Exploring the contribution and significance of animal protein in the diet of bonobos by stable isotope ratio analysis of hair

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In primates, age, sex, and social status can strongly influence access to food resources. In *Pan*, these criteria are assumed to influence access to vertebrate meat. However, the significance of meat in terms of its role in the nutrition of *Pan* is still debated. Here we present a study using stable carbon and nitrogen isotope ratios in hair samples from habituated, wild bonobos (*Pan paniscus*) to explore these issues. Over a period of 5 mo hair samples were collected from fresh bonobo nests at LuiKotale, Democratic Republic of Congo. Hair samples were assigned to known individuals and were of sufficient length to allow the evaluation of isotopic variation over several months. Samples of plant foods and sympatric fauna were also analyzed. The $\delta^{13}C$ and $\delta^{15}N$ results of the bonobo hair were remarkably homogeneous over time and for the group as a whole. There are no differences in diet between the sexes. Within the group of males, however, there was a positive correlation between dominance status and $\delta^{15}N$. The isotopic data indicate that the contribution of fauna to bonobo diet is marginal and that plant food is the dietary protein source. In only some cases did elevated $\delta^{15}N$ hair values correlate with observed faunivory and not correspond to the $\delta^{15}N$ measured in the dominant plant foods. Given the large variation in hunting and meat eating of *Pan* across the African continent, the detection of seasonal changes in faunivory by elevated $\delta^{15}N$ values in sectioned ape hair is a promising approach.

feeding ecology | great apes

Reconstructing hominin diets and possible meat-eating behavior is a key research area in the field of human evolution (1, 2) because adaptations for the consumption of animal protein and fat have been related to brain developmental trends in the evolution of the human lineage (3). As our closest living relatives, bonobos (*Pan paniscus*) and chimpanzees (*Pan troglodytes*) are often used as referential models in the context of diet composition, feeding behavior, and food processing (4, 5). The diet of both *Pan* species is dominated by plant foods: fruits account for more than 50% of the daily dietary intake and are complemented by leaves, herbs, and, at least in some populations, underground storage organs. Both species supplement their plant diet with insects and meat from vertebrates acquired by hunting (6). Behavioral observations from meat-eating events suggest that both *Pan* species consider meat a highly attractive food; meat is generally considered to be a high-quality food resource that offers nutrients that are difficult to obtain from other foods (7). Conflicts among those who compete for access to meat are frequent, and dominant individuals may take carcasses from subordinates. Longitudinal data from one population suggest that meat consumption by female chimpanzees can shorten interbirth intervals (8). Given the close link between the nutritional status of females and reproductive success, the inferred nutritional function of meat eating seems plausible, but requires further exploration. Although existing evidence demonstrates that meat is part of the diet of most or all *Pan* populations, how meat consumption relates to the overall diet remains unknown (7). Hunting and meat eating is less frequently observed in bonobos (*Pan paniscus*) compared with some chimpanzee populations (9). Observational data from two sites show that females eat meat more often and in larger amounts than males (10). In Salonga, bonobos especially target immature primates and mature forest antelopes (*Cephalophinae*) that have an estimated body mass of 4–12 kg (11). After hunts, females are observed to be more successful in monopolizing meat, and meat is rarely shared with males (10).

