Title

Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis

Journal

JOURNAL OF HUMAN EVOLUTION, 66

ISSN

0047-2484

Authors

Oelze, Vicky M
Head, Josephine S
Robbins, Martha M
et al.

Publication Date

2014

DOI

10.1016/j.jhevol.2013.10.003

Peer reviewed

Journal of Human Evolution xxx (2013) 1–12

Contents lists available at ScienceDirect

Journal of Human Evolution

journal homepage: www.elsevier.com/locate/jhevol

Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis

Vicky M. Oelze [a,b,*], Josephine S. Head [a], Martha M. Robbins [a], Michael Richards [b,c], Christophe Boesch [a]

[a] Max Planck Institute for Evolutionary Anthropology, Department of Primatology, Deutscher Platz 6, 04103 Leipzig, Germany
[b] Max Planck Institute for Evolutionary Anthropology, Department of Human Evolution, Deutscher Platz 6, 04103 Leipzig, Germany
[c] Department of Anthropology, University of British Columbia, 6303 NW Marine Drive, Vancouver, British Columbia, Canada V6T 1Z1

ARTICLE INFO

Article history:
Received 30 May 2013
Accepted 9 October 2013
Available online xxx

Keywords:
Carbon and nitrogen isotopes
Palaeodietary reconstruction
Great ape
Africa
Niche partitioning

ABSTRACT

The feeding ecology of sympatric great ape species yields valuable information for palaeodietary reconstructions in sympatric early hominin species. However, no isotopic references on sympatrically living apes and their feeding ecology are currently available. Here we present the first isotopic study on sympatric great apes, namely western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) from Loango National Park, Gabon. We successfully analyzed the stable carbon and nitrogen isotope ratios in a selection of food plants ($n = 31$) and hair samples ($n = 30$) retrieved from sleeping nests to test whether niche partitioning among sympatric chimpanzees and gorillas is detectable using isotope analysis of hair. Ape hair strands with roots were sectioned into sequential segments ($n = 100$) to investigate temporal isotopic variation related to seasonal variations in food resources. We found significant $\delta^{13}C$ differences between herbaceous plants and fruits, most likely due to canopy effects. While the $\delta^{13}C$ values of chimpanzees indicate the consumption of fruit, the low $\delta^{13}C$ values in gorilla hair indicate folivory, most likely the consumption of ^{13}C-depleted herbaceous vegetation. Our isotopic data also confirmed dietary overlap between chimpanzees and gorillas, which varied by season. Gorillas showed significant variation in $\delta^{13}C$ values in response to season due to shifting proportions of herbaceous plants versus fruits. In chimpanzees, significant seasonal variation in $\delta^{15}N$ was likely related to the seasonal availability of fruit species with particularly high $\delta^{15}N$ values. In summary, we found isotopic evidence for niche partitioning and seasonal dietary variation among sympatric great apes at Loango. These findings provide a valuable reference for palaeodietary research on fossil hominins using $\delta^{13}C$ analyses, particularly for studies focusing on sympatric taxa and on temporal isotopic variation within incremental tissues such as tooth enamel.

Introduction

Studies on the behavioral ecology of sympatric gorillas and chimpanzees provide information for various aspects of palaeoanthropological research (Stanford, 2006). Chimpanzees can thrive in a wide spectrum of habitat types, which range from evergreen tropical rainforests to the dry savannas of East and West Africa, whereas the different subspecies of *Gorilla* live only in evergreen tropical rainforest in two areas of Central Africa (Junker et al., 2012). The different feeding strategies of these great ape species are of particular interest in Central Africa because in nearly all regions where the two species co-occur they have overlapping home ranges and face inter-specific competition over resources. Studies on the feeding ecologies of sympatrically living western lowland gorillas (*Gorilla gorilla gorilla*) and central chimpanzees (*Pan troglodytes troglodytes*) suggest that while both species are feeding generalists and opportunistic frugivores, chimpanzees are more persistent frugivores and consume fewer herbaceous plants than gorillas (Tutin et al., 1991; Morgan and Sanz, 2006; Stanford, 2006; Doran-Sheehy et al., 2009). By analyzing fecal samples and food remains of unhabituated gorillas and chimpanzees from Loango National Park, Head et al. (2011) showed a high degree of dietary overlap in the consumption of fruits, but larger differences in all other food categories. Gorillas avoided fatty fruits, which were

* Corresponding author.
E-mail address: viktoria_oelze@eva.mpg.de (V.M. Oelze).

0047-2484/$ – see front matter © 2013 Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.jhevol.2013.10.003

preferred by chimpanzees and consumed more herbaceous and tree leaf species than chimpanzees. Moreover, the dietary overlap between the two ape species appeared to follow seasonal shifts. These findings may suggest different fallback food strategies to cope with seasonal changes in the availability of preferred food plants and nutrients.

Understanding dietary patterns of sympatric extant apes provides information for palaeodietary reconstructions in fossil ape and hominin species, particularly for studies on hominin feeding niches of species that lived contemporarily in the same geographical region (Stanford, 2006). Well known examples include *Paranthropus boisei* coexisting with early *Homo* in East Africa (summarized e.g., by Stanford, 2006) and a more recent discovery of fossils suggests the presence of several contemporary species of the genus *Homo* (Leakey et al., 2012). Reconstructing the dietary partitioning among sympatric hominins can provide insights on their niche specific behavioral and physiological adaptations. The selective pressure to adapt to food shortage periods by falling back on other food resources is increasingly recognized in the study of primate evolution. Fallback foods are commonly defined as highly abundant food resources of low nutritional quality, which are utilized when preferred foods are scarce (Marshall and Wrangham, 2007; Constantino and Wright, 2009). Although so-called fallback foods have rarely been tested for their actual nutritional content and quality (Doran-Sheehy et al., 2009), it has been proposed that the distinct manner in which sympatric great apes fallback on less-preferred foods during periods of low food availability may explain some of their socioecological (ranging patterns, party size and composition) and morphological (masticatory and digestive anatomy) differences. For example, lowland gorillas utilize digestively challenging filler fallback foods such as leaves and piths when ripe fruits are rare, whereas sympatric chimpanzees tend to fallback on insect extraction, for which complex tool kits and cognitive skills are required (Yamagiwa and Basabose, 2009). Despite the assumed importance of fallback food consumption in hominin diversification, the identification of seasonal fallback food consumption remains challenging for palaeodietary reconstructions (summarized in Constantino and Wright, 2009).

Long-term dietary signals recorded and retained in the carbon isotopic ratios ($^{13}C/^{12}C = \delta^{13}C$) of tooth enamel may provide direct evidence on niche partitioning, dietary seasonality and potentially even fallback food consumption. To date, $\delta^{13}C$ values have been analyzed in fossil tooth enamel of many African hominin taxa, revealing high levels of inter-specific dietary diversity in the reliance on C_4- and C_3-plants (van der Merwe et al., 2008; Lee-Thorp et al., 2010, 2012). Particularly, laser ablation $\delta^{13}C$ analysis provided insights into dietary variation during tooth formation within single individuals of *Paranthropus robustus* and *Australopithecus africanus* (Sponheimer et al., 2006b; Lee-Thorp et al., 2010) and has the potential to be applied to many other fossil taxa in the future. While most hominins appear to have consumed significant proportions of C_4-based resources including C_4-grasses, sedges, or possibly also savanna-grazing herbivores (Lee-Thorp et al., 2010; Ungar and Sponheimer, 2011; Sponheimer et al., 2013), the early East African hominin *Ardipithecus ramidus* appears to have had a mainly C_3-based diet more similar to that of present day chimpanzees (White et al., 2009; Sponheimer et al., 2013). More recently, this ape-like C_3-pattern was also reported from two *Australopithecus sediba* specimens from South Africa (Henry et al., 2012), challenging the widely accepted perception that evolutionary changes in locomotion and feeding repertoire of our fossil ancestors were largely driven by adaptations to savannah habitats (Schoeninger, 2012). As chimpanzees that live in semi-arid woodland-savanna mosaics predominantly forage for fruits in few and isolated forest patches (Pruetz, 2006; Sponheimer et al., 2006a), it appears possible that early African hominins employed similar strategies (Stanford, 2006, 2012). We suggest that improved isotopic evidence of great ape feeding ecology will enable a better understanding of isotopic variation under various ecological conditions and provide valuable analogies for palaeodietary reconstructions of folivory or frugivory in early hominins.

The analysis of $\delta^{13}C$ and $\delta^{15}N$ in body tissue has a wide applicability in describing niche utilization and feeding preferences in sympatric primates, as demonstrated by Schoeninger and colleagues (Schoeninger et al., 1997, 1998). Protein-deriving amino acids are the main contributors for the synthesis of proteinous tissues including hair and bone collagen, and thus isotopic feeding reconstructions using hair are biased towards dietary protein (Ambrose and Norr, 1993; Tieszen and Fagre, 1993; Jim et al., 2004). While in terrestrial ecosystems $\delta^{13}C$ ratios are particularly useful to distinguish among fodder plants with different photosynthetic pathways (C_3, CAM and C_4) and at different canopy heights (Tieszen, 1991; van der Merwe and Medina, 1991), $\delta^{15}N$ levels mainly correspond to trophic level (herbivore versus omnivore or insectivore diets), but are also affected by the consumption of ^{15}N-depleted food plants, such as legumes (Ambrose, 1991). As local isotopic baseline values are largely determined by climate, substrate and biome complexity (Heaton, 1987), it has become accepted practice in isotopic research to include samples of plants to assess the local bio-availability of isotope ratios in a given habitat (Sandberg et al., 2012).

Isotopic research on great apes, summarized by Sandberg et al. (2012), to date has been limited to studies on unhabituated chimpanzees (Schoeninger et al., 1999; Carter, 2001; Sponheimer et al., 2006b; Smith et al., 2010), one group of fully habituated chimpanzees (Fahy et al., 2013), one community of habituated bonobos (Oelze et al., 2011), and recently one group of habituated mountain gorillas (Blumenthal et al., 2012). Here we present the first isotope dataset on free-ranging western lowland gorillas and central chimpanzees, and the first isotope study that compares dietary preferences in two sympatric great apes species. Using hair samples of great apes collected in Loango National Park, Gabon, we followed the approach that Cerling and colleagues (Cerling et al., 2009) concisely referred to as 'History of Animals using Isotope Records (HAIR)' and gained long-term dietary signatures potentially enabling investigations of dietary seasonality.

The objectives of this isotope study on sympatric great apes are to:

1) explore dietary differences between gorillas and chimpanzees by means of stable isotopes,
2) identify isotopically-diagnostic great ape food resources,
3) explore potential seasonal isotopic variation in gorillas and chimpanzees, and
4) compare isotopic signatures to other indirect measures of feeding behavior (Head et al., 2011) to evaluate the applicability of isotopic methods to the study of unhabituated ape populations.

Materials and methods

Hair samples were collected from nests of chimpanzees and gorillas as part of ongoing habituation efforts in the Loango National Park, Gabon (Boesch et al., 2007, 2009; Head et al., 2011, 2012). The Loango Ape Project study area (2°04′ south and 9°33′ east) covers 80 km^2 on a long strip of land bordered to the west by the Atlantic Ocean and to the east by a large lagoon. The study area contains a variety of habitat types and the forest composition is quite different from other locations where sympatric apes have been studied (Furuichi et al., 1997; Morgan, 2000), and includes

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003

mature and secondary forest, coastal forest, swamp forest and savannah. The swamp forest includes mangrove, seasonally inundated forest and permanently inundated forest, which is characterized by an abundance of terrestrial herbs. Mean annual rainfall is approximately 2215 mm, and temperature ranges from 22.9 °C to 27.2 °C. There is a long rainy season (October to April) that is often interrupted by a short dry season (December to January). The long dry season stretches from May to September (Head et al., 2011).

