318							
24	*Carapa* sp.	Caesalpinaceae	38	304	G	G					4
25	*Rauvolphia vomitoria*	Apocynaceae	17	268							
26	*Xylopia hypolampra*	Annonaceae	19.8	74							
27	*Panda oleosa*	Pandaceae	52	71	G	C/G				2	4
28	*Odyendya gabonensis*	Simaroubaceae	47.8	68			C/G				
29	*Hexalobus crispiflorus*	Annonaceae	46.9	66	C/G	C	G	0.9	3.9	24	43
30	*Arungana madagascariensis*	Guttifiere	19.4	62	C	G				6	

[a] Frequency calculated as percentage of fecal samples containing seeds of that fruit species

[b] Frequency calculated as number of months observed on trails as a percentage of total duration of study

rainfall and fruit availability (all months, $n=37$, Pearson correlation $r^2=0.078$, $p=0.646$; June 2007–June 2009, $n=25$, Pearson correlation $r^2=0.155$, $p=0.458$).

Composition of Diet

Gorillas consumed more food types than chimpanzees based on data from combined fecal analysis, trail signs, and direct observations (Table I). Gorillas ate 203 food items from 145 species, whereas chimpanzees ate 176 food items from 116 species. 73% of gorilla fruits and 62% of chimpanzee fruits were shared, whereas 23% and 54% of other food items consumed by the gorillas and chimpanzees respectively were shared. Bark was consumed only by gorillas. Fruit was the most numerous food class for both species, consisting of 40% and 55% total number of food parts consumed for gorillas and chimpanzees respectively. 92% of all chimpanzee feces examined contained seeds vs. 81.5% of all gorilla feces.

   Both ape species consumed weaver ants (*Oecophylla longinoda*) on several occasions, but for all other ant species their choices were not the same. We observed both chimpanzees and gorillas eating larvae once, and we found larvae in gorilla feces once. We sometimes found animal remains (hairs and bone) in chimpanzee feces, but never in gorilla feces. Chimpanzees also regularly exploited nests to obtain honey from ≥4 different species of bee (*Apis mellifera*, *Meliponula bocandei*, *M. nebulata*, and *M. lendliana*: Boesch *et al.* 2009).

Dietary Overlap and Responses to Changes in Fruit Abundance from Fecal Analysis

We found that total overlap in fruit consumption (from fecal remains, combining all months of the study) was high, at 76% and 63% for gorillas and chimpanzees respectively. However, when overlap was calculated on a bimonthly basis using Renkonen's method (Fig. 2), it varied between 0.3% and 69% (mean=27.5%). The degree of overlap fluctuated on a seasonal basis, but did not correlate to fruit availability ($n=18$, Pearson correlation $r^2=0.12$, $p=0.617$). All of the 10 fruits most frequently consumed by gorillas, based on fecal analysis, were also eaten by
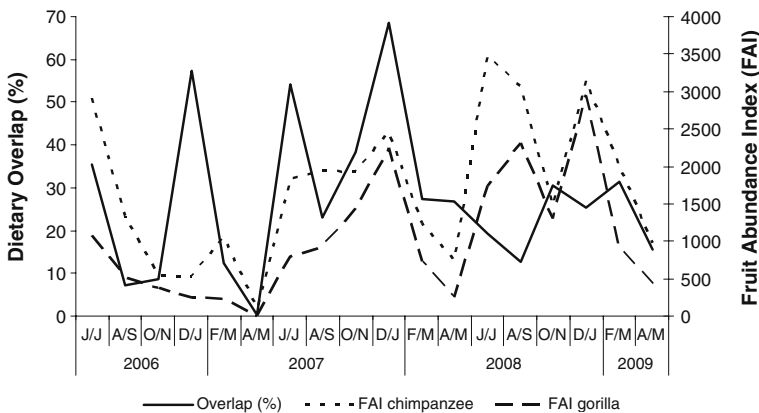

Fig. 2 Dietary overlap between chimpanzees and gorillas per month, and abundance of fruit within their range. Fruit abundance is 1000 times the values on the *y*-axis.

chimpanzees (Table III), but only 4 of the 10 fruits most frequently consumed by chimpanzees were eaten by gorillas.