Biochemical analysis of tissue provides important information on diet composition and allows a better understanding of what is actually incorporated into the body (12). By analyzing the stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) in animal tissue, a stepwise enrichment between trophic levels is observed, which can reveal the main source of protein (13, 14). The analysis of carbon and nitrogen isotope ratios has been widely applied in nutritional animal ecology (15), as well as in archaeology to reconstruct human and hominin paleodiets (12, 16, 17). The method relies on the fractionation of isotopes due to the different kinetic and thermodynamic properties of the light versus heavy isotopes during chemical and physical processes in the biosphere (18). The fractionation of carbon isotopes in terrestrial ecosystems is related mainly to photosynthetic pathways of plants. Consumers in environments dominated by C_3 plants show lower $\delta^{13}C$ values than in ecosystems dominated by C_4 plants (19, 20). In dense tropical forest habitats, plants are ^{13}C-depleted due to low light intensity and photosynthetic recycling of ground-respired CO_2. This "canopy effect" causes ^{13}C-depleted values in primary forests with the most negative values near the forest floor and the least negative values in the canopy (21, 22). Although the trophic level effects cause only minor fractionation in $\delta^{13}C$ (~1–2%), $\delta^{15}N$ values show a significant stepwise enrichment of 2–5% for each trophic level in the food chain (13). By analyzing tissue such as collagen or keratin, the protein fraction of the diet can be identified to derive mainly from plant or animal protein. However, in terrestrial ecosystems, nitrogen fractionation can also relate to temperature, salinity, and precipitation (23, 24). Therefore, to understand the variability in a species' isotope signature, it is imperative to analyze samples from different food-web levels of the same ecosystem. A variety

of material, such as hair, feathers, and plant fibers, provide reliable isotope information to reconstruct the isotopic ecology of a certain habitat (25, 26).

Numerous studies have applied stable isotope ratio analysis to explore the contribution of different plant sources (e.g., C_3 and C_4 plants) and niche separation, as well as intraspecific and interspecific variation of the composition of the diets of nonhuman primates (26–30). Other studies on African forest and savanna isotope ecology provide some information on primates but do not have corresponding diet data (20, 25). To date, isotopic information on hominoid primates is restricted to samples from chimpanzees. A study by Schoeninger et al. (28) involved hair samples from two populations living in open savanna habitats at Ugalla (Tanzania) and Ishasha (Democratic Republic of Congo). It showed that chimpanzees focused on plant foods from forest patches and woodland, and not on C_4-dominated grassland foods. This finding was supported by a more recent study by Sponheimer et al. (29) of savanna chimpanzees at Fongoli in Senegal. Using samples of bone collagen from various chimpanzees from the Kibale forest, Uganda, Carter (31) found that the chimpanzees had a wide range of $\delta^{13}C$ and $\delta^{15}N$ values, suggesting more variation in terms of diet composition, including C_4 plants originating from domesticated plant species such as sugarcane or corn. A more recent study of a collection of historic chimpanzee crania from northern Liberia found no significant sex differences in diet, but could not reconstruct the chimpanzee's food sources as no environmental background isotopic data were included (32). Compared with the nutritional value of various types of food plants, knowledge about the nutritional contribution of animal food remains elusive. We conducted stable isotope ratio analyses on hair samples from individually known bonobos from LuiKotale, a long-term study site in the Democratic Republic of Congo. The major goal of this study was to explore bonobo isotope ecology and identify their major dietary protein sources. We examined if field observations of meat and plant food consumption could be correlated to isotopic changes in the bonobo hair and evaluated the utility of this technique for future isotopic studies on extant African apes. In addition, the data were used to examine isotopic variations on a temporal scale and in relation to time, age, sex, and social status of subjects. To understand the isotopic variability of different food sources in the natural habitat, a variety of plant food items and sympatric animal species from different ecological niches were also analyzed.

Results

The isotopic results of the floral (n = 33), faunal (n = 32), and bonobo hair (n = 143) samples from Salonga are shown in Tables S1–S3. All plant samples represent fruits, leaves, or piths of species that are known to be eaten or at least partly ingested (e.g., bark) by the LuiKotale bonobos. From observational data we could additionally classify the five most important food plants for each month during the study period (Table S4). The plants show a wide range of $\delta^{13}C$ values, −36.2‰ to −24.7‰ (mean = −29.0 ± 2.7‰ 1σ), and of $\delta^{15}N$ values, 2.6‰ to 9.3‰ (mean = 5.6 ± 1.3‰ 1σ). Similar heterogeneity is found in the faunal samples. Animals from Salonga forest display $\delta^{13}C$ values ranging from −33.6‰ for a diurnal butterfly to −20.2‰ measured in an unidentified bird species. The mean $\delta^{13}C$ for the faunal samples is −24.9 ± 2.0‰ (1σ). The $\delta^{15}N$ values range between 3.8‰ in termites and 17.6‰ in the feather of an unidentified bird species. The mean $\delta^{15}N$ for the faunal samples is 10.7 ± 2.7‰ (1σ).