Hair samples of great apes were collected from fresh nests in 2009. Additional hair samples were collected from gorillas during ongoing habituation efforts in 2011, resulting in several hair samples from two silverbacks from the Indegho and Atananga groups. Hairs were collected from both ground and tree nests, which were confirmed as chimpanzee or gorilla nests based on species-specific signs (feces or feeding remains) that are commonly used to distinguish them from one another (see Head et al., 2011 for details). Gorilla silverback nests were identified based on their location (on the ground) and the presence of long silver hairs, which are exclusively produced by adult male gorillas. With the exception of silverbacks, approximate age and sex of other sampled individuals was unknown. All tissue samples were stored in paper envelopes or plastic tubes and kept dry with silica gel.

All plant items were collected in November 2010 and May 2011 but without focusing on resampling the same plant materials in different seasons. Plant foods were selected for analysis using the list of important ape foods in Loango generated by Head et al. (2011), based on frequency in ape fecal remains and on feeding trails. Additionally, we collected food items that were consumed by two semi-habituated gorilla groups during direct feeding observations. For each collected plant sample, canopy height was measured using a range finder where plants were >10 m in height, and roughly estimated where plants were <10 m height. Plant samples (several grams each) were dried and stored in tubes containing silica gel to prevent the material from decomposing.

Isotope analysis

Stable isotope ratios of hair strands may indicate dietary or even physiological changes over time. This has been successfully shown for domestic and wild mammals (e.g., Schwertl et al., 2003; Cerling and Viehl, 2004; Cerling et al., 2004b) and also for humans (e.g., O'Connell and Hedges, 1999; Huelsemann et al., 2009; Mekota et al., 2009). Although the hair matrix is exposed to environmental influences (e.g., ultraviolet radiation and abrasion), it has been shown that the isotopic composition of carbon and nitrogen remains intact over longer periods of time (Auerswald et al., 2011). Other advantages of hair keratin samples are that they can be easily and non-invasively retrieved in sufficient amounts from unhabituated apes, and sequential isotope data can be obtained for single individuals over several months.

All ape hair strands were purified before isotopic analysis and cleaned in a mixture of methanol and chloroform (2:1 v/v) for 24 h in a rotator to remove potential lipids or dirt (O'Connell et al., 2001). Samples were then rinsed with ultrapure deionized water and dried in an incubator over-night at 40 °C and transferred to a microscope workspace. We selected long hairs with intact roots for sequential sectioning under a stereo microscope with 50× magnification. Moreover, taking a certain 'growth cycle error' (Williams et al., 2011) into account, we only selected hairs that could be assigned to the telogen phase of the hair growth cycle. In this physiologically inactive phase, the root bulb appears to be enlarged and without pigmentation (white-yellowish color). As hair is preferentially shed in this final stage of the hair cycle, almost all hairs containing roots were in the telogen phase. Short and particularly thin hairs were excluded from analysis to avoid analysis of hair that may belong to infants sharing their mother's sleeping nest (Oelze et al., 2011). Additionally, fractured hair and single hairs without roots were measured as bulk samples. Hair samples with intact roots selected for sectioning were aligned with fine tweezers at the root bulb under the microscope and, depending on the amount (length and weight) of hair, cut into 0.5 cm–2.0 cm sections with a scalpel. We used human scalp hair growth rates because there is a lack of information on great ape hair growth rates, and thus we expected some imprecision in these estimates. If we assume that 1 cm of hair corresponds to 30 days (Tobin, 2005), each 0.5 cm section should match up approximately with two weeks of hair growth and a 2.0 cm section with approximately two months.

While most hair sections were measured in single analyses, several hair samples were run in dublicates to check for analytical reproducibility. Finally, each hair sub-sample (≥0.4 mg) was transferred into tin capsules for isotopic measurement. All plant items were freeze-dried and homogenized manually with a clean pestle and mortar. Subsequently, ~2 mg of ground plant fiber were weighed in duplicates into tin capsules for isotopic measurement. All measurements were performed in a Flash EA 2112 (Thermo-Finnigan®, Bremen, Germany) coupled to a DeltaXP mass spectrometer (Thermo-Finnigan®, Bremen, Germany) at the Max Planck Institute for Evolutionary Anthropology in Leipzig, Germany. As plant materials often have very low nitrogen content (%N), we visually inspected the signal intensity during nitrogen isotope analysis in the analytical software Isodat (Thermo-Finnigan®, Bremen, Germany). In seven plant samples, low signal intensity (below 800 mV) indicated nitrogen amounts insufficient for detection. These samples were re-analyzed with larger amounts (typically between 3 and 4 mg). Overall, the analytical precision was better than 0.2‰ (1σ) for $\delta^{13}C$ and $\delta^{15}N$ according to repeated analyses of international (IAEA N1, N2, CH6 and CH7) and internal laboratory standards (7× Methionine, 2× bovine liver) included in each run. In all subsequent figures these analytical errors are smaller than the area represented by the symbols.

Statistical analysis

We used R (version 2.15.1, R-Team, 2010) to conduct several generalized linear mixed models (GLMM). The GLMMs enable investigation of complex multi-factorial natural phenomena in ecology and evolution, e.g., by including interactions between predictor variables and by integrating random effects. Considering random effects is particularly important when variation is measured through time or when multiple responses are measured per individual (reviewed in Bolker et al., 2009), e.g., by conducting multiple measurements along a single hair strand as reported in this study. To test whether $\delta^{13}C$ and $\delta^{15}N$ values in plants were influenced by canopy height and/or by plant part unit, we used two separate GLMMs (Baayen, 2008) for the response variables $\delta^{13}C$ and $\delta^{15}N$ using the function 'lmer' of the R-package lme4 (Bates et al., 2012). These models included the fixed effects 'canopy height' and 'plant part unit' to assess the differences between canopy levels and between photosynthetic and non-photosynthetic plant parts. Additionally, we controlled for random effects of 'species food' and 'plant species/family' (see Table 1). To fulfill the assumption of normality of residuals, we z-transformed canopy height and for the $\delta^{13}C$ model we transformed the $\delta^{13}C$ values ($\delta^{13}C - (\min \delta^{13}C)^2$). We checked for potential presence of collinearity (using variance inflation factors, Field, 2005) and whether residuals were normally distributed and homogeneous (visual inspection of qq-plot and the residuals plotted against fitted values) and found no issues with these assumptions. To test model stability, we used the package influence.ME (Nieuwenhuis et al., 2012), which checks for

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003

Table 1
Isotope ratios of food plants from Loango National Park.

Species/family	Family	Plant part unit	Species food*	Sampling season	Freq** chimp.	Freq** gorillas	Canopy level (m)	%C	%N	Atomic C/N ratio	$\delta^{13}C‰$	$\delta^{15}N‰$
Strychnos aculeata	Loganiaceae	Fruit	C	Nov 2010	***	0.0	Liana	49.5	0.8	73.8	−28.9	3.5
Pycnanthus angolensis	Myristicaceae	Fruit	C	Nov 2010	17.4	0.0	27.5	54.2	0.8	76.2	−27.7	0.2
Staudtia gabonensis	Myristicaceae	Fruit	C	Nov 2010	28.2	0.0	27.0	43.2	1.6	31.7	−30.5	4.7
Dacryodes normandii	Burseraceae	Fruit	C	Nov 2010	7.9	0.0	26.0	43.8	1.9	26.3	−29.0	4.0
Garcinia sp.	Guttiferae	Fruit	C	Nov 2010	0.5	0.0	14.0	34.9	2.0	21.3	−31.2	4.2
										Mean	**−29.4**	**3.3**
										SD (1σ)	**1.4**	**1.8**
Cissus dinklagei	Vitaceae	Fruit	C/G	Nov 2010	16.7	17.7	Liana	30.5	0.9	39.0	−25.9	0.6
Teghumelia africana	Moraceae	Fruit	C/G	Nov 2010	***	***	31.0	29.8	0.4	81.0	−25.7	2.4
Mammea africana	Guttiferae	Fruit	C/G	Nov 2010	***	***	29.3	37.7	0.7	60.3	−27.9	1.8
Uapaca guineensis	Euphorbiaceae	Fruit	C/G	Nov 2010	2.5	9.5	24.0	41.6	2.0	24.1	−26.3	4.4
Vitex doniana	Verbenaceae	Fruit	C/G	May 2011	14.4	21.6	23.0	49.8	0.7	77.9	−31.0	0.9
Gilbertiodendron sp.	Leguminosae	Fruit	C/G	Nov 2010	***	***	22.0	28.5	0.8	44.5	−27.5	1.5
Pachypodanthium staudtii	Annonaceae	Fruit	C/G	Nov 2010	7.5	2.6	21.4	38.8	2.1	25.2	−27.4	4.4
Pseudospondias longifolia	Anacardiaceae	Fruit	C/G	May 2011	10.8	9.3	17.8	45.5	1.5	36.0	−30.0	3.4
Irvingia gabonensis	Irvingaceae	Fruit	C/G	Nov 2010	***	***	16.7	67.2	1.6	50.4	−27.5	4.2
Uvaristrum pierreanum	Annonaceae	Fruit	C/G	Nov 2010	1.4	4.1	13.6	48.3	0.2	276.2	−27.5	0.9
Salacia sp.?	Celastraceae	Fruit	C/G	Nov 2010	0.9	4.3	2.6	46.0	1.4	38.6	−34.0	3.7
										Mean	**−28.2**	**2.6**
										SD (1σ)	**2.5**	**1.5**
										Fruit mean	**−28.6**	**2.8**
										Fruit SD (1σ)	**2.2**	**1.6**
Mbikoddi sp.	Plant	Leaf	G	May 2011			Liana	48.9	2.7	21.5	−33.3	2.6
Coula edulis	Olacaceae	Nut/seed	G	May 2011	0.7		20.2	51.5	0.8	77.3	−29.2	2.4
Antonotha macrophylla	Caesalpiniaceae	Leaf	G	May 2011			19.0	50.1	2.7	21.8	−30.1	3.6
Baphia sp.	Papilionaceae	Bark	G	May 2011			12.0	49.1	1.8	31.7	−27.7	0.1
Baphia sp.	Papilionaceae	Leaf	G	May 2011			12.0	47.8	2.6	21.1	−29.5	−1.2
Myrianthus arboreus	Moraceae	Bark	G	May 2011			11.5	49.6	1.1	53.6	−28.2	7.0
Myrianthus arboreus	Moraceae	Bark	G	May 2011			11.5	38.3	1.3	33.7	−28.7	4.1
Salacia sp. (beach)	Celastraceae	Leaf and flower	G	May 2011			2.0	49.5	1.6	35.9	−28.3	4.8
										Mean	**−29.4**	**2.9**
										SD (1σ)	**1.8**	**2.6**
Thalia welwetschtii (marantacee swamp)	Marantaceae	Leaf	G	May 2011			1.5	44.8	2.4	21.8	−31.2	5.1
Thalia welwetschtii (marantacee swamp)	Marantaceae	Stem pith	G	May 2011			1.5	40.1	0.6	77.3	−31.1	3.9
Aframomum sp.	Zingiberaceae	Leaf	G	May 2011			0.8	42.4	1.8	27.2	−34.0	3.2
Halopegia azurea (marantacee forest)	Marantaceae	Leaf	G	May 2011			0.8	40.5	1.6	29.1	−37.2	1.8
Rhynchospora corymbosa	Cyperaceae	Stem and leaf	G	May 2011			0.8	46.0	2.3	23.7	−29.5	5.0
Aframomum sp.	Zingiberaceae	Stem pith	G	May 2011			0.8	39.0	1.8	25.3	−33.6	3.8
Halopegia azurea (marantacee forest)	Marantaceae	Stem pith	G	May 2011			0.8	35.6	1.7	25.3	−37.3	1.5
Anchomanes difformis	Araceae	Leaf	G	May 2011			0.6	41.2	3.1	15.7	−37.9	3.4
Anchomanes difformis	Araceae	Stem pith	G	May 2011			0.6	42.2	1.4	35.5	−36.1	0.6
Cola flavoutina	Sterculiaceae	Leaf	G	May 2011			0.3	43.2	3.0	17.0	−36.6	13.3
										Mean	**−34.4**	**4.2**
										SD (1σ)	**3.0**	**3.5**
										Total mean	**−30.5**	**3.2**
										Total std (1σ)	**3.5**	**2.5**
										Total min	**−37.9**	**−1.2**
										Total max	**−25.7**	**13.3**

Frequencies (freq*) of consumption are based on Head et al. (2011: Table 2). * Food of great ape species (C: chimpanzee, G: gorilla, C/G: both); ** frequency is calculated as the % of feces that contained the seeds of the species over a three year period; *** seeds are not ingested.

influential observations in mixed models by excluding observations one by one and comparing the resulting estimated coefficients and by calculating Cook's distance values. Changes in the estimates when removing each observation from the $\delta^{13}C$ model suggested a single influential case. However, removing this single influential case from the $\delta^{13}C$ model did not produce different results as compared with the full model. In the $\delta^{15}N$ model, four influential cases suggested overall instability of the model. Excluding these cases from the model did not affect the results. The two full models were compared with the null models using likelihood ratio tests (R function ANOVA with argument test set to 'Chisq'). *P*-values for the effect of 'species food' were based on Markov Chain Monte Carlo sampling (Baayen, 2008) and were calculated using the functions pvals.fnc and aovlmer.fnc of the R package languageR (Baayen, 2011).

