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SHORT COMMUNICATION

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Stable isotope data from bonobo (*Pan paniscus*) faecal samples from the Lomako Forest Reserve, Democratic Republic of the Congo

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1 | INTRODUCTION

Behavioural observations of bonobos (*Pan paniscus*) have revealed that their preferred foods are fruit, yet they consume terrestrial herbaceous vegetation (THV) throughout the year (Badrian, Badrian, & Susman, 1981; Badrian & Malenky, 1984; White, 1992). THV accounts for ~2% of bonobo diets but many bonobo sites are characterised by dense understories, obscuring feeding observations on the ground. THV has been viewed as an important food source for *P. paniscus*, and some evidence suggests that the THV consumed by bonobos bears higher nutritional yields than that consumed by chimpanzees (*Pan troglodytes*) in East Africa (Malenky & Wrangham, 1994).

Stable isotope analysis has been used to supplement feeding observations of nonhuman primates (NHPs) and has helped further our knowledge of the dietary patterns of *Pan* spp. (Loudon, Sandberg, Wrangham, Fahey, & Sponheimer, 2016; Schoeninger, Most, Moore, & Somerville, 2016). The $\delta^{13}C$ and $\delta^{15}N$ values of an animal reflect the foods they ate and are permanently recorded in their tissues or excreta (Sandberg, Loudon, & Sponheimer, 2012). Since NHPs consume plants, botanical $\delta^{13}C$ and $\delta^{15}N$ values aid interpretations of their stable isotope compositions. Most tropical grasses use the C_4 photosynthetic pathway and have tissue $\delta^{13}C$ values between −11‰ and −14‰ (O'Leary, 1988). In contrast, trees, shrubs and temperate grasses follow the C_3 photosynthetic pathway and have $\delta^{13}C$ values averaging about −27‰ and range between −23‰ and −31.5‰. The range of $\delta^{13}C$ values in C_3 plants is in part due to a "canopy effect." Plants growing under dense canopy cover have lower $\delta^{13}C$ values than plants in open areas due to the incorporation of ^{13}C-depleted CO_2 produced by decaying leaves (Medina & Minchin, 1980) and lower light intensities (Ehleringer, Field, Lin, & Kuo, 1986). Plant organs also vary in carbon isotope compositions with nonphotosynthetic organs typically exhibiting higher $\delta^{13}C$ values compared to leaves (Codron et al., 2005). Nitrogen isotopic variation is more difficult to interpret. However, animal tissues are usually ^{15}N-enriched relative to diet and there is a stepwise increase in $\delta^{15}N$ values (~3‰) with each trophic level (Schoeninger & DeNiro, 1984).

We explore the stable isotope ecology of *P. paniscus* through analysis of faeces from the Iyema bonobos inhabiting the Lomako Forest in the Democratic Republic of the Congo (DRC). To contextualise these data, we compare them to stable isotope data from hair (after transformation to hair-equivalent values) collected from other *Pan* communities and to the $\delta^{13}C$ and $\delta^{15}N$ values of available plants from other *Pan* sites. Based on the structural attributes of the Lomako forests, we expect the Iyema community will exhibit lower $\delta^{13}C$ values compared to *Pan* communities living in forests with discontinuous canopies or communities in anthropogenically disturbed forests or open savannahs (Loudon et al., 2016). We predict that the

TABLE 1 $\delta^{13}C$ and $\delta^{15}N$ mean and standard deviations for Lomako plant organs, plants collected at differing canopy levels, and bonobo faecal values after correcting for faecal-diet offsets

Plant organ	*N*	$\delta^{13}C$‰	$\delta^{15}N$‰	Height	*N*	$\delta^{13}C$‰	$\delta^{15}N$‰
Fruit	20	−30.2 ± 2.7	6.1 ± 1.8	Ground (0–2m)	7	−36.8 ± 2.9	6.1 ± 3.0
Leaves	9	−36.7 ± 3.3	4.7 ± 2.8	Mid-canopy (2–10m)	14	−31.6 ± 4.2	6.0 ± 1.6
Pith	5	−33.6 ± 4.0	6.4 ± 3.0	Canopy (>10m)	13	−30.9 ± 3.0	6.0 ± 2.2
Seed	5	−29.1 ± 1.7	6.4 ± 1.8	Liana[a]	5	−28.9 ± 1.5	4.8 ± 2.8
Bonobos[b]	57	−29.2 ± 0.5	5.8 ± 0.6	Bonobos[b]	57	−29.2 ± 0.5	5.8 ± 0.6