Compared with the ecological data from plants and animals, the variability of isotopes in the hair samples from bonobos was low (Fig. 1 and Fig. 2). The $\delta^{13}C$ values range from −26.7‰ to −25.2‰ (mean = −25.8 ± 0.3‰ 1σ), and the $\delta^{15}N$ values range from 7.7‰ to 9.1‰ with a mean of 8.4 ± 0.3‰ (1σ). There were no significant differences in the mean isotope values between females and males (exact Mann–Whitney U test: for $\delta^{13}C$—U = 19, $N_{females}$ = 11,
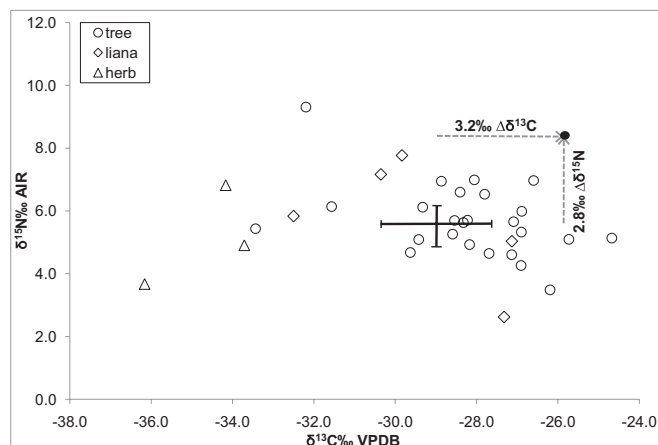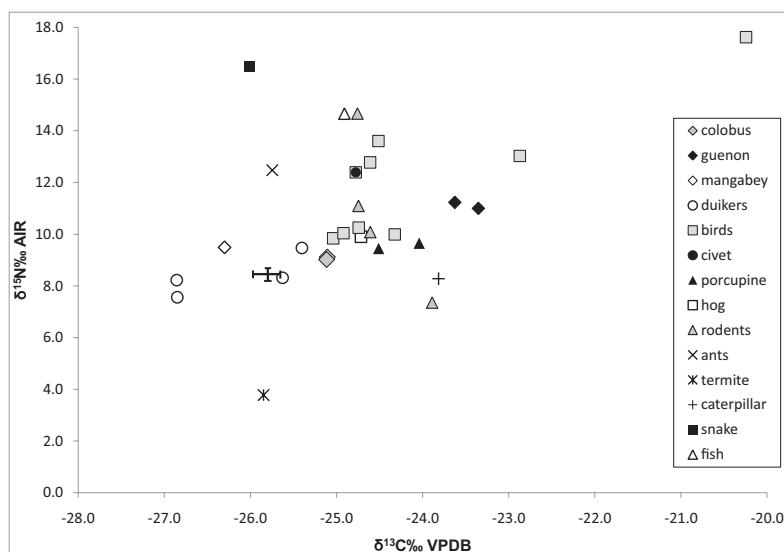

Fig. 1. Isotope ratios of plant samples from Salonga sorted by plant type, mean value for all floral samples (SD 1σ), and the mean value (black dot) of all bonobo hair samples (n = 143). The dashed arrows display the fractionation (Δ) between mean plant diet and the mean bonobo hair keratin values. The analytical error for $\delta^{13}C$ and $\delta^{15}N$ is <0.2%.