To test whether the isotope values in chimpanzee and gorilla hair sections were influenced by season in different ways we used two separate GLMMs, one for $\delta^{13}C$ and one for $\delta^{15}N$ (Baayen, 2008). As predictors we included 'season' in the form of a circular date (sin(Date) + cos(Date)), 'species' (gorilla and chimpanzee) and the interaction of season and species as fixed effects. The 'hair ID' of individual hair samples was included as a random effect to account for repeated measures on single hair samples. We also included random slopes terms to allow for individual hair samples to vary in

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003

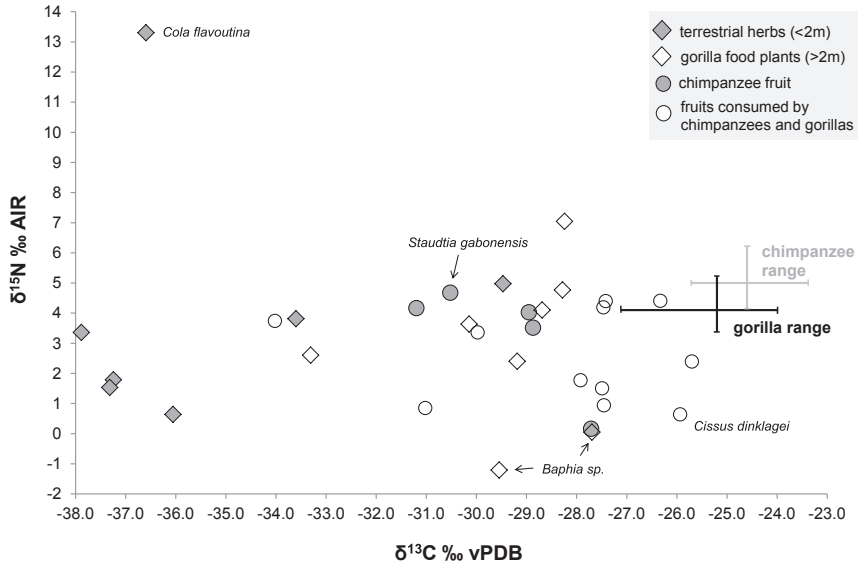

Figure 1. Food plants of gorillas, chimpanzees and of both great ape species (also see Table 1) compared to the average results obtained both from chimpanzees and gorillas.

their relationship to season. We log-transformed the $\delta^{15}N$ values to fulfill the assumption of normally distributed residuals. To test whether repetitive sampling of a single silverback (Indegho) had any effect on our two models in terms of pseudo-replication, we ran separate models excluding this silverback from the dataset and including only this silverback, but the overall results of these test models were similar to the original models (see below). We checked whether the assumptions of normally distributed and homogeneous residuals were fulfilled by visually inspecting a qq-plot and the residuals plotted against fitted values (both indicated no deviations from these assumptions). Model stability was tested by excluding individual hair samples one by one from the data and comparing the estimates derived with those obtained from the model based on all data, which indicated no influential cases. Variance Inflation Factors were calculated from the results of a standard linear model (excluding the random effect) and suggested no collinearity. The significance of each full model as compared with its corresponding null model (comprising only the random effect 'hair ID' and the random slopes terms) was established using a likelihood ratio test. *P*-values for the individual effects (p_{mcmc}) were based on Markov Chain Monte Carlo sampling (Baayen, 2008).

To test the effect of season on $\delta^{13}C$ and $\delta^{15}N$ ratios in both ape species, we ran four separate post hoc GLMMs and checked the assumptions in the same manner as outlined in the two previous models outlined above.

Results and discussion

Floral baseline

While the baseline $\delta^{13}C$ values at Loango are comparable with most other great ape sites, the $\delta^{15}N$ baseline values appear to be rather site specific. The mean plant $\delta^{15}N$ value of 3.3‰ (±2.5‰, 1σ) for Loango was ~2‰ lower than those calculated from the Congo Basin forests and Taï National Park (Ituri: 5.4‰ ± 1.8‰, 1σ; Salonga: 5.6‰ ± 1.3‰, 1σ; Taï: 4.9‰ ± 1.7‰, 1σ), but higher than in Bwindi (2.2‰ ± 2.7‰) and quite similar to the mean value of 3.8‰ ± 1.6‰ documented in Kibale National Park, Uganda (Carter, 2001). Thus, Loango herbivores and other consumers can be expected to be lower in $\delta^{15}N$ compared with the data from the Congo Basin or Taï. The Loango floral data showed a high degree of $\delta^{15}N$ variation among the different plant types, with both the lowest and highest $\delta^{15}N$ values extracted from leaves of the preferred gorilla food plants *Baphia* sp. (−1.2‰, the bark value is 0.1‰) and *Cola flavoutina* (13.3‰), respectively (see Fig. 1). *Baphia* can be assigned to the woody legume subfamily (Leguminosae: Papilionoideae). Hence, along with *Gilbertiodendron* sp. (*Leguminosae*) the depletion in ^{15}N is connected to the nodular N-fixing capability of these plants (Ambrose, 1991). Furthermore, we support the notion that some tropical liana species may be capable of nodulation (Gehring and Vlek, 2004; Gehring et al., 2005), as the $\delta^{15}N$ value of the liana *Cissus dinklagei* (0.6‰) is close to that of atmospheric nitrogen. The same liana subspecies also revealed the lowest plant $\delta^{15}N$ value (2.6‰) within the Salonga data set (Oelze et al., 2011). On the other hand, we cannot explain the elevated $\delta^{15}N$ value in the leaves of the shrub *Cola flavoutina* (13.3‰ ± 0.6‰, 1σ, from duplicate analysis), but assume a link to its complex nitrogen pathway, e.g., due to symbiosis with ectomycorrhizal fungal communities (Högberg, 1990).

Mean $\delta^{13}C$ ratio analyzed from bulk plant specimens from Loango including fruits, leaves, stem piths, nuts and flowers (see Table 1) was −30.5‰ (±3.5‰, 1σ, see Table 1). Although the mixed habitat structure typical of the Loango region differs from the evergreen forests of the Congo Basin, the mean $\delta^{13}C$ vegetation value from Loango was remarkably similar to the datasets from the West African closed canopy forest of Taï National Park with a mean of −30.8 (±4.1‰, 1σ) (Fahy et al., 2013), and to the rainforests of Ituri in Democratic Republic of Congo (D.R.C.) with a mean $\delta^{13}C$ value of −31.2‰ (±2.8‰, 1σ) (Cerling et al., 2004a), and Salonga, also located in D.R.C., with a mean of −29.0‰ (±2.7‰, 1σ) (Oelze et al., 2011). In Salonga, fruits from high canopy levels were predominantly sampled for the study of bonobo diet, but the low $\delta^{13}C$ values measured in three terrestrial herbs (−33.7‰ to −36.2‰) suggest that the mean $\delta^{13}C$ value for this evergreen forest should actually be ~1‰ lower and more similar to Ituri, where the sampling focus was dedicated to all canopy layers (Cerling et al., 2004a). Contrary to this, plant samples reported for mountain gorilla habitat in Bwindi, Uganda, largely consisted of leaves and other foliage but still had a relatively high isotopic mean of −28.1‰ (±2.2‰, 1σ) compared with the other sites (Blumenthal et al., 2012). In addition, the terrestrial herbaceous vegetation from the Bwindi mountainous forest had higher $\delta^{13}C$ values (mean = −29.2‰ ± 1.4‰, min = −31.9‰) than those from the

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003

Congo Basin or Loango. We agree with Blumenthal and colleagues (Blumenthal et al., 2012) that the observed baseline difference of ~2–~3‰ in $\delta^{13}C$ between these forests is more likely the result of much less dense canopy cover in mountain gorilla habitats (M. Robbins, Personal observation) than the result of differences in atmospheric $\delta^{13}C$ due to differences in altitude (Körner et al., 1988).

Within the plant food items sampled for this study, we found a significant relationship between $\delta^{13}C$ and canopy height. The full $\delta^{13}C$ model was clearly significant (GLMM likelihood ratio test: $\chi^2 = 30.69$, df = 5, $p < 0.001$), but only the factor 'canopy height' caused the observed variation in $\delta^{13}C$ ($p_{mcmc} = 0.003$), whereas 'plant part unit' had no effect ($p_{mcmc} = 0.329$). Across terrestrial C_3-plant species, photosynthetic plant parts are commonly found to be ^{13}C-depleted by 1–3‰ as compared with non-photosynthetic parts (reviewed in Cernusak et al., 2009). However, according to our model these differences are insignificant compared to the larger differences caused by canopy height. Nevertheless, given that our sample size is small, we cannot exclude that a slight depletion of (herb) leaves as compared to fruits (Cernusak et al., 2009) also contributed to this general pattern. We found the lowest mean $\delta^{13}C$ value of −34.4‰ (±3.0‰, 1σ, $n = 10$) in herbaceous vegetation (<2 m height), whereas high canopy fruits had a much higher mean value of −28.6‰ (±2.2‰, 1σ). We conclude that this pattern is caused by the so called 'canopy effect' and relates to photosynthesis under low light intensity and reduced air circulation in the forests' understory (van der Merwe and Medina, 1991). This stratification in $\delta^{13}C$ by canopy level has been described for several tropical ecosystems (Martinelli et al., 1998; Cerling et al., 2004a; Voigt, 2010; Oelze et al., 2011; Fahy et al., 2013). At Bwindi, Uganda, herbaceous plants had a low mean $\delta^{13}C$ value of −29.2‰ (±1.4‰, 1σ) while fruits had a higher mean $\delta^{13}C$ value of −26.3‰ ± 0.3‰, 1σ (Blumenthal et al., 2012). However, the largest $\delta^{13}C$ differences at Bwindi were found between tree leaves and fruits (Blumenthal et al., 2012). Given that all tree leaves ($n = 24$) were represented by a single tree species (*Myrianthus holstii*), it cannot be fully excluded that leaves of other food tree species would reveal a different $\delta^{13}C$ distribution.

In contrast to $\delta^{13}C$, we found no relationship between $\delta^{15}N$ and canopy height or plant part at Loango (GLMM likelihood ratio test: $\chi^2 = 5.54$, $df = 5$, $p = 0.353$). We conclude that the differences between the food categories consumed by chimpanzees and gorillas at Loango species are mainly driven by $\delta^{13}C$ and canopy effects. The $\delta^{13}C$ differences between terrestrial vegetation and higher canopy fruits were also observed in C_3-food plants consumed by mountain gorillas (Blumenthal et al., 2012) and by bonobos (Oelze et al., 2011), suggesting that this pattern can be found among different habitat types inhabited by great apes.