Notes. The $\delta^{13}C$ data presented here were not corrected for the burning of fossil fuels.
[a]Lianas are vines that grew from the mid- or high canopy downward, drawing nutrients from trees at that strata and thus impacting their carbon stable isotope values. [b]The bonobo values presented here reflect faecal-diet offsets by adding 0.7‰ to the $\delta^{13}C_{faecal}$ values and subtracting 2.0 to the $\delta^{15}N_{faecal}$ values.

Iyema $\delta^{13}C$ and $\delta^{15}N$ values should align closely to the values of the LuiKotale bonobo community based on the canopy cover and the feeding ecology of each community (Oelze et al., 2011; White, 1992). We also predict that the Iyema bonobos stable isotope compositions will closely resemble Lomako fruit values and should overlap on isotopic bi-plots.

2 | MATERIALS AND METHODS

Fifty-seven bonobo faecal samples were collected from the Iyema field site in the Lomako Forest (00°55′N, 21°06′E) located in the DRC in June–July 2014. Iyema is a ~16-km^2 study area, consisting of primary rainforests and some secondary rainforests and swamp forests (White, 1992). The forest floor is carpeted with THV, and all levels of the canopy are characterised by dense foliage consisting of shrubs, lianas and trees of various heights forming a continuous canopy (Badrian & Malenky, 1984). The bonobos are semi-habituated, and a best abundance estimation model suggests there are 26–66 individuals in the community (Brand et al., 2016). Faecal samples were collected after defecation, and we recorded the date, geographic location and, when possible, the age/sex of the individual. For some individuals, we collected multiple samples. Faeces provide stable isotope data on the undigested portion of an individual's diet on the order of days, limiting our abilities to examine seasonal differences but provide short-term feeding data. We collected plant organs (i.e., fruits, leaves, piths and seeds) from three different heights including ground level (0–2 m), mid-canopy (2–10 m) and high canopy (10+ m). We also collected from lianas that originated in the mid- or high canopy and drew nutrients from trees, and then grew downward. We note lianas specifically, since their $\delta^{13}C$ values can be impacted by the height at which they drew nutrients. All samples were dried on-site using a camp stove and placed in labelled bags with desiccant. This research complied with the University of Oregon's Institutional Animal Care and Use Committee (#12-09), adhered to the legal requirements of the DRC, and was approved by the Institut Congolais pour la Conservation de la Nature (#0492).

Samples were ground into powder, weighed to ~1.5 mg, placed in tin capsules and combusted in an elemental analyser for stable carbon and nitrogen isotope abundances using a flow-through inlet system on a continuous flow isotope ratio mass spectrometer. $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios are expressed using the delta (δ) notation in parts per thousand or permil (‰) relative to the Vienna PeeDee Belemnite (VPDB) and atmospheric N_2 (AIR) standards, respectively.

To examine the relationship between the stable isotope values of the Iyema bonobos and the plants at Lomako, we added 0.7‰ to the $\delta^{13}C$ values and subtracted 2.0‰ from the $\delta^{15}N$ values of faeces (Sponheimer, Robinson, Ayliffe, et al., 2003). To compare the Iyema values to published hair stable isotope compositions from other chimpanzee and bonobo communities, we adjusted the faecal values to their hair equivalents by adding 3.7‰ to the faecal $\delta^{13}C$ values (Sponheimer, Robinson, Ayliffe, et al., 2003) and 1.0‰ to the faecal $\delta^{15}N$ values (Sponheimer, Robinson, Roeder, et al., 2003). To control for changes in the $\delta^{13}C$ compositions of atmospheric CO_2 linked to the burning of fossil fuels (McCarroll & Loader, 2004), we added 1.83‰ to the Iyema $\delta^{13}C_{hair}$ values. Previously published hair isotope data were adjusted to pre-industrial equivalents, and the *Pan* data sets required to make such adjustments are available here: https://figshare.com/articles/Supporting_Data_Loudon_et_al_2016_AJP/3179371