N_{males} = 9, P = 0.8357; for $\delta^{15}N$—U = 22, P = 0.9452). The males had a mean $\delta^{13}C$ value of −25.7 ± 0.3‰ (1σ) and a mean $\delta^{15}N$ value of 8.4 ± 0.3‰ (1σ) whereas the females had a mean $\delta^{13}C$ value of −25.8 ± 0.3‰ (1σ) and a mean $\delta^{15}N$ value of 8.5 ± 0.2‰ (1σ). $\delta^{15}N$ values correlated significantly with male rank (Spearman correlation: ρ = −0.717, n = 9, P = 0.037) as well as with the relative age of subjects (U = 8, N_{adult} = 5, $N_{adolescent}$ = 4, P = 0.032). No differences were found when relating $\delta^{13}C$ values with rank (ρ = 0.333, n = 9, P = 0.948) or when comparing $\delta^{13}C$ values of adult and adolescent males (U = 8, N_{adult} = 5, $N_{adolescent}$ = 4, P = 0.73).

Discussion

Floral Samples. The isotopic results for the plant samples are presented in Fig. 1 in relation to the mean bonobo value. The food plants collected at Salonga revealed a high variability in isotope ratios (Table S1 and Fig. 1) and, in this respect, resemble what has been described for other tropical forests (22, 25, 33). A study on the isotope ecology of the Ituri Forest, also located in Democratic Republic of Congo, provides the best dataset for comparison. Cerling et al. (25) measured $\delta^{13}C$ and $\delta^{15}N$ values in foliage, fruits, and seeds from different canopy levels (n = 71) and reported isotope values remarkably similar to what was found at Salonga. The mean $\delta^{13}C$ value (−31.2 ± 2.8‰ 1σ) in Ituri was only 1.5‰ more negative than the floral samples from Salonga (−29.0 ± 2.7‰ 1σ). This is most likely due to the intentional sampling of lower canopy levels in the Ituri study whereas in Salonga most plant food samples derive from higher canopy levels. Similar ^{13}C-depleted values (−31.4 ± 0.5‰ 1σ) have been reported from closed canopy forests in Kenya (34). Salonga and Ituri are part of the same evergreen lowland forest of the Congo basin and are strongly affected by the canopy effect and thus ^{13}C-depleted (19, 22). Conversely, Kibale National Park in Uganda (31) comprises a mosaic of habitats that include evergreen forests, open woodlands, and savanna. Correspondingly, the botanical samples from this site are more variable and enriched in terms of ^{13}C (−26.4 ± 6.1‰ 1σ) in relation to the Democratic Republic of Congo. Nitrogen isotope ratios are known to be elevated in rainforests compared with open woodlands and forests in temperate climates, due to more complex pathways of nitrogen assimilation (33, 35, 36). Not surprisingly, the mean $\delta^{15}N$ values of the plants from Ituri (5.4 ± 1.8‰ 1σ) and Salonga (5.6 ± 1.3‰ 1σ) are nearly identical. However, the Kibale plants were less ^{15}N-enriched (mean of 3.8 ± 1.6‰)

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Fig. 2. Isotope ratios of the sampled faunal species from Salonga and the mean value (1σ SD) for all bonobo hair. The data point of a diurnal butterfly was excluded from this graph due to its extremely depleted ^{13}C value (−33.6%). Analytical error is <0.2%.

compared with Salonga, presumably resulting in a lower baseline δ^{15}N value for consumers in this ecosystem.

Faunal Samples. The variation of isotope results observed in the animal species at Salonga is similar to those reported from other African forests (12, 25). Depletion of ^{13}C due to the canopy effect was mostly reflected in ground-dwelling species, such as the duiker (*Cephalophus*), Congo peacock (*Afropavo congensis*), and guinea fowl (*Guttera*) as well as in ground-living insects (e.g., army ants and termites). The highest δ^{13}C values were measured in species living and feeding in the higher levels of the forest canopy, represented by the guenon (*Cercopithecus*), squirrel (*Protoxerus stangeri*), and two unidentified birds (Fig. 2). Some primates such as bonobos, red colobus (*Procolobus thollori*), and the mangabey (*Cercocebus aterrimus*) had relatively low δ^{13}C values, although they can be considered as arboreal-feeding species. Their isotope values were very similar to those of the duikers, which feed mainly on fruits dropped by arboreal primates and some additional herbs (11). We suggest that bonobos, colobus, and mangabeys feed in the intermediate forest levels, which are not as strongly enriched in ^{13}C, and also may occasionally feed on subcanopy food sources. The guenon seems to exclusively feed in the highest canopy levels and therefore occupies a different ecological niche than the other primates in our dataset.