In lowland forests, herbaceous vegetation grows in higher densities in swamps and seasonally inundated habitats. In these biotopes medium sized trees are often rare, but the understory consisting of Marantaceae and Zingiberaceae plants is commonly covered by high crowned trees (White, 2001). While there are no typical Marantaceae forests at Loango, Marantaceae herbaceous plants commonly grow on the edges of swamps or in seasonally inundated areas. Marantaceae and Zingiberaceae herbs (see Table 1) from Loango averaged at −34.1‰ in $\delta^{13}C$ (±2.8‰ 1σ, $n = 6$) and are thus ~4‰ lower than the mean plant value. Also in Salonga, Marantaceae herbs had a mean of −34.7‰ (±1.3‰ 1σ, $n = 3$) (Oelze et al., 2011) and at Taï National Park in Ivory Coast the lowest $\delta^{13}C$ value within a data set of 99 food plants was found in leaves of the Marantaceae species *Haloplegia* (−39.4‰) (Fahy et al., 2013). This clearly indicates that ^{13}C-depletion in terrestrial herbaceous vegetation can be observed across geographical areas. These plants are crucial to the diet of several primate species including bonobos, chimpanzees and gorillas (Malenky et al., 1994). Given that their isotopic signatures are strikingly different from other plants such as fruits, they can be considered to be particularly useful tracer food items for this and future isotopic studies on extant primates.

Our plant isotopic data may be particularly interesting for future palaeodietary work on the $\delta^{13}C$ ratios in dental tissues of extinct hominin species. Isotopic evidence suggests that most landscapes inhabited by early hominins had low levels (<40%) of woody cover (Cerling et al., 2011). Nevertheless, before four million years ago the few available woodland and forest patches were important foraging grounds for early hominins, which correspondingly reveal C_3-based dietary signatures (Sponheimer et al., 2013). The gradient in plant $\delta^{13}C$ ratios we report here for a mosaic of habitats including forest, savanna and swamps may provide a useful analogy for past environments inhabited by hominins. Wrangham et al. (2009) emphasized the relevance of shallow-water habitats for hominin feeding ecology. They summarize that freshwater was seasonally available at most fossil bearing sites and conclude that aquatic plants such as herbaceous macrophytes, floodplain herbs and particularly their underground storage organs may have been an important seasonal fallback food for hominins. Our data suggests that a refined inspection of the isotopic variation within the C_3-signatures measured in hominin tooth enamel (e.g., by laser ablation mass spectrometry) could provide evidence on whether the C_3-diet mainly consisted of high canopy fruits or of low canopy foods such as terrestrial herbaceous vegetation, which are often associated with aquatic regimes.

Hair isotope data quality

The length and weight of single ape hairs strands allowed for up to nine sequential isotope values (~nine months) in a single chimpanzee sample and ten sequential values (~ten months) in two silverback gorilla samples (Table 2). Reproducibility of stable isotope analyses was tested in 13 hair samples (marked with * in Tables 2 and 3), resulting in an analytic error of <0.1‰ in $\delta^{13}C$ and $\delta^{15}N$ within each duplicate measurement. The quality of hair isotope measurements was controlled by inspecting the atomic C/N ratios. Only hair isotope data with C/N ratios between 2.9 and 3.8 were considered acceptable (O'Connell and Hedges, 1999; O'Connell et al., 2001). As a consequence, 19 gorilla and two chimpanzee hair sections with C/N ratios between 1.6 and 1.9 indicated incomplete sample combustion and were excluded from the dataset (see Tables 2 and 3).

Gorilla and chimpanzee niche separation

The differences in mean $\delta^{13}C$ and $\delta^{15}N$ ratios of the two ape species were found to be highly significant (Welch two sample *t*-tests, $\delta^{13}C$: $t_{21} = -4.632$, $p < 0.001$; $\delta^{15}N$: $t_{24} = -5.81$, $p < 0.001$). Fig. 2 illustrates that isotope values of chimpanzees and gorillas cluster differently, but also show an area of overlap. The differences in isotopic signatures between gorillas and chimpanzees most likely mirror the isotopic characteristics in the predominant food sources (Fig. 1). While the chimpanzee's diet is dominated by plants with higher $\delta^{13}C$ values, which we confirmed to be fruits, the feeding niche of gorillas additionally contains higher proportions of terrestrial vegetation with lower $\delta^{13}C$ values, most likely due to canopy effects (Figs. 1 and 2). In Fig. 3, we combined gorilla and chimpanzee hair isotope ratios from different years and seasons by month. Here, the largest differences between the two ape species in both isotope systems can be observed during the dry season. This niche differentiation between frugivory and folivory in sympatric chimpanzees and gorillas has been described across field sites (e.g., Kuroda, 1992; Tutin and Fernandez, 1993; Rogers et al., 2004; Morgan and Sanz, 2006). At Loango, Head et al. (2011) described

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003

Table 2
Loango gorilla (*Gorilla gorilla gorilla*) $\delta^{13}C$ and $\delta^{15}N$ data measured in single hair sections and bulk hair strands.

Species	Hair ID number	Sample date	Section date	cm start	cm end	Info	C%	N%	Atomic C/N ratio	$\delta^{13}C‰$	$\delta^{15}N‰$	Mean $\delta^{13}C‰$	Mean $\delta^{15}N‰$
Gorilla gorilla	21019	27/03/2009	6-Mar-09	0.0	1.5	Indegho sb	42.8	14.5	3.4	−25.0	4.0	−25.3	4.1
Gorilla gorilla			23-Jan-09	1.5	3.0		43.7	14.5	3.5	−25.6	4.1		
Gorilla gorilla	21019	27/03/2009	13-Feb-09	0.0	3.0	Indegho sb	43.6	14.7	3.5	−25.5	4.3	−25.4	4.3
Gorilla gorilla			21-Nov-08	3.0	6.0		44.2	14.4	3.6	−25.3	4.2		
Gorilla gorilla			4-Jul-08	6.0	13.0		43.5	13.7	3.7	−25.3	4.4		
Gorilla gorilla	21018	02/04/2009	12-Feb-09	0.0	3.5		20.9	14.5	1.7	~~−25.7~~	~~4.2~~	−25.0	3.8
Gorilla gorilla			6-Nov-08	3.5	7.0		20.8	13.5	1.8	~~−25.0~~	~~4.6~~		
Gorilla gorilla			19-Mar-09	0.0	1.0		42.2	14.5	3.4	−24.8	3.8		
Gorilla gorilla			19-Feb-09	1.0	2.0		43.2	14.7	3.4	−25.0	3.8		
Gorilla gorilla			22-Jan-09	2.0	3.0		43.4	14.6	3.5	−25.2	3.9		
Gorilla gorilla	21016	03/04/2009	13-Mar-09	0.0	1.5	sb	21.5	15.0	1.7	~~−24.5~~	~~3.6~~		
Gorilla gorilla			30-Jan-09	1.5	3.0		21.5	14.4	1.7	~~−25.1~~	~~3.6~~		
Gorilla gorilla			12-Dec-08	3.0	5.0		21.6	13.4	1.9	~~−25.6~~	~~3.8~~		
Gorilla gorilla	21017	04/04/2009	n.a	0.0	1.5		20.3	14.4	1.6	~~−24.6~~	~~4.3~~		
Gorilla gorilla	21017	04/04/2009	7-Mar-09	0.0	2.0		21.8	15.1	1.7	~~−24.5~~	~~4.3~~		
Gorilla gorilla			10-Jan-09	2.0	4.0		27.1	18.3	1.7	~~−24.4~~	~~4.1~~		
Gorilla gorilla			15-Nov-08	4.0	6.0		21.7	13.5	1.9	~~−25.0~~	~~4.1~~		
Gorilla gorilla	21014	05/04/2009	n.a	–	–	Atananga sb	44.6	15.0	3.5	−25.1	3.8	−25.1	3.8
*Gorilla gorilla**	21013	27/04/2009	n.a.	–	–		43.4	14.0	3.6	−25.6	4.2	−25.6	4.2
Gorilla gorilla	21012	01/05/2009	n.a.	–	–		42.9	13.7	3.6	−24.8	4.8	−24.8	4.8
Gorilla gorilla	21008	03/05/2009	26-Apr-09	0.0	0.5	Indegho sb	45.3	15.5	3.4	−24.7	3.7	−25.2	3.9
Gorilla gorilla			12-Apr-09	0.5	1.0		45.3	15.5	3.4	−24.6	3.7		
Gorilla gorilla			29-Mar-09	1.0	1.5		45.1	15.6	3.4	−24.8	3.8		
Gorilla gorilla			15-Mar-09	1.5	2.0		44.0	14.5	3.5	−25.0	3.8		
Gorilla gorilla			1-Mar-09	2.0	2.5		45.1	15.4	3.4	−24.9	3.9		
Gorilla gorilla			15-Feb-09	2.5	3.0		45.3	15.4	3.4	−25.0	4.0		
Gorilla gorilla			1-Feb-09	3.0	3.5		47.3	14.4	3.8	−26.2	3.9		
Gorilla gorilla			18-Jan-09	3.5	4.0		43.7	14.9	3.4	−25.4	3.9		
Gorilla gorilla			4-Jan-09	4.0	4.5		42.2	14.0	3.5	−25.7	4.0		
Gorilla gorilla			30-Nov-08	4.5	6.5		44.4	14.1	3.7	−25.7	4.3		
Gorilla gorilla	21009	03/05/2009	5-Apr-09	0.0	2.0	Indegho sb	43.4	14.7	3.4	−25.4	3.8	−25.5	4.2
Gorilla gorilla			8-Feb-09	2.0	4.0		45.2	15.3	3.5	−25.6	4.1		
Gorilla gorilla			14-Dec-08	4.0	6.0		44.9	14.9	3.5	−25.8	4.4		
Gorilla gorilla			2-Nov-08	6.0	8.0		44.7	14.6	3.6	−25.0	4.5		
Gorilla gorilla	21010	12/05/2009	n.a.	–	–		40.4	13.2	3.6	−25.9	4.3	−25.9	4.3
*Gorilla gorilla**	21011	12/05/2009	n.a.	–	–		43.5	14.5	3.5	−25.2	4.0	−25.2	4.0
*Gorilla gorilla**	21007	19/05/2009	28-Apr-09	0.0	1.5		44.3	15.3	3.4	−24.5	3.9	−24.7	3.9
Gorilla gorilla			17-Mar-09	1.5	3.0		43.7	15.1	3.4	−24.8	4.0		
Gorilla gorilla			27-Jan-09	3.0	5.0		44.1	15.2	3.4	−24.7	3.8		
Gorilla gorilla	21006	23/05/2009	2-May-09	1.0	1.5	Indegho sb	21.7	15.4	1.6	~~−24.0~~	~~3.6~~		
Gorilla gorilla			21-Mar-09	1.5	3.0		21.8	15.4	1.7	~~−24.4~~	~~3.6~~		
Gorilla gorilla			31-Jan-09	3.0	5.0		21.5	15.1	1.7	~~−24.7~~	~~4.0~~		
Gorilla gorilla	21006	23/05/2009	9-May-09	0.0	1.0	Indegho sb	21.4	15.1	1.7	~~−25.2~~	~~4.0~~	−25.2	4.4
Gorilla gorilla			11-Apr-09	1.0	2.0		21.8	15.2	1.7	~~−25.4~~	~~4.2~~		
Gorilla gorilla			14-Mar-09	2.0	3.0		21.9	14.9	1.7	~~−25.4~~	~~4.1~~		
Gorilla gorilla			14-Feb-09	3.0	4.0		22.0	15.1	1.7	~~−26.0~~	~~4.2~~		
Gorilla gorilla			17-Jan-09	4.0	5.0		21.7	15.0	1.7	~~−25.6~~	~~4.2~~		
Gorilla gorilla			20-Dec-08	5.0	6.0		45.5	15.2	3.5	−25.4	4.2		
Gorilla gorilla			22-Nov-08	6.0	7.0		44.2	14.6	3.5	−25.4	4.5		
Gorilla gorilla			25-Oct-08	7.0	8.0		43.6	14.3	3.6	−25.4	4.4		
Gorilla gorilla			27-Sep-08	8.0	9.0		43.5	14.4	3.5	−24.9	4.5		
Gorilla gorilla			30-Aug-08	9.0	10.0		42.6	13.9	3.6	−24.9	4.3		
*Gorilla gorilla**	21005	26/05/2009	n.a.	–	–		20.7	14.2	1.7	~~−25.2~~	~~4.3~~		
Gorilla gorilla	22978	12/02/2011	29-Jan-11	0.0	1.0		18.3	6.3	3.4	−25.1	5.2	−24.9	4.9
Gorilla gorilla			1-Jan-11	1.0	2.0		18.3	6.3	3.4	−24.9	5.0		
Gorilla gorilla			4-Dec-10	2.0	3.0		44.0	14.6	3.5	−25.0	4.7		
Gorilla gorilla			6-Nov-10	3.0	4.0		44.0	14.5	3.5	−24.6	4.6		
Gorilla gorilla	22979	10/03/2011	n.a.	0.0	0.5		118.9	30.4	4.6	~~−23.0~~	~~6.1~~	−25.7	4.6
Gorilla gorilla			17-Feb-11	0.5	1.0		43.7	14.9	3.4	−25.6	4.5		
Gorilla gorilla			3-Feb-11	1.0	1.5		44.2	14.9	3.5	−25.9	4.7		
Gorilla gorilla			20-Jan-11	1.5	2.0		45.4	15.1	3.5	−25.7	4.5		
Gorilla gorilla			6-Jan-12	2.0	2.5		45.0	15.1	3.5	−25.6	4.8		
Gorilla gorilla			23-Dec-10	2.5	3.0		44.0	14.6	3.5	−25.7	4.6		
Gorilla gorilla			2-Dec-10	3.0	4.0		43.4	14.2	3.6	−25.8	4.6		
Gorilla gorilla	22980	27/04/2011	13-Apr-11	0.0	1.0	Indegho sb	39.3	13.4	3.4	−25.6	4.2	−25.8	4.3
Gorilla gorilla			16-Mar-11	1.0	2.0		45.0	15.2	3.4	−25.8	4.1		
Gorilla gorilla			16-Feb-11	2.0	3.0		44.4	14.9	3.5	−26.1	4.3		
Gorilla gorilla			19-Jan-11	3.0	4.0		44.4	14.7	3.5	−26.1	4.5		
Gorilla gorilla			22-Dec-10	4.0	5.0		43.9	14.2	3.6	−25.9	4.6		
Gorilla gorilla			29-Sep-10	5.0	10.0		44.0	13.8	3.7	−25.3	4.0		
*Gorilla gorilla**	22981	28/04/2011	14-Apr-11	0.0	1.0	Atananga sb	44.5	15.2	3.4	−24.5	3.6	−24.9	3.9
Gorilla gorilla			17-Mar-11	1.0	2.0		44.5	15.1	3.4	−24.7	3.7		
Gorilla gorilla			17-Feb-11	2.0	3.0		46.3	15.4	3.5	−24.9	3.9		
Gorilla gorilla			20-Jan-11	3.0	4.0		46.2	15.4	3.5	−25.0	4.0		