Chimpanzees consistently consumed a greater number of fruit species on a bimonthly basis (mean=7.7, range=3–21 species, $n=18$) than did gorillas (mean=6.9, range=3–16 species, $n=18$), even though the analysis excludes seeds not swallowed by chimpanzees. There was no difference in the mean number of fruit species per fecal sample per bimonth (1.7 and 2 for gorillas and chimpanzees respectively; $n=18$, Wilcoxon rank sum test $p=0.136$). Chimpanzee feces contained more fruit than gorilla feces in 89% of bimonths (Wilcoxon rank sum test, $n=18$, $p=0.001$; Fig. 3a and b), confirming our expectation that chimpanzees are significantly more frugivorous than gorillas.

Given our findings that all fruit species were not consumed by both apes, we used availability specific to fruits known to be consumed by each ape species, e.g., excluding those that each species never consumed, to create separate fruit availability indexes (FAIs) for gorillas and chimpanzees. Using the entire phenology dataset set we found no relationship between fruit availability and fruit consumption for the gorillas ($n=18$, Pearson correlation $r^2=0.372$, $p=0.128$), and the relationship between fruit availability and fruit consumption for the chimpanzees is just short of being significant ($n=18$; $r^2=0.463$, $p=0.053$). Because the FAI for the first 6 bimonths of the study did not include 8 species that were later added to the phenology, we reran the analysis using only the last 12 bimonths of data. We found a positive correlation between fruit availability and fruit consumption for both species ($n=12$; chimpanzees, $r^2=0.697$, $p=0.012$; gorillas, $r^2=0.744$, $p=0.006$). In sum,

Table III Top 10 fruit species consumed by chimpanzees and gorillas based on frequency in fecal samples (%)

Species	Frequency in chimpanzee feces (%) and rank (x)	Frequency in gorilla feces (%) and rank (x)
Staudtia gabonensis	28.2 (1)	0
Pycnanthus angolensis	17.4 (2)	0
Cissus dinklagei	16.7 (3)	17.7 (2)
Vitex doniana	14.4 (4)	21.6 (1)
Ficus sp.	12.3 (5)	10.2 (4)
Pseudospondias longifolia	10.8 (6)	9.3 (6)
Beilschmieda sp.	9 (8)	0
Monodora myristicaceae	9 (8)	0
Unknown species	9 (8)	0
Dacryodes normandii	7.9 (10)	0
Myrianthus arboreus	4.2 (16)	15.9 (3)
Uapaca paludosa	2.5 (19)	9.5 (5)
Erythrophleum ivorense	4 (17)	8.9 (7)
Scytopetalum	0.7 (36)	8.4 (8)
Chitranthus sp.	0.5 (45)	5.1 (9)
Syzygium guineensis	0.2 (46)	4.7 (10)

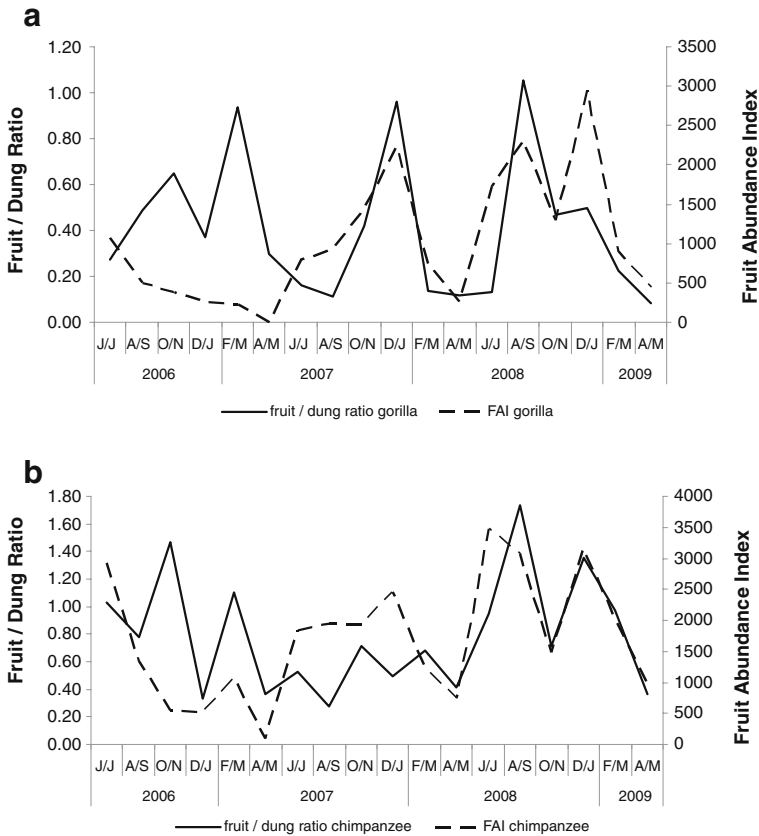Numbers in parentheses indicate rank

Fig. 3 a Mean fruit/dung ratio of fecal samples on a monthly basis for gorillas, and abundance of fruit within their range. Fruit abundance is 1000 times the values on the y-axis. b Mean fruit/dung ratio of fecal samples on a monthly basis for chimpanzees, and abundance of fruit within their range. Fruit abundance is 1000 times the values on the y-axis.

these results suggest that the apes respond to fluctuations in fruit availability by consuming more as it becomes increasingly available.