The complexity of the nitrogen assimilation pathways in the tropical forest results in high δ^{15}N values, even in herbivorous species. The lowest δ^{15}N values were found in folivore species such as termites (3.8%), caterpillars (8.3%), colobus monkeys (~9.0%), and ungulates (8.4 ± 0.8% 1σ). In the duikers, we observed the same pattern as in δ^{13}C: duikers reveal δ^{15}N values very similar to the bonobos, mangabey, and colobus monkeys due to their dietary adaptation of largely consuming fruits dropped by arboreal primates. It should be noted that the values of fruigvorous and folivorous mammals exceed those of forest-living primates reported elsewhere (27, 30, 37). This difference may result from the relatively high floral baseline values of Salonga (Fig. 1). As expected, the nitrogen isotope ratios were found to be more enriched in the higher levels of the food chain. Omnivorous and insectivorous mammals such as guenons, civets, river hog, and insectivorous birds had δ^{15}N values between 9.5% and 13%. Carnivore isotope signatures were found in ants (12.5%), a snake (16.5%), one unidentified rodent (14.7%), and in the feathers of an unidentified bird (17.6%). On the basis of

the δ^{13}C result (−20.2%) and the high δ^{15}N value of the unidentified bird, it is possible to say that it was a raptor-hunting arboreal species (Fig. 2).

Bonobo Hair Samples. We measured isotope ratios of 143 hair samples from serially sectioned hair deriving from at least 21 mature individuals (Figs. 1–4 and Table S3). If the growth rate of bonobo hair is similar to that of humans, the isotope values should provide information on the diet consumed over a period of about 9 mo (December 2008–August 2009). The mean δ^{13}C value of −25.8 ± 0.3% (1σ) in Salonga bonobo hair is the most negative value reported for African apes and for groups with sympatric duikers (see above). Although bonobos of this population occasionally move into grassland, there was no evidence for the consumption of C_4 plants. These results strongly contrast with the data from chimpanzee populations living in open woodlands or even in savanna landscapes. Mean isotope values of plants from Kibale (−26.4 ± 6.1% 1σ) indicate that this environment could be less depleted in ^{13}C than the forest of Salonga (−29.0 ± 2.7% 1σ). The higher mean δ^{13}C value in samples of Kibale chimpanzees (−22.9 ± 0.7% 1σ) can also be explained by the chimpanzee's opportunistic feeding strategies. Carter (31) suggested that chimpanzees were ^{13}C-enriched due to regular raids on C_4 field crops such as maize and sugarcane in the villages. However, the comparison of δ^{13}C values in samples from Salonga bonobos and Kibale chimpanzees is complicated by the fact that Kibale chimpanzee data were obtained from bone collagen with questionable C/N ratios (31, 38). Moreover, various values for hair-collagen offsets are found in the literature, making a direct comparison of collagen and hair keratin values difficult (39, 40). The same applies to the dataset from the Liberian Ganta chimpanzees; here, direct comparison is further hindered by the need to consider fossil fuel effects, as the Ganta bone collection derives from a historical context (41).

The Salonga bonobo hair samples had a mean δ^{15}N value of 8.4 ± 0.3% (1σ), and this result represents the highest measured δ^{15}N value from adult African apes to date. This indicates that, compared with other African ape habitats, food sources at Salonga are ^{15}N-enriched. The diet-tissue fractionation ($\Delta_{plant\ diet-keratin}$) between the plant foods (mainly fruits) and bonobo hair is 3.2% for $\Delta\delta^{15}N_{plant\ diet-keratin}$ and 2.8% for $\Delta\delta^{13}C_{plant\ diet-keratin}$, representing one trophic level (16, 17). Looking at the isotope values of sympatric animal and plant species, it is obvious that plants are the