(*continued on next page*)

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003

Table 2 (*continued*)

Species	Hair ID number	Sample date	Section date	cm start	cm end	Info	C%	N%	Atomic C/N ratio	$\delta^{13}C_{‰}$	$\delta^{15}N_{‰}$	Mean $\delta^{13}C_{‰}$	Mean $\delta^{15}N_{‰}$
Gorilla gorilla			23-Dec-10	4.0	5.0		45.1	14.7	3.6	−25.2	4.3		
Gorilla gorilla			25-Nov-10	5.0	6.0		44.7	14.0	3.7	−25.1	3.8		
Gorilla gorilla			28-Oct-10	6.0	7.0		44.3	13.8	3.8	−25.0	3.5		
Gorilla gorilla	27234	03/08/2011	20-Jul-11	0.0	1.0	sb	43.1	13.4	3.7	−24.7	3.4	−25.8	3.5
Gorilla gorilla			22-Jun-11	1.0	2.0		43.1	13.9	3.6	−25.1	3.4		
Gorilla gorilla			25-May-11	2.0	3.0		43.0	13.2	3.8	−25.1	3.6		
Gorilla gorilla			27-Apr-11	3.0	4.0		42.2	13.2	3.7	−26.0	3.6		
Gorilla gorilla			30-Mar-11	4.0	5.0		40.1	12.1	3.8	−26.6	3.4		
Gorilla gorilla			16-Feb-11	5.0	7.0		41.4	12.9	3.8	−27.1	3.7		
										$n = 64$		**$n = 17$**	
										Mean		**−25.3**	**−25.3**
										Std (1σ)		**0.5**	**0.4**
										Min		**−27.1**	**−25.9**
										Max		**−24.5**	**−24.7**

The mean date of each hair section is calculated with hair growth rates of 1 cm/30 days and under the assumption that the sampling date corresponds to the hair roots (sb = silverback).

Table 3
Loango chimpanzee (*Pan troglodytes troglodytes*) $\delta^{13}C$ and $\delta^{15}N$ data measured in single hair sections and bulk hair strands.

Species	Hair ID number	Sample date	Section date	cm start	cm end	Info	C%	N%	Atomic C/N ratio	$\delta^{13}C_{‰}$	$\delta^{15}N_{‰}$	Mean $\delta^{13}C_{‰}$	Mean $\delta^{15}N_{‰}$
Pan troglodytes	21022	02/04/2009	12-Mar-09	0.5	1.0		43.2	14.4	3.5	−24.2	4.8	−24.3	4.8
Pan troglodytes			26-Feb-09	1.0	1.5		44.8	14.8	3.5	−24.2	4.8		
Pan troglodytes			12-Feb-09	1.5	2.0		44.8	14.8	3.5	−24.0	4.9		
Pan troglodytes			22-Jan-09	2.0	3.0		45.1	14.6	3.6	−24.3	4.9		
Pan troglodytes			18-Dec-08	3.0	4.5		45.7	14.8	3.6	−24.7	4.9		
*Pan troglodytes**	21021	02/05/2009	n.a.	–	–		42.8	13.9	3.6	−24.1	5.1	−24.1	5.1
Pan troglodytes	21032	22/09/2009	1-Sep-09	0.0	1.5	Nest 1	45.0	15.0	3.5	−24.7	4.3	−24.8	4.4
Pan troglodytes			21-Jul-09	1.5	3.0		59.8	20.0	3.5	−24.8	4.5		
Pan troglodytes	21033	22/09/2009	n.a.	–	–	Nest 2	49.4	16.4	3.5	−25.0	4.1	−24.7	5.0
Pan troglodytes	21031	28/09/2009	14-Sep-09	0.0	1.0		44.4	14.8	3.5	−24.4	5.5		
Pan troglodytes			17-Aug-09	1.0	2.0		45.0	15.2	3.5	−24.6	5.1		
Pan troglodytes			20-Jul-09	2.0	3.0		44.8	15.0	3.5	−24.7	5.0		
Pan troglodytes			22-Jun-09	3.0	4.0		45.0	14.9	3.5	−24.6	5.5		
Pan troglodytes	21030	29/09/2009	15-Sep-09	0.0	1.0		44.1	14.2	3.6	−24.3	5.4	−24.6	5.3
Pan troglodytes			18-Aug-09	1.0	2.0		44.9	15.3	3.4	−24.3	5.6		
Pan troglodytes			21-Jul-09	2.0	3.0		44.1	14.8	3.5	−24.6	5.4		
Pan troglodytes			9-Jun-09	3.0	5.0		43.9	14.7	3.5	−24.9	5.0		
Pan troglodytes	21029	19/10/2009	5-Oct-09	0.0	1.0		45.3	15.0	3.5	−24.4	4.5	−24.4	5.0
Pan troglodytes			7-Sep-09	1.0	2.0		45.3	15.4	3.4	−24.5	4.8		
Pan troglodytes			10-Aug-09	2.0	3.0		44.8	15.1	3.5	−24.4	5.3		
Pan troglodytes			29-Jun-09	3.0	5.0		45.8	15.3	3.5	−24.2	5.2		
Pan troglodytes	21024	01/11/2009	25-Oct-09	0.0	0.5	Nest 1	44.3	14.5	3.6	−24.6	4.3	−24.6	4.6
Pan troglodytes			11-Oct-09	0.5	1.0		45.6	14.9	3.6	−24.6	4.2		
Pan troglodytes			27-Sep-09	1.0	1.5		45.6	14.7	3.6	−24.7	4.6		
Pan troglodytes			13-Sep-09	1.5	2.0		45.4	14.5	3.7	−24.5	4.6		
Pan troglodytes			30-Aug-09	2.0	2.5		45.1	14.3	3.7	−24.6	4.4		
Pan troglodytes			16-Aug-09	2.5	3.0		45.5	14.3	3.7	−24.5	4.5		
Pan troglodytes			2-Aug-09	3.0	3.5		45.0	14.1	3.7	−24.6	4.6		
Pan troglodytes			19-Jul-09	3.5	4.0		45.1	14.1	3.7	−24.8	4.9		
Pan troglodytes			28-Jun-09	4.0	5.0		45.4	14.1	3.8	−24.5	5.1		
Pan troglodytes	21025	01/11/2009	18-Oct-09	0.0	1.0	Nest 2	44.6	14.8	3.5	−24.6	4.1	−24.7	4.5
Pan troglodytes			20-Sep-09	1.0	2.0		44.4	15.0	3.5	−24.8	4.2		
Pan troglodytes			23-Aug-09	2.0	3.0		44.0	15.1	3.4	−24.7	4.4		
Pan troglodytes			26-Jul-09	3.0	4.0		44.2	15.4	3.4	−24.7	4.8		
Pan troglodytes			14-Jun-09	4.0	6.0		44.4	15.9	3.3	−24.6	4.8		
Pan troglodytes	21026	01/11/2009	n.a.	–	–	Nest 3	43.4	13.9	3.7	−23.4	5.1	−23.4	5.1
*Pan troglodytes**	21027	01/11/2009	n.a.	–	–	Nest 4	43.4	13.9	3.7	−25.6	5.4	−25.6	5.4
Pan troglodytes	21028	01/11/2009	11-Oct-09	0.0	1.5	Nest 5	43.5	13.7	3.7	−25.7	4.3	−24.9	4.8
Pan troglodytes			30-Aug-09	1.5	3.0		43.6	14.1	3.6	−24.7	4.8		
Pan troglodytes			31-May-09	4.0	7.0		45.0	14.9	3.5	−24.4	5.3		
*Pan troglodytes**	21023	02/11/2009	n.a.	–	–		44.3	14.4	3.6	−24.6	5.2	−24.6	5.2
*Pan troglodytes**	27233	30/07/2011	16-Jul-11	0.0	1.0		47.1	15.7	3.5	−24.1	5.2	−24.8	5.9
Pan troglodytes			18-Jun-11	1.0	2.0		44.3	14.6	3.5	−24.6	5.8		
Pan troglodytes			21-May-11	2.0	3.0		44.3	13.8	3.7	−24.6	6.2		
Pan troglodytes			23-Apr-11	3.0	4.0		41.7	13.1	3.7	−25.0	6.2		
Pan troglodytes			26-Mar-11	4.0	5.0		43.5	13.4	3.8	−25.4	5.9		
Pan troglodytes			26-Feb-11	5.0	6.0		42.2	12.1	4.1	~~−25.1~~	~~5.8~~		
Pan troglodytes			15-Jan-11	6.0	8.0		47.4	13.5	4.1	~~−24.7~~	~~5.5~~		
										$n = 46$		**$n = 13$**	
										Mean		**−24.6**	**5.0**
										Std (1σ)		**0.4**	**0.5**
										Min		**−25.7**	**4.1**
										Max		**−23.4**	**6.2**

The mean date of each hair section is calculated with hair growth rates of 1 cm/30 days and the sampling date corresponding to the hair roots.