We compared the bonobo communities to three broad habitat categories inhabited by *P. troglodytes* that we refer to as "forest," "savannah" and "anthropogenically-disturbed." Those communities inhabiting environments with a grass understory are defined as "savannah." We compared the $\delta^{13}C$ and $\delta^{15}N$ values of plants collected at Lomako to those from Kibale (Blumenthal, Rothman, Chritz, & Cerling, 2016), Loango (Oelze, Head, Robbins, Richards, & Boesch, 2014), Salonga (Oelze et al., 2011) and the Tai National Forest (Fahy, Richards, Riedel, Hublin, & Boesch, 2013). We used Welch's analysis of variance (ANOVA) and Tukey's honest significant difference (HSD) pairwise tests to compare the $\delta^{13}C$ and $\delta^{15}N$ values of plants, faeces, or hair, for each community or habitat category ($\alpha = 0.05$).

3 | RESULTS AND DISCUSSION

To date, the Iyema bonobo $\delta^{13}C_{faecal}$ values are the lowest published for any *Pan* community (−29.9‰ ± 0.5, $n = 57$) and they have among the highest $\delta^{15}N_{faecal}$ values (7.8 ± 0.6‰, $n = 57$; see Supporting

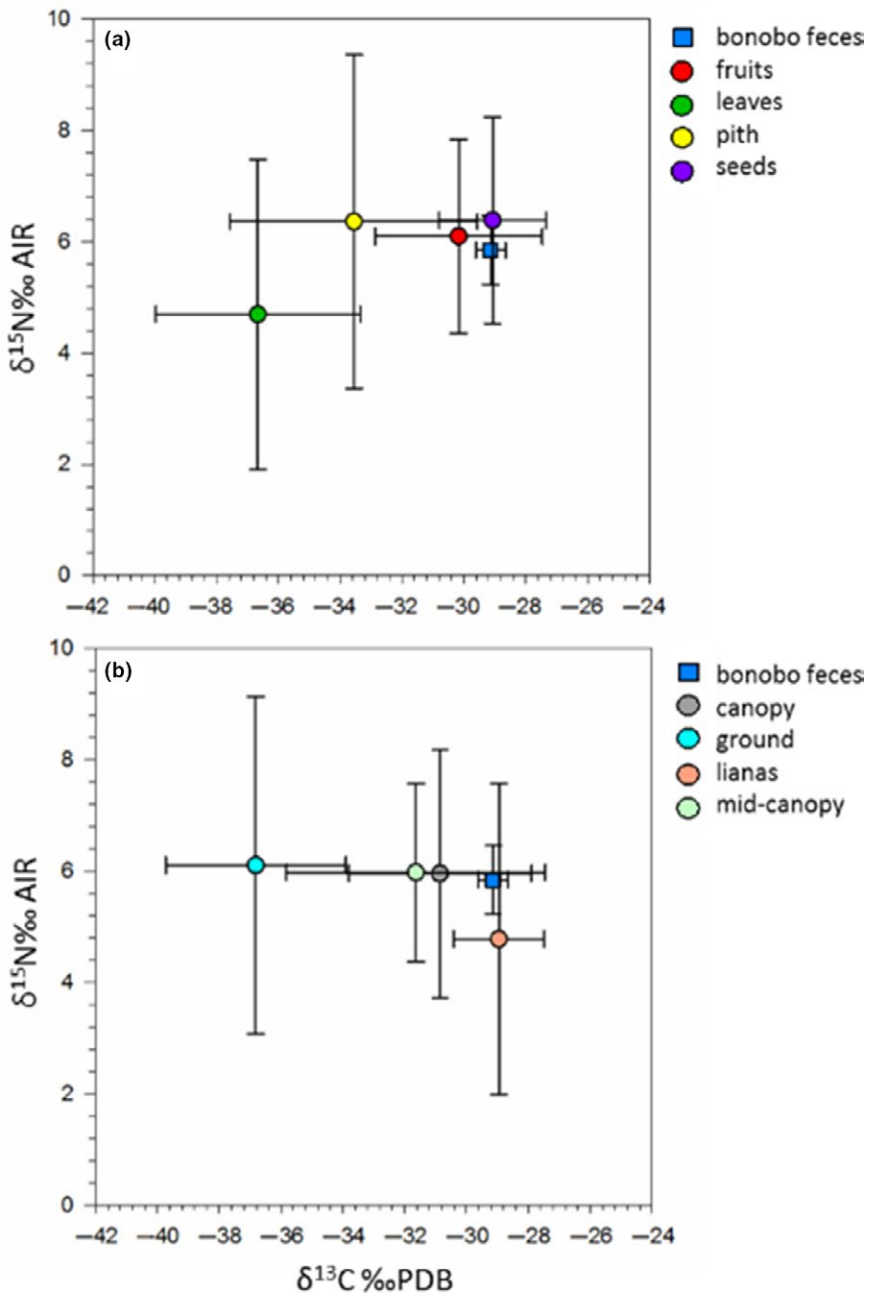

FIGURE 1 Iyema bonobo faecal $\delta^{13}C$ and $\delta^{15}N$ values converted to their dietary equivalents plotted with values from Lomako plant organs (a) and canopy height (b)

Information Table S1 for bonobo data). The bonobo faecal stable isotope data are driven by the Lomako plants which have very low $\delta^{13}C$ values (−32.0‰ ± 4.0, n = 39) and high $\delta^{15}N$ values (5.8‰ ± 2.2, n = 39; plant data are presented in Supporting Information Table S2). When we converted the $\delta^{13}C_{faecal}$ and $\delta^{15}N_{faecal}$ values to their dietary equivalents, the Iyema bonobos had diets with isotopic