Dietary Variability and Responses to Changes in Fruit Abundance from Trail Signs

Consumption of fibrous foods by gorillas varied over the 12 mo measured via daily trail signs. The number of fibrous foods consumed was the highest for the 3 mo that both fruit availability and fruit consumption were lowest (<20%; Fig. 4), but we found no correlation between fruit availability and fiber consumption (Pearson correlation, $n=12$, $r^2=-0.41$, $p=0.18$), and no correlation between fruit availability and fruit consumption by gorillas (Pearson correlation, $n=12$, $r^2=0.45$, $p=0.15$). Splitting the fiber data into bark, tree leaves, and herbs revealed that gorillas consumed leaves more often than herbs in 9 out of 12 mo, and bark more frequently than herbs in 7 out of 12 mo.

Fruit consumption by chimpanzees did not show the same fluctuations as for the gorillas, and remained above 70% (percentage of trail signs that were fruit) in all
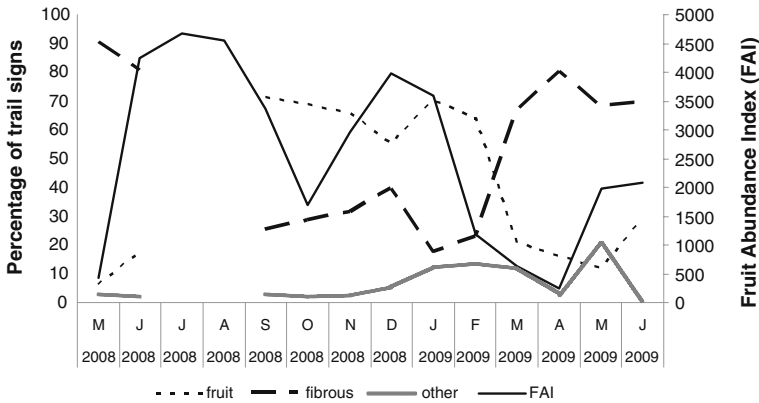
Fig. 4 Monthly consumption of fruit and fiber by gorillas, and monthly fruit abundance index. Fruit abundance is 1000 times the values on the *y*-axis.

months studied (Fig. 5). Similarly, for chimpanzees there is no correlation between fiber consumption and fruit availability (Pearson correlation, $n=12$, $r^2=-0.29$; $p=0.34$) or between fruit consumption and fruit availability (Pearson correlation, $n=12$, $r^2=0.5$, $p=0.06$).

Discussion

Forest Composition

Our results show that Loango National Park has a minimal herb density and different seasonal fruiting pattern than reported for other ape habitats, illustrating that there can be high variability between sites (Table IV). More than 50% of the 30 most common tree species provided fruit for chimpanzees and gorillas (Table II),
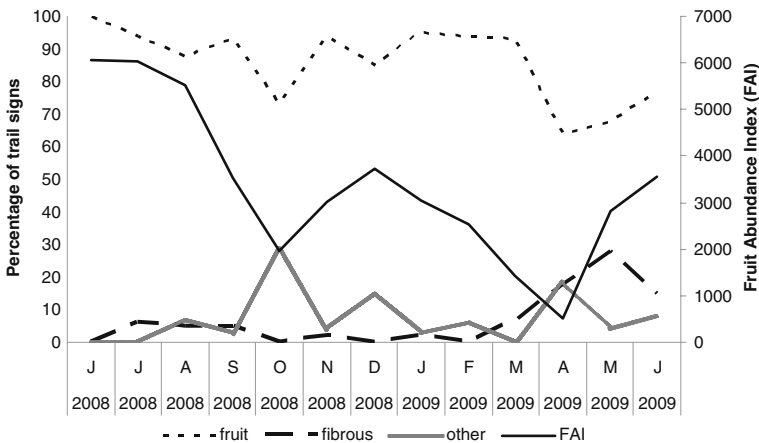

Fig. 5 Monthly consumption of fruit and fiber by chimpanzees, and monthly fruit abundance index. Fruit abundance is 1000 times the values on the *y*-axis.