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003

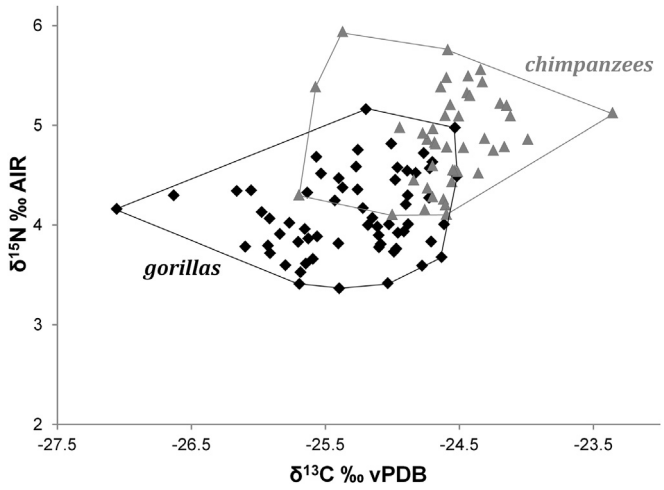

Figure 2. Distribution and overlap of $\delta^{13}C$ and $\delta^{15}N$ data values measures in bulk hair samples and hair sections of sympatric gorillas and chimpanzees from Loango.

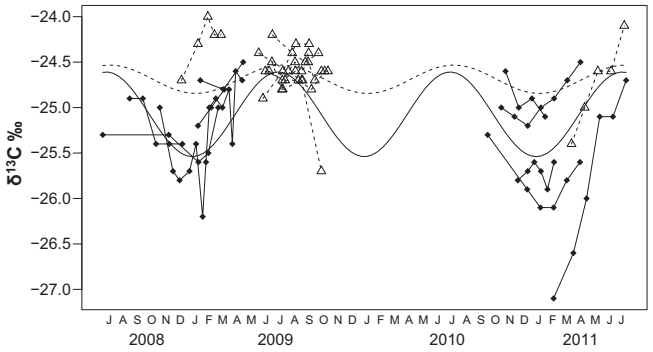

Figure 4. GLMM results for chimpanzees (dashed black line) and gorillas (solid black line) modeling the response of carbon stable isotopes to season. The amplitude of seasonal variation in gorillas is significantly larger than in chimpanzees. Model robustness is indicated as gray lines, representing alternative models each excluding single individual hair samples ($n = 21$). Here, overall model robustness is high and the alternative model lines hardly vary (gorilla) or do not vary (chimpanzee) from the original model.

the chimpanzees as being significantly more frugivorous based on fecal analysis and feeding remains. The data collected over a period of three years revealed that gorillas consumed a variety of herbaceous vegetation (16 species), while chimpanzees only utilized one herbaceous plant species. On the other hand, gorillas ignored lipid rich fruit species, which were almost exclusively eaten by chimpanzees, e.g., *Staudtia gabonensis*. Although gorillas and chimpanzees seem to have successfully reduced feeding competition, some isotopic and thus dietary overlap between both species can be observed. Isotopic similarity in carbon and nitrogen and thus dietary overlap between chimpanzees and gorilla is highest at the very end of the dry season and the first weeks of the rainy season (September/October). Here, the $\delta^{13}C$ and $\delta^{15}N$ values of several chimpanzee and gorilla hair sections clearly overlap. Head et al. (2011) showed seasonal dietary overlap between chimpanzees and gorillas ranging from 0.3% to 69.0%, with highest overlap rates in the peak of the rainy season (December/January). As the dataset is imbalanced during this particular time frame, we cannot further investigate dietary overlap in the mid rainy season with our present data (Fig. 3). Nevertheless, dietary evidence of niche differentiation and dietary overlap obtained from isotopic ratios of hair are well in line with indirect measures of great ape feeding ecology available for the field site of Loango, and also with long-term direct observations from several sites across Africa.

The fact that the niche differentiation between two hominid species within a C_3-plant dominated ecosystem is also expressed in the respective $\delta^{13}C$ signatures of body tissue is relevant for future palaeodietary reconstruction of folivory and frugivory in sympatric fossil primate species. Several early hominin species fed in environments dominated by C_3-vegetation (Sponheimer et al., 2013). Future studies could investigate whether these diets were more gorilla-like and thus more opportunistically shifting between folivory and frugivory or if their feeding repertoire rather resembled the persistent frugivory of present day chimpanzees.

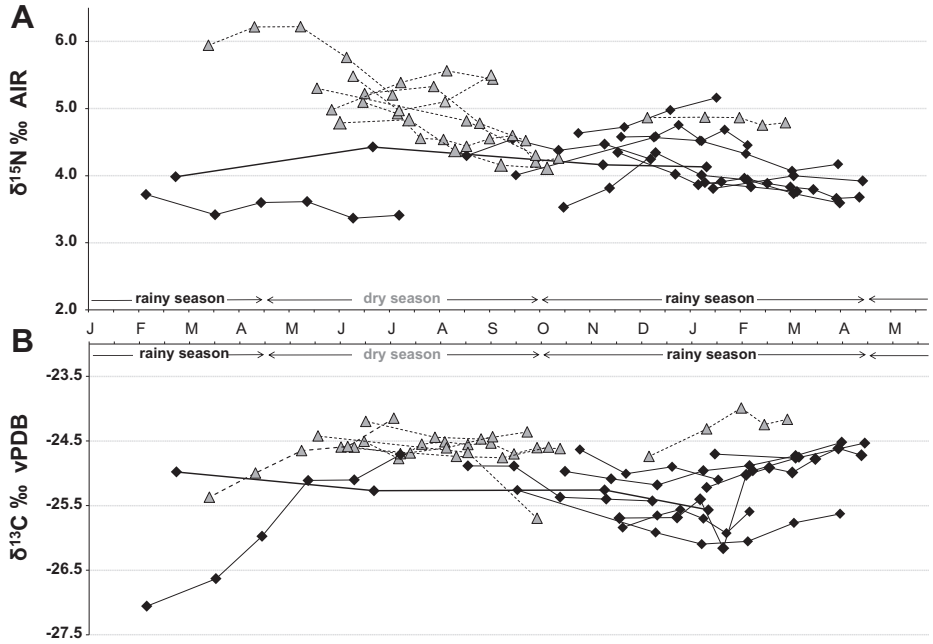

Figure 3. Seasonal nitrogen (A) and carbon (B) isotopic variation in gorilla (black diamonds) and chimpanzee (gray triangles) hair combined from the field seasons 2008/2009 and 2010/2011. Isotopic overlap in carbon and nitrogen is highest during the transition from dry season to rainy season.

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003

Great ape seasonality

We predicted that the pronounced differences in precipitation and food availability in Loango would have an effect on the stable isotope ratios of hair in both great ape species throughout the year. This assumption was supported by our statistical analysis, with which we tested if isotope ratios in chimpanzee and gorilla hair sections were influenced by season in different ways.

Overall, the full $\delta^{13}C$ model was clearly significant as compared with the null model (likelihood ratio test: $\chi^2 = 14.29$, df = 4, $p < 0.006$), and there is a tendency that the interaction between species and season has some effect ($p_{mcmc} = 0.057$). The model results (curved lines) for $\delta^{13}C$ are illustrated in Fig. 4 and suggest that chimpanzees and gorillas differ as to the intensity with which their isotope ratios respond to season. While the $\delta^{13}C$-variability in the gorilla model (solid line) follows pronounced seasonal shifts, the chimpanzee model (dashed line) indicates less variation in $\delta^{13}C$ throughout the year. The post hoc $\delta^{13}C$ model we ran for gorillas was highly significant (likelihood ratio test: $\chi^2 = 11.53$, df = 2, $p = 0.003$) and showed that the relationship between $\delta^{13}C$ and the fixed effect of season was significant ($p_{mcmc} = 0.001$). In chimpanzees, the $\delta^{13}C$ values were not affected by season (likelihood ratio test: $\chi^2 = 0.58$, $df = 2$, $p = 0.745$), but isotopic variation differed between individual hair strands. These observations for $\delta^{13}C$ are best explained by a constant reliance on higher canopy fruits in chimpanzees and changing proportions of herbaceous vegetation versus higher canopy resources in gorillas. In gorillas, the model predicts the lowest $\delta^{13}C$ values (and thus presumably the highest degree of herbaceous vegetation) during the middle of the rainy season. However, the fruit availability index for gorillas based on phenology recordings at Loango National Park (Head et al., 2011) suggested a peak in fruit availability in December and January. More evidence from direct observations on the feeding ecology of this gorilla population may help to disentangle these slightly contradicting findings.

Blumenthal et al. (2012) recently explored the potential of using stable isotope analysis in fresh feces to describe short term shifts in fruit consumption among mountain gorillas. However, while this approach may be an analytical tool in habituated communities that can be followed (and also directly observed) on a daily basis, this method may not be useful for studying unhabituated apes, unless time- and cost intensive genetic methods are used for fecal identification. We propose that isotope analysis in hair is an innovative and cost-effective approach to assess shifts in folivory and frugivory in unhabituated gorillas, mainly because hair samples can be easily obtained from gorilla ground nests and hair length allows for up to ten months of sequential isotope data from the same individual.

The results of the $\delta^{15}N$ model reveal a quite distinct seasonal pattern (Fig. 5). The full $\delta^{15}N$ model for both species was highly significant ($\chi^2 = 55.09$, $df = 6$, $p < 0.001$) and the interaction between species and season was clearly significant as well ($p_{mcmc} < 0.001$). The seasonal patterns of both species are opposite each other and the amplitude of the gorilla model line (solid) is less intense than the amplitude of the chimpanzee model line (dashed). The post-hoc $\delta^{15}N$ model for gorillas was not significant ($\chi^2 = 5.38$, $df = 2$, $p = 0.067$), whereas in chimpanzees variation in $\delta^{15}N$ was highly significant ($\chi^2 = 33.86$, $df = 4$, $p < 0.001$) and clearly related to season ($p_{mcmc} < 0.001$). In the Loango chimpanzees, the highest $\delta^{15}N$ values are measured in hair sections representing the very early dry season and a trend of decreasing $\delta^{15}N$ values towards the end of the dry season can be observed across several individuals. Given that chimpanzees are principally frugivorous, it appears likely that this variation in $\delta^{15}N$ is caused by the consumption of specific ^{15}N-enriched plants during the first weeks of the dry season. In a previous study (Head et al., 2011), seeds of the fatty fruit *Staudtia gabonensis* were found in 68% of all chimpanzee feces

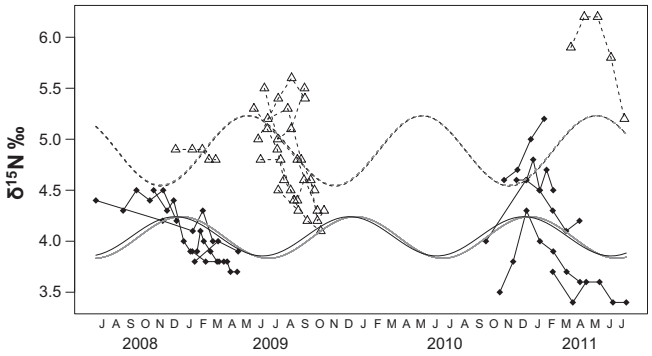

Figure 5. GLMM results for chimpanzees (dashed black line) and gorillas (solid black line) modeling the response of nitrogen stable isotopes to season. In this model all $\delta^{15}N$ values needed to be log transformed; the actual data ranges from ~3‰ to 6‰ (see Figure 3). The seasonal $\delta^{15}N$ response in chimpanzees is significantly larger than in gorillas. Model robustness is very high and indicated as grey lines; the alternative model lines hardly vary (gorilla) or do not vary (chimpanzee) from the original model.

collected during the dry season, implying that this fruit is particularly important to the dietary adaptation of the Loango chimpanzees at this time of the year. We found that *Staudtia gabonensis* has the highest ^{15}N-signature (4.7‰) among the most relevant chimpanzee plant foods and the consumption of these fruits is likely reflected in sequential segments of hair. Other chimpanzee fruits with comparable isotopic 'properties' include *Dacryodes normandii* and *Garcinia* sp. (see Table 1), but they seem less relevant to the chimpanzees diet (Head et al., 2011). We conclude that seasonal dependence on fruits of *Staudtia gabonensis* led to the observed shifts in chimpanzee hair $\delta^{15}N$ values. The fact that gorillas did not show a similar $\delta^{15}N$ pattern may support the previous observation that gorillas at Loango avoid fat rich fruits like *Staudtia gabonensis* (Head et al., 2011).