compositions similar to seeds and fruits, and their diets were isotopically similar to nonleaf canopy plant parts (Table 1; Figure 1). These data accord well with observations and faecal analyses collected at Lomako. Badrian et al. (1981) observed that fruit accounted for 49% of the bonobo diet, Badrian and Malenky (1984) found that fruit consisted of 54% of their diet, and White (1992) found that fruit accounted for 72% of feeding observations. The high $\delta^{15}N_{faecal}$ values of the Iyema bonobos are consistent with a fruit-rich diet, although piths and seeds are good fits from this perspective. The $\delta^{13}C_{faecal}$ and $\delta^{15}N_{faecal}$ data are most consistent with the Iyema bonobos having diets of chiefly fruits and/or seeds when plotted in isotopic bi-space (Figure 1). In terms of canopy stratification, White (1992) found that the Lomako bonobos spent 5.4% of all observations on the ground and feeding on THV accounted for 2.1% of observations. Analyses of Lomako THV suggest it provides high nutritional yields (Malenky & Stiles, 1991; Malenky & Wrangham, 1994) and that it is used as a protein source for the bonobos (White, 1996). However, isotopically, we could not detect the consumption of THV, which is consistent with its consumption being rare as noted by White (1992). In general, the stable isotope data suggest that the Iyema bonobos preferentially eat plants at the canopy and mid-canopy including lianas which originate at these strata (Figure 1).

TABLE 2 Site, mean annual precipitation, $\delta^{13}C_{hair}$ and $\delta^{15}N_{hair}$ mean and standard deviation data, and sample size for chimpanzee (*Pan troglodytes*) and bonobo (*Pan paniscus*) communities, and ecological category or *Pan* species