Table IV Cross site comparison of resource availability and dietary composition of chimpanzees and gorillas from 7 different study sites

Ape species	Loango Chimpanzee	Loango Gorilla	Lopé[1] Chimpanzee	Lopé Gorilla	Goualougo[2] Chimpanzee	Goualougo Gorilla	Nouabalé-Ndoki[3] Chimpanzee	Nouabalé-Ndoki Gorilla	Bai Hokou[4] Gorilla	Mondika[5] Gorilla
Tree stem density (hectare)	323		384.5		No data		No data		No data	419.5
Tree diversity (no. of species)	171		137[1b]		No data		110		143	269
Herb density (herbs/m²)[d]	0.26 (0.04[e])		1.88[e]		No data		2.25[5]		0.82 (1.11[e])	0.78[e]
Ape density (km²)	1.5[6]	0.82–1.06[6]	1	1	1.5–2.2	2.3	2.7	1.9–2.6	0.9	4.48[7]
Total no. of food items	176	203	182	220	158	107	114	182	230	127
Total fruits	97	82	114	100	56%[b]	No data	100	115	89	70
Total stems	6	20	8	16	8%[b]	No data	6	14	14	14
Total leaves	24	60	19	48	16%[b]	No data	3	29	84	33
Total bark	0	14	0	12	3%[b]	No data	1	2		8
Total other	22	27	41	56	17%[b]	No data	5	22	13	2
Mean no. of fruit species per feces	2	1.7	2.7	3	2.33±1.22	1.63±1.42	2.4	3	3.2	3.5
Percentage of feces containing fruit remains	92[a]	81.5[a]	98	96	98.8	79.9	No data	100	98	95
Dietary overlap with other ape species (fruits)	62%	73%	82%	79%	No data	No data	59%	51%	No data	No data
Dietary overlap with other ape species (all foods)	50%	43%	73%	57%	58%	84%	64%[c]	13%[c]	No data	No data

[1] Tutin and Fernandez (1993) and Tutin et al. (1991, 1997); [1b] White (1992); [2] Morgan and Sanz (2006); [3] Nishihara (1992, 1995), Kuroda (1992) and Kuroda et al. (1996); [4] Remis (1997) and Remis et al. (2001); [5] in Doran et al. (2002); [6] Arandjelovic et al. (2010); [7] A. Todd pers comm

[a] Criteria of fruit remains was different in Loango; we considered only seeds to represent fruit remains in a feces

[b] Figures for total number of each food category are a percentage and not actual values

[c] Figures represent dietary overlap of other food items (excluding fruits)

[d] Herb density includes seedlings unless otherwise indicated

[e] Herb density includes only herbs consumed by gorillas (monocotyledon family)

suggesting that the forests in Loango contain a rich and diverse array of food resources for both ape species. Terrestrial herbs from the monocotyledon families most frequently consumed by gorillas in other locations (Marantaceae, Commelinaceae, and Zingiberaceae) were scarce in Loango (0.04/m^2; range at other sites 0.78–1.16 /m^2 [Rogers *et al.* 2004]), and the only other frequently consumed gorilla herb species found in Loango (Cyperaceae) becomes accessible only during the dry season (because of its location in deep swamps), which is not the low fruit season in Loango.

Seasonality and Dietary Variability

Conversely to reports from other field sites (Doran *et al.* 2002; Furuichi *et al.* 2001; Nishihara 1992; White 1994), the dry season in Loango does not correspond with the low fruit season, nor did rainfall and fruit availability correlate. The relatively high fruit availability during the dry season was due to only a few highly abundant species, i.e., *Vitex doniana* and *Staudtia gabonensis*, which are important in the diets of gorillas and chimpanzees respectively (but gorillas never eat *S. gabonensis*). Ripe fruits of *Vitex doniana* were available for 5–7 mo of each year studied, constituted on average 50% of gorilla fruit availability in these months, and were observed in 44% of all gorilla feces analyzed during those months. *Staudtia gabonensis* was available for 4–5 mo each year, constituted on average 38% of chimpanzee fruit availability in these months, and seeds were present in 68% of chimpanzee feces analyzed during those months. These 2 fruit species therefore appear to be of particular dietary importance for the apes in Loango during the dry season. Interestingly, both of these species are rare or not important in the diet of the apes at some other sites (Rogers *et al.* 1990; C. Sanz, Goualougo, and C. Devos, Mikongo forest, Lopé, *pers comm.*), although *Vitex doniana* is important in the diets of gorillas during the rainy season at Bai Hokou (Remis 1997).