While $\delta^{15}N$ cannot be detected in fossilized specimens, the $\delta^{13}C$ ratios have been successfully measured in a large number of fossil hominin teeth (Sponheimer et al., 2013). Although they differ in their temporal scaling, hair and tooth enamel have an incremental nature in common and continuously retain the temporal aspects of in vivo dietary signatures. Laser ablation isotope analysis along the tooth's growth trajectory has the potential to unravel temporal dietary variation. Even though the accurate timing of tooth enamel increments (perikymata) remains difficult and partial isotopic overprinting during enamel maturation may dampen the original signal, the sequence of before and after can be captured and may indicate seasonality (Lee-Thorp et al., 2010 and references therein). Thus far, two studies have presented such seasonal isotopic data that revealed variation of up to 7‰ $\delta^{13}C$ in *Australopithecus africanus* and *Paranthropous robustus*, indicating shifts between C_3 and C_4-based foods (Sponheimer et al., 2006b; Lee-Thorp et al., 2010). We suggest that seasonal shifts could also be detected in fossil primates that predominantly foraged in C_3-habitats, such as *Ardipithecus ramidus* and *A. sediba* (White et al., 2009; Henry et al., 2012). Isotopic variation of several ‰ would indicate shifting proportions of fruits versus foliage, particularly herbaceous vegetation, and could thus provide evidence on fallback food selection.

Conclusions

We evaluated the isotope ecology of sympatric great apes living in a mosaic habitat by analyzing the $\delta^{13}C$ and $\delta^{15}N$ ratios in food plants and ape hair samples from Loango National Park. The significant differences in $\delta^{13}C$ we found between terrestrial herbaceous vegetation and high canopy fruits were related to canopy effects. Thus, we could show that folivory on herbaceous vegetation

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003

and frugivory can be distinguished by means of $\delta^{13}C$. The gorilla hair isotope values revealed evidence for the consumption of significant amounts of terrestrial herbaceous plants, while chimpanzee isotope values indicated that fruits were the main dietary resource. Hence, our isotopic data found a niche differentiation of these sympatric apes, yet also supported the previously reported dietary overlap between the Loango chimpanzees and gorillas. Using sequential hair sections we reconstructed seasonal isotopic variation over the course of seasons and several years. The amount of dietary overlap between chimpanzees and gorillas appeared to vary with time, as previously shown using fecal analysis (Head et al., 2011). Compared with chimpanzees, gorillas revealed a much stronger variation in $\delta^{13}C$ in response to season, most likely due to varying proportions of herbaceous vegetation versus fruits in different seasons. On the other hand, the highly significant shifts in $\delta^{15}N$ values of chimpanzees were most likely connected to the consumption of ^{15}N-enriched fruit like *Staudtia gabonensis* during the early dry season, which was supported by previous indirect evidence (Head et al., 2011).

Our results have several implications for palaeoanthropology. First, we identified C_3-herbaceous vegetation to be a diagnostic food item for future palaeodietary studies. Particularly the relevance of aquatic herbs as a seasonal fallback food could be investigated in fossil specimens using $\delta^{13}C$ analysis. Second, we argue that niche partitioning can be identified in sympatric hominin species that predominantly fed in C_3-habitats. Thirdly, we suggest that, similar to the sequential analysis of hair, refined sequential analysis of tooth enamel using laser ablation IRMS may provide novel insights into the inter- and intra-individual seasonal dietary variation of fossil hominins that foraged in C_3-habitats.

In his recent review, Sandberg et al. (2012) has emphasized that one of the main advantages of isotopic investigations in primatology lies in the fact that dietary information can be obtained from wild populations without time and financially demanding habituation programs or long term field work. Additionally, habituation may also have negative effects on ape populations, such as disease transmission and the loss of fear towards humans and thus increased vulnerability to poaching (reviewed by Fedigan, 2010). Here, we demonstrate that isotope analysis is a useful method for dietary reconstruction, which allows the investigation of niche separation and seasonality in sympatric apes. At this rather early stage of isotopic research on unhabituated apes, additional evidence from fecal analysis and feeding trails appears particularly useful in aiding plant sample collection and the interpretations of isotopic data. However, we found that pronounced differences in feeding niche (frugivory versus folivory of herbaceous plants) and also seasonal shifts between these food categories can be detected by means of stable isotope analysis. Thus, studying the isotope ecology of great apes could provide a time and thus cost effective alternative to direct observations, at least for some aspects of primate feeding ecology.

Acknowledgments

We thank the Agence Nationale des Parcs Nationaux (ANPN), the Centre National de la Recherche Scientifique et Technique (CENAREST) and the Institut de Recherche en Ecology Tropicale (IRET) of Gabon for their collaboration and for permission to conduct our research in Loango National Park. We thank the field assistants of the Loango Ape Project for assistance during sample collection and Sven Steinbrenner for technical support during isotope analysis. Colleen Stephens, Roger Mundry and Jessica Junker are acknowledged for their statistical advice and support. Finally we thank the editor and the two anonymous reviewers for providing constructive comments to an earlier version of the manuscript. This project was supported by the Max Planck Society, and by the ANPN, Africa's Eden and WCS staff with logistical support in Gabon.

References

Ambrose, S.H., 1991. Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. J. Archaeol. Sci. 18, 293–317.
Ambrose, S.H., Norr, L., 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert, J.B., Grupe, G. (Eds.), Prehistoric Human Bone: Archaeology at the Molecular Level. Springer-Verlag, New York, pp. 1–37.
Auerswald, K., Rossmann, A., Schäufele, R., Schwertl, M., Monahan, F.J., Schnyder, H., 2011. Does natural weathering change the stable isotope composition (^{2}H, ^{13}C, ^{15}N, ^{18}O and ^{34}S) of cattle hair? Rapid Commun. Mass Sp. 25, 3741–3748.
Baayen, R.H., 2008. Analyzing Linguistic Data. Cambridge University Press, Cambridge.
Baayen, R.H., 2011. languageR: data sets and functions with 'analyzing linguistic data: a practical introduction to statistics'. R Package Version 1.4 Ed.
Bates, D., Maechler, M., Bolker, B., 2012. lme4: Linear mixed-effects models using S4 classes. R Package Version 0.999999-0.
Blumenthal, S.A., Chritz, K.L., Rothman, J.M., Cerling, T.E., 2012. Detecting intra-annual dietary variability in wild mountain gorillas by stable isotope analysis of feces. Proc. Natl. Acad. Sci. 109, 21277–21282.
Boesch, C., Head, J., Tagg, N., Arandjelovic, M., Vigilant, L., Robbins, M., 2007. Fatal chimpanzee attack in Loango National Park. Gabon. Int. J. Primatol. 28, 1025–1034.
Boesch, C., Head, J., Robbins, M.M., 2009. Complex tool sets for honey extraction among chimpanzees in Loango National Park. Gabon. J. Hum. Evol. 56, 560–569.
Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H., White, J.S.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24, 127–135.
Carter, M.L., 2001. Sensitivity of stable isotopes (^{13}C, ^{15}N and ^{18}O) in bone to dietary specialization and niche separation among sympatric primates in Kibale National Park, Uganda. Ph.D. Dissertation, University of Chicago.
Cerling, T.E., Viehl, K., 2004. Seasonal diet changes of the forest hog (*Hylochoerus meinertzhageni* Thomas) based on the carbon isotopic composition of hair. Afr. J. Ecol. 42, 88–92.
Cerling, T.E., Hart, J.A., Hart, T.B., 2004a. Stable isotope ecology of the Ituri Forest. Oecologia 138, 5–12.
Cerling, T.E., Passey, B.H., Ayliffe, L.K., Cook, C.S., Ehleringer, J.R., Harris, J.M., Dhidha, M.B., Kasiki, S.M., 2004b. Orphans' tales: seasonal dietary changes in elephants from Tsavo National Park, Kenya. Palaeogeogr. Palaeoclimatol. Palaeoecol. 206, 367–376.
Cerling, T.E., Wittemyer, G., Ehleringer, J.R., Remien, C.H., Douglas-Hamilton, I., 2009. History of Animals using Isotope Records (HAIR): a 6-year dietary history of one family of African elephants. Proc. Natl. Acad. Sci. 106, 8093–8100.
Cerling, T.E., Wynn, J.G., Andanje, S.A., Bird, M.I., Korir, D.K., Levion, N.E., Macharia, A.N., Quade, J., Remien, C.H., 2011. Woody cover and hominin environments in the past 6 million years. Nature 476, 51–56.
Cernusak, L.A., Tcherkez, G., Keitel, C., Cornwell, W.K., Santiago, L.S., Knohl, A., Barbour, M.M., Williams, D.G., Reich, P.B., Ellsworth, D.S., Dawson, T.E., Griffiths, H.G., Farquhar, G.D., Ian, J., Wright, I.J., 2009. Why are non-photosynthetic tissues generally 13C enriched compared with leaves in C3 plants? Review and synthesis of current hypotheses. Funct. Plant Biol. 36, 199–213.
Constantino, P.J., Wright, B.W., 2009. The importance of fallback foods in primate ecology and evolution. Am. J. Phys. Anthropol. 140, 599–602.
Doran-Sheehy, D., Mongo, P., Lodwick, J., Conklin-Brittain, N.L., 2009. Male and female western gorilla diet: Preferred foods, use of fallback resources, and implications for ape versus old world monkey foraging strategies. Am. J. Phys. Anthropol. 140, 727–738.
Fahy, G.E., Richards, M., Riedel, J., Hublin, J.-J., Boesch, C., 2013. Stable isotope evidence of meat eating and hunting specialization in adult male chimpanzees. Proc. Natl. Acad. Sci. 110, 5829–5833.
Fedigan, L.M., 2010. Ethical issues faced by field primatologists: asking the relevant questions. Am. J. Primatol. 72, 754–771.
Field, A., 2005. Discovering Statistics Using SPSS. Sage Publications, London.
Furuichi, T., Inagaki, H., Angoue-Ovono, S., 1997. Population density of chimpanzees and gorillas in the Petit Loango Reserve, Gabon: Employing a new method to distinguish between nests of the two species. Int. J. Primatol. 18, 1029–1046.
Gehring, C., Vlek, P.L.G., 2004. Limitations of the ^{15}N natural abundance method for estimating biological nitrogen fixation in Amazonian forest legumes. Basic Appl. Ecol. 5, 567–580.
Gehring, C., Vlek, P.L.G., de Souza, L.A.G., Denich, M., 2005. Biological nitrogen fixation in secondary regrowth and mature rainforest of central Amazonia. Agr. Ecosyst. Environ. 111, 237–252.
Head, J., Boesch, C., Makaga, L., Robbins, M.M., 2011. Sympatric chimpanzees and gorillas in Loango National Park, Gabon: Dietary composition, seasonal changes and inter-site comparisons. Int. J. Primatol. 32, 755–775.
Head, J.S., Robbins, M.M., Mundry, R., Makaga, L., Boesch, C., 2012. Remote video-camera traps measure habitat use and competitive exclusion among