Site	Rainfall (mm)	*N*	$\delta^{13}C$‰	$\delta^{15}N$‰	Reference for isotope data
Lake Kerere (Uganda)	1,750	9	−20.6 ± 0.4	5.9 ± 0.2	Loudon et al., 2016
Miranga Village (Uganda)	1,700	5	−19.5 ± 1.0	5.8 ± 0.1	Loudon et al., 2016
"Disturbed forest" *P. troglodytes*		14	−20.2 ± 0.9	5.8 ± 0.2	
Cameroon	1,700	38	−23.5 ± 0.7	9.3 ± 0.8	Macho & Lee-Thorp, 2014
Chambura Gorge (Uganda)	950	7	−21.6 ± 0.9	8.4 ± 0.5	Loudon et al., 2016
Gombe (Tanzania)	1,250	13	−21.8 ± 0.3	3.5 ± 0.3	Schoeninger et al., 2016
Kanyanchu (Uganda)	1,500	4	−22.2 ± 0.1	7.7 ± 0.3	Loudon et al., 2016
Kanyawara (Uganda)	1,671	6	−21.7 ± 0.4	6.8 ± 0.9	Loudon et al., 2016
Loango (Gabon)	2,215	14	−22.8 ± 0.5	5.0 ± 0.4	Oelze et al., 2014
Tai National Forest (Côte d'Ivoire)	1,830	31	−23.6 ± 0.6	7.3 ± 0.6	Fahy et al., 2013
"Forest" *P. troglodytes*		113	−23.0 ± 0.9	7.3 ± 2.1	
Fongoli (Senegal)	900	36	−20.6 ± 0.4	2.9 ± 0.3	Sponheimer et al., 2006
Ishasha (DRC)	750	9	−21.8 ± 0.3	6.9 ± 2.1	Schoeninger et al., 1999
Ugalla (Tanzania)	1,012	8	−20.7 ± 0.3	2.3 ± 0.7	Schoeninger et al., 1999
"Savannah" *P. troglodytes*		58	−20.8 ± 0.6	3.5 ± 1.8	
Iyema (DRC)	2,000	57	−24.4 ± 0.5	8.8 ± 0.6	This study
LuiKotale (DRC)	2,000	33	−23.9 ± 0.2	8.4 ± 0.2	Oelze et al., 2011
"Bonobos" *P. paniscus*		90	−24.2 ± 0.5	8.7 ± 0.5	

Note. All $\delta^{13}C_{hair}$ values presented here have been adjusted to account for the burning of fossil fuels.

We found differences in the $\delta^{13}C_{plant}$ ($F_{4, 87.7}$ = 13.7; p < 0.0001) and $\delta^{15}N_{plant}$ values ($F_{4,93.6}$ = 8.8; p < 0.0001) among the five *Pan* communities (Supporting Information Table S3). The $\delta^{13}C$ values of the Lomako plants are lower than the plants at Salonga (p < 0.0001), which is inhabited by the LuiKotale bonobos (Oelze et al., 2014), and the plants at Kibale (p < 0.0001). Differences in foliar $\delta^{13}C$ values across wide geographic regions are influenced by mean annual precipitation (Loudon et al., 2016). The differences in the $\delta^{13}C$ values between Salonga and Lomako occurred despite both sites are characterised by continuous canopies. Moreover, at Lomako, we found that the ground-level plants had $\delta^{13}C$ values that were 5.9‰ lower than those of canopy plants (Supporting Information Table S3). In the closed canopy forests of Kibale, differences between the $\delta^{13}C$ values of leaves collected in the understory versus the subcanopy and canopies were ~2.9‰ (Blumenthal et al., 2016). Despite the differences in the $\delta^{13}C$ values of the plants at