As we predicted, fruit consumption correlates positively with fruit availability for both ape species when considering only fruits consumed by each species. Therefore, our results are consistent with studies using direct observations that found that the percentage of feeding time spent eating ripe fruit by chimpanzees and gorillas increased when fruit availability was higher (Masi *et al.* 2009; Wrangham *et al.* 1998). We did not find a relationship between fruit availability and fiber consumption for either species, which may be due to our crude measure of fiber consumption based on daily presence/absence of each food item found on the apes' trails. Other studies that used fecal analysis to measure foliage consumption by chimpanzees found that it did increase during times of fruit scarcity (Kuroda *et al.* 1996; Tutin and Fernandez 1993) and that patterns of fiber consumption by chimpanzees showed seasonal variation similar to that by gorillas, but that they consumed foliage in smaller quantities.

Though there is no correlation between fruit availability and the number of fibrous species consumed by gorillas, there is large variation between months and an increase in the number of fibrous species consumed when fruit availability was lowest. It therefore seems possible that longer-term data collection in Loango and a more precise methodology could support the findings of Kuroda *et al.* (1996) and Remis *et al.* (2001) that gorillas react to fruit shortages by switching to a more folivorous diet when ripe fruit is scarce. Fruit consumption by chimpanzees showed

much less variation between months than for gorillas, and percentage of trail signs that consisted of fruit always remained above 70% (gorilla fruit trail signs were as low as 6% in some months), suggesting that chimpanzees in Loango exhibit less dietary flexibility than the gorillas, consistent with observations elsewhere (Kuroda *et al.* 1996).

Dietary Overlap

Overall the diets of gorillas and chimpanzees in Loango showed a high degree of overlap in the fruit category, but they diverged in all other food categories. Contrary to our predictions, the low abundance of terrestrial herbs did not result in increased overlap between the 2 ape species; gorillas instead appear to exploit other sources of fiber through regular consumption of tree leaves and bark. Gorillas consumed more tree leaf and herb species than did chimpanzees, as has been found elsewhere (Kuroda 1992; Tutin and Fernandez 1993; Tutin *et al.* 1991, 1996), and chimpanzees consistently consumed more fruit than gorillas did throughout the study, supporting the idea that the gorillas' larger body size enables them to consume a higher volume of foliage and to follow a more generalist regimen than the predominantly fruit specializing chimpanzees (Remis 2006; Remis *et al.* 2001). Dietary overlap measured via Renkonen's method exhibited large seasonal variation; in some months chimpanzees and gorillas were not competing for the same fruit species, whereas in other months overlap was very high. Overlap does not correlate with overall fruit availability, but this may be because patterns of fruit consumption by apes are very complex, and certain fruit species are consumed only when others preferred fruit species are not available (Doran *et al.* 2002).

Gorillas in Loango avoided fruit species that may be high in crude lipids such as *Staudtia gabonensis*, *Pycnanthus angolensis*, and *Dacryodes normandii* (analyzed at Lopé by Rogers *et al.* 1990), which corresponds to findings at other sites (Masi 2008; Remis *et al.* 2001; Rogers *et al.* 1990; Tutin and Fernandez 1993; *cf.* Calvert 1985), but these fruit species were heavily exploited by chimpanzees (Table III) and thus appeared to be a feature of niche differentiation between the 2 ape species (Rogers *et al.* 1990). In every month of the study, 1–4 of these lipid-rich fruits were available, and were the primary cause of differences in fruit consumption by the 2 ape species. This indicates that the chimpanzees in Loango have a much more consistent supply of ripe fruits throughout the year and therefore they perhaps do not need to turn to leaves or herbs as often as do the gorillas.

Intersite Variation in Resource Availability and Ape Diet

Sympatric species can occupy a wide range of habitats, leading to variation in dietary overlap between sites (Cords 1990; Eckardt and Zuberbühler 2004). Mean number of seed species per feces for both gorillas and chimpanzees, the total number of food items, and dietary overlap in Loango were comparable to those at other sites, despite the forest containing a higher diversity of tree species than in Lopé, Nouabalé-Ndoki or Bai Hokou. Our study suggests that gorillas and chimpanzees in Loango do not consume a greater number of fruit species than elsewhere, and the percentage of feces containing fruit remains is actually lower than at other sites for both ape species, except for gorillas at Goualougo. This may be because other

studies have included fleshy remains as indicators of fruit presence (Nishihara 1995; Remis *et al.* 2001; Tutin and Fernandez 1993), whereas we considered only feces that contained fruit seeds because we could not always reliably assign fleshy parts to a particular fruit species.