sympatric chimpanzee, gorilla and elephant in Loango National Park, Gabon. J. Trop. Ecol. 28, 571–583.
Heaton, T.H.E., 1987. The $^{15}N/^{14}N$ ratios of plants in South Africa and Namibia: relationship to climate and coastal/saline environments. Oecologia 74, 236–246.
Henry, A.G., Ungar, P.S., Passey, B.H., Sponheimer, M., Rossouw, L., Bamford, M., Sandberg, P., de Ruiter, D.J., Berger, L., 2012. The diet of *Australopithecus sediba*. Nature. http://dx.doi.org/10.1038/nature11185.
Högberg, P., 1990. ^{15}N natural abundance as a possible marker of the ectomycorrhizal habit of trees in mixed African woodlands. New Phytol. 115, 483–486.
Huelsemann, F., Flenker, U., Koehler, K., Schaenzer, W., 2009. Effect of a controlled dietary change on carbon and nitrogen stable isotope ratios of human hair. Rapid Commun. Mass Sp. 23, 2448–2454.
Jim, S., Ambrose, S.H., Evershed, R.P., 2004. Stable carbon isotopic evidence for differences in the dietary origin of bone cholesterol, collagen and apatite: Implications for their use in palaeodietary reconstruction. Geochim. Cosmochim. Ac. 68, 61–72.
Junker, J., Blake, S., Boesch, C., Campbell, G., Toit, L. du, Duvall, C., Ekobo, A., Etoga, G., Galat-Luong, A., Gamys, J., Ganas-Swaray, J., Gatti, S., Ghiurghi, A., Granier, N., Hart, J., Head, J., Herbinger, I., Hicks, T.C., Huijbregts, B., Imong, I.S., Kuempel, N., Lahm, S., Lindsell, J., Maisels, F., McLennan, M., Martinez, L., Morgan, B., Morgan, D., Mulindahabi, F., Mundry, R., N'Goran, K.P., Normand, E., Ntongho, A., Okon, D.T., Petre, C.-A., Plumptre, A., Rainey, H., Regnaut, S., Sanz, C., Stokes, E., Tondossama, A., Tranquilli, S., Sunderland-Groves, J., Walsh, P., Warren, Y., Williamson, E.A., Kuehl, H.S., 2012. Recent decline in suitable environmental conditions for African great apes. Divers. Distrib. 18, 1077–1091.
Körner, C., Farquhar, G.D., Roksandic, Z., 1988. A global survey of carbon isotope discrimination in plants from high altitude. Oecologia 74, 623–632.
Kuroda, S., 1992. Ecological interspecies relationships between gorillas and chimpanzees in the Ndoki-Nouabalé Reserve, Northern Congo. In: Itoiywa, N., Sugiyama, Y., Sackett, G.P., Thompson, R.K.R. (Eds.), Primate Topics, Behaviour, Ecology and Conservation, Vol 2. University of Tokyo Press, Tokyo, pp. 385–394.
Leakey, M.G., Spoor, F., Dean, M.C., Feibel, C.S., Anton, S.C., Kiarie, C., Leakey, L.N., 2012. New fossils from Koobi Fora in northern Kenya confirm taxonomic diversity in early *Homo*. Nature 488, 201–204.
Lee-Thorp, J.A., Sponheimer, M., Passey, B.H., de Ruiter, D.J., Cerling, T.E., 2010. Stable isotopes in fossil hominin tooth enamel suggest a fundamental dietary shift in the Pliocene. Phil. Trans. R. Soc. B 365, 3389–3396.
Lee-Thorp, J.A., Likius, A., Mackaye, H.T., Vignaud, P., Sponheimer, M., Brunet, M., 2012. Isotopic evidence for an early shift to C4 resources by Pliocene hominins in Chad. Proc. Natl. Acad. Sci. 109, 20369–20372.
Malenky, R.K., Kuroda, S., Vineberg, E.O., Wrangham, R.W., 1994. The significance of terrestrial herbaceous foods for bonobos, chimpanzees, and gorillas. In: Wrangham, R.W., McGrew, W.C., deWaal, F.B.M., Heltne, P.G. (Eds.), Chimpanzee Cultures. Harvard University Press, Cambridge, pp. 59–75.
Marshall, A.J., Wrangham, R.W., 2007. Evolutionary consequences of fallback foods. Int. J. Primatol. 28, 1218–1235.
Martinelli, L.A., Almeida, S., Brown, I.F., Moreira, M.Z., Victoria, R.L., Sternberg, L.S.L., Ferreira, C.A.C., Thomas, W.W., 1998. Stable carbon isotope ratio of tree leaves, boles and fine litter in a tropical forest in Rondônia, Brazil. Oecologia 114, 170–179.
Mekota, A.M., Grupe, G., Ufer, S., Cuntz, U., 2009. Identifying starvation episodes using stable isotopes in hair forensic approach on serial hair analysis. Rechtsmedizin 19, 431–438.
Morgan, B., 2000. Ecology of mammalian frugivores in the Reserve de Faune du Petit Loango, Gabon. Ph.D. Dissertation, Cambridge University.
Morgan, D., Sanz, C., 2006. Chimpanzee feeding ecology and comparisons with sympatric gorillas in the Goualougo Triangle, Republic of Congo. In: Hohmann, G., Robbins, M.M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, pp. 97–122.
Nieuwenhuis, R., Te Grotenhuis, M., Pelzer, B., 2012. influenceME: tools for detecting influential data in mixed effects models. R. Journal 4, 38–47.
O'Connell, T.C., Hedges, R.E.M., 1999. Investigations into the effect of diet on modern human hair isotopic values. Am. J. Phys. Anthropol. 108, 405–429.
O'Connell, T.C., Hedges, R.E.M., Healey, M.A., Simpson, A.H.R.W., 2001. Isotopic comparison of hair, nail and bone: modern analyses. J. Archaeol. Sci. 28, 1247–1255.
Oelze, V.M., Fuller, B.T., Richards, M.P., Fruth, B., Surbeck, M., Hublin, J.-J., Hohmann, G., 2011. Exploring the contribution and significance of animal protein in the diet of bonobos by stable isotope ratio analysis of hair. Proc. Natl. Acad. Sci. 108, 9792–9797.
Pruetz, J.D., 2006. Feeding ecology of savanna chimpanzees (*Pan troglodytes verus*) at Fongoli, Senegal. In: Hohmann, G., Robins, M.M., Boesch, C. (Eds.), Feeding Ecology in Apes and Other Primates. Cambridge University Press, Cambridge, pp. 161–182.
R-Team, 2010. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna.
Rogers, M.E., Abernethy, K., Bermejo, M., Cipolletta, C., Doran, D., McFarland, K., Nishihara, T., Remis, M., Tutin, C.E.G., 2004. Western gorilla diet: A synthesis from six sites. Am. J. Primatol. 64, 173–192.
Sandberg, P.A., Loudon, J.E., Sponheimer, M., 2012. Stable isotope analysis in primatology: a critical review. Am. J. Primatol. 74, 969–989.
Schoeninger, M.J., 2012. Palaeoanthropology: The ancestral dinner table. Nature 487, 42–43.
Schoeninger, M.J., Iwaniec, U.T., Glander, K.E., 1997. Stable isotope ratios indicate diet and habitat use in New World monkeys. Am. J. Phys. Anthropol. 103, 69–83.
Schoeninger, M.J., Iwaniec, U.T., Nash, L.T., 1998. Ecological attributes recorded in stable isotope ratios of arboreal prosimian hair. Oecologia 113, 222–230.
Schoeninger, M.J., Moore, J., Sept, J.M., 1999. Subsistence strategies of two 'savanna' chimpanzee populations: the stable isotope evidence. Am. J. Primatol. 49, 297–314.
Schwertl, M., Auerswald, K., Schnyder, H., 2003. Reconstruction of the isotopic history of animal diets by hair segmental analysis. Rapid Commun. Mass Sp. 17, 1312–1318.
Smith, C.C., Morgan, M.E., Pilbeam, D., 2010. Isotopic ecology and dietary profiles of Liberian chimpanzees. J. Hum. Evol. 58, 43–55.
Sponheimer, M., Loudon, J.E., Codron, D., Howells, M.E., Pruetz, J.D., Codron, J., de Ruiter, D.J., Lee-Thorp, J.A., 2006a. Do 'savanna' chimpanzees consume C-4 resources? J. Hum. Evol. 51, 128–133.
Sponheimer, M., Passey, B.H., de Ruiter, D.J., Guatelli-Steinberg, D., Cerling, T.E., Lee-Thorp, J.A., 2006b. Isotopic evidence for dietary variability in the early hominin *Paranthropus robustus*. Science 314, 980–982.
Sponheimer, M., Alemseged, Z., Cerling, T.E., Grine, F.E., Kimbel, W.H., Leakey, M.G., Lee-Thorp, J.A., Manthi, F.K., Reed, K.E., Wood, B.A., Wynn, J.G., 2013. Isotopic evidence of early hominin diets. Proc. Natl. Acad. Sci. http://dx.doi.org/10.1073/pnas.1222579110.
Stanford, C.B., 2006. The behavioral ecology of sympatric African apes: Implications for understanding fossil hominoid ecology. Primates 47, 91–101.
Stanford, C.B., 2012. Chimpanzees and the behaviour of *Ardipithecus ramidus*. A. Rev. Anthropol. 41, 139–149.
Tieszen, L.L., 1991. Natural variations in the carbon isotope values of plants: implications for archaeology, ecology and paleoecology. J. Archaeol. Sci. 18, 227–248.
Tieszen, L.L., Fagre, T., 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO_2, bone collagen, bioapatite, and soft tissues. In: Lambert, J.B., Grupe, G. (Eds.), Prehistoric Human Bone. Springer, Berlin, pp. 121–155.
Tobin, D.J., 2005. The biogenesis and growth of hair. In: Tobin, D.J. (Ed.), Hair in Toxicology. An Important Bio-monitor. The Royal Society of Chemistry, Cambridge, pp. 3–33.
Tutin, C.E.G., Fernandez, M., 1993. Composition of the diet of chimpanzees and comparisons with that of sympatric lowland gorillas in the Lopé Reserve, Gabon. Am. J. Primatol. 30, 195–211.
Tutin, C.E.G., Fernandez, M.M., Rogers, M.E., Williamson, E.A., McGrew, W., 1991. Foraging profiles of sympatric lowland gorillas and chimpanzees in the Lopé Reserve, Gabon. Phil. Trans. R. Soc. B 334, 179–186.
Ungar, P.S., Sponheimer, M., 2011. The diets of early hominins. Science 334, 190–193.
van der Merwe, N.J., Medina, E., 1991. The canopy effect, carbon isotope ratios and foodwebs in Amazonia. J. Archaeol. Sci. 18, 249–259.
van der Merwe, N.J., Masao, F.T., Bamford, M.K., 2008. Isotopic evidence for contrasting diets of early hominins *Homo habilis* and *Australopithecus boisei* of Tanzania. S. Afr. J. Sci. 104, 153–155.
Voigt, C.C., 2010. Insights into strata use of forest animals using the 'canopy effect'. Biotropica 42, 634–637.
White, L.J.T., 2001. Forest-sananna dynamics and the origins of Marantaceae forest in Central Gabon. In: Weber, W., White, L.J.T., Vedder, A., Naughton-Treves, L. (Eds.), African Rain Forest Ecology and Conservation an Interdisciplinary Perspective. Yale University Press, New Haven, pp. 165–182.
White, T.D., Ambrose, S.H., Suwa, G., Su, D.F., DeGusta, D., Bernor, R.L., Boisserie, J.-R., Brunet, M., Delson, E., Frost, S., Garcia, N., Giaourtsakis, I.X., Haile-Selassie, Y., Howell, F.C., Lehmann, T., Likius, A., Pehlevan, C., Saegusa, H., Semprebon, G., Teaford, M., Vrba, E., 2009. Macrovertebrate paleontology and the Pliocene habitat of *Ardipithecus ramidus*. Science 326 (67), 87–93.
Williams, L.J., White, C.D., Longstaffe, F.J., 2011. Improving stable isotopic interpretations made from human hair through reduction of growth cycle error. Am. J. Phys. Anthropol. 145, 125–136.
Wrangham, R., Cheney, D., Seyfarth, R., Sarmiento, E., 2009. Shallow-water habitats as sources of fallback foods for hominins. Am. J. Phys. Anthropol. 140, 630–642.
Yamagiwa, Y., Basabose, A.K., 2009. Fallback foods and dietary partitioning among *Pan* and *Gorilla*. Am. J. Phys. Anthropol. 104, 739–750.

Please cite this article in press as: Oelze, V.M., et al., Niche differentiation and dietary seasonality among sympatric gorillas and chimpanzees in Loango National Park (Gabon) revealed by stable isotope analysis, Journal of Human Evolution (2013), http://dx.doi.org/10.1016/j.jhevol.2013.10.003