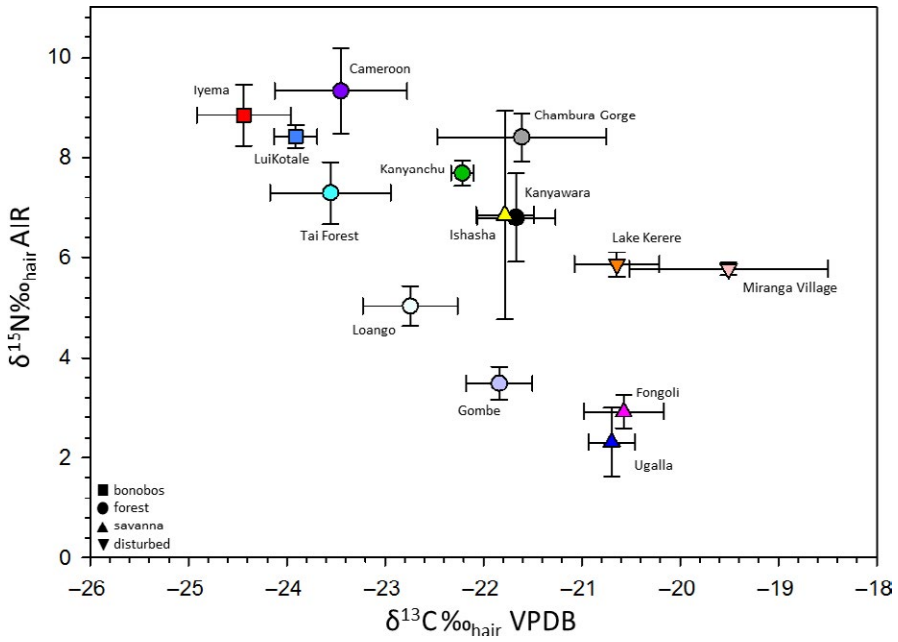

FIGURE 2 Means and standard deviations of hair $\delta^{13}C$ and $\delta^{15}N$ values for *Pan* communities. All values were adjusted for the effects that fossil fuel burning has had on $13CO_2$ atm. Squares represent bonobos (*Pan paniscus*), circles represent "forest" chimpanzee (*Pan troglodytes*) communities, triangles represent "savannah" chimpanzee communities, and inverse triangles represent chimpanzee communities living in habitats with high degrees of anthropogenic disturbance

these sites, the Salonga and Kibale forests are both characterised by continuous canopies.

We found differences in the $\delta^{13}C_{hair}$ ($F_{13,46.2}$ = 271.3; p < 0.0001) and $\delta^{15}N_{hair}$ values among the 14 *Pan* communities ($F_{13,44.1}$ = 636.8; p < 0.0001; Table 2; Figure 2). Pairwise comparisons revealed that the Iyema bonobos had lower $\delta^{13}C_{hair}$ values (p < 0.001) than all the communities, and higher $\delta^{15}N_{hair}$ values (p < 0.0001) for nine of the communities, with the exceptions being Cameroon, Kanyanchu, Chambura Gorge and LuiKotale. Comparisons between the *Pan* ecological categories (i.e., bonobos and *P. troglodytes* in "forest," "savannah" and "anthropogenically-disturbed habitats") yielded differences in $\delta^{13}C_{hair}$ ($F_{3,54.7}$ = 523.8; p < 0.0001) and $\delta^{15}N_{hair}$ values ($F_{3,97.2}$ = 491.9; p < 0.0001; Table 2 and Supporting Information Figure S1). Pairwise comparisons showed that the bonobo communities exhibited lower $\delta^{13}C_{hair}$ values (p < 0.0001) and higher $\delta^{15}N_{hair}$ values (p < 0.0001) than the *Pan* communities living in the other ecological categories.

Carbon isotope analyses of "savannah" chimpanzee communities have proven useful for understanding the behaviour and ecology of extinct hominins, and it is thought that "savannah" *Pan* and early hominins utilised similar biomes (Schoeninger, Moore, & Sept, 1999; Sponheimer et al., 2006). The stable carbon isotope compositions of these "savannah" communities are indistinguishable from those of *Ardipithecus ramidus* and *Australopithecus anamensis* (Loudon et al., 2016). In stark contrast, the $\delta^{13}C$ values of the Iyema community resemble those of *Gigantopithecus* sp. (Nelson, 2014; Qu et al., 2014) which probably ate plants within a closed canopy and may have preferentially consumed THV which seems likely given its large body size.

Carbon isotope data for extinct and extant hominoids have revealed a continuum of habitat and dietary patterns. On one end of this continuum lie the modern-day bonobo communities that yield the lowest $\delta^{13}C$ values and consume C_3 plants growing in rainforests with continuous canopies. In contrast, "savannah" chimpanzees occupy the other end of the continuum whose values align with consumption of plants in open environs and resemble some species of *Ardipithecus* and *Australopithecus* (Sponheimer et al., 2013).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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