We found large differences in the apes' responses to certain fruit species that are considered important fallback foods—those that dominate the diet during a multimonth period in most or all years, particularly during times of low fruit availability (Doran *et al.* 2002; Rogers *et al.* 2004; Tutin and Fernandez 1993)— between Loango and other sites. *Duboscia macrocarpa* and *Klainedoxa gabonensis* are important fallback foods for one or both ape species at Nouabalé-Ndoki (Kuroda *et al.* 1996; Nishihara 1995), Mondika (Doran *et al.* 2002), Moukalaba-doudou (Takenoshita 2008), Lopé (Tutin and Fernandez 1993; Tutin *et al.* 1991), and Goualougo (Morgan and Sanz 2006). In Loango, *Klainedoxa gabonensis* is more abundant than in Mondika (1.32 stems/ha and 0.7 stems/ha respectively), and *Duboscia macrocarpa* less abundant (0.7 stems h/a and 2.1 stems/ha respectively) (Doran *et al.* 2002), and fruit was available during 76% ($n=26$ mo) and 59% ($n=16$ mo) of months respectively. However, in Loango, chimpanzees have never been observed to consume either fruit species, whereas gorillas have been observed to consume the fruits of *Klainedoxa gabonensis* only once. Therefore the apes' avoidance of these fruits in Loango supports the idea that fruit availability remained adequate year round because of the presence of other species, and the apes rarely or never needed to consume these fruits.

Our results suggest that tree leaves may play an important role in the diet of gorillas in Loango, particularly during times of low fruit availability, as shown by studies using direct observations (Doran-Sheehy *et al*. 2009; Masi *et al.* 2009). The number of tree leaf species eaten by gorillas is significantly higher in Loango than at any other site, and this is likely related to the very low herb density in Loango. The reduced herb density in Loango does not seem to be associated with an increased reliance on fruit, as proposed by Kuroda *et al.* (1996); instead the results suggest that Loango gorillas may have increased their exploitation of tree leaves to compensate for a lack of herbs.

The lack of herbaceous vegetation does not appear to have led to a reduced density of gorillas in Loango in comparison to other locations, as proposed by Furuichi *et al.* (1997), Rogers *et al.* (2004), and Wrangham *et al.* (1993) (Table IV). Our results therefore support the idea that forests with minimal terrestrial herbs can support healthy western gorilla populations. In addition to food availability, current ape density may be affected by past impacts such as disease or hunting. Both Nouabalé-Ndoki and Mondika had higher densities of herbaceous vegetation and gorillas than Loango did, whereas Lopé had a comparable density of gorillas to Loango despite a much higher density of herbaceous vegetation (Table IV). Two studies at nearby Petit Loango found extremely low ape densities, which may have been underestimates because they were constrained by time (1 mo: Furuichi *et al.* 1997) or sampling area (mainly coastal forest: Morgan 2000). We have observed high heterogeneity in habitat types and usage by both ape species in Loango. They may not use particular habitats for long periods of time, particularly the coastal forest, when food availability is low (J. Head, *unpubl. data*). Our results highlight the large differences that can be found within a small area, and emphasize the need for caution when generalizing from a single study site to a larger area.

Our results show that chimpanzees and gorillas have a pattern of niche differentiation similar to that found in other locations, suggesting that each species has evolved a certain range of dietary flexibility as a response to variation in food availability and the presence of a potential competitor. It is possible that greater digestive flexibility leads to the more variable dietary patterns of gorillas compared to chimpanzees and reduces interspecific competition. Our results are similar to patterns of dietary overlap and niche separation between sympatric woolly monkeys (*Lagothrix lagotricha poeppigii*) and spider monkeys (*Ateles belzebuth belzebuth*), in which woolly monkeys follow a more generalized diet and avoid lipid-rich fruits and the spider monkeys specialize on fewer, richer resources and heavily exploit lipid-rich fruits (Dew 2005). We have not yet found evidence that the presence of one species is potentially affecting the presence of the other, e.g., *Cercocebus galeritus* and *Papio cynocephalus* (Wahunga 1998). Further investigation on small-scale patterns of habitat use by the chimpanzees and gorillas in Loango will provide further information on how they live sympatrically and help us to understand the limits of distribution for both species across Africa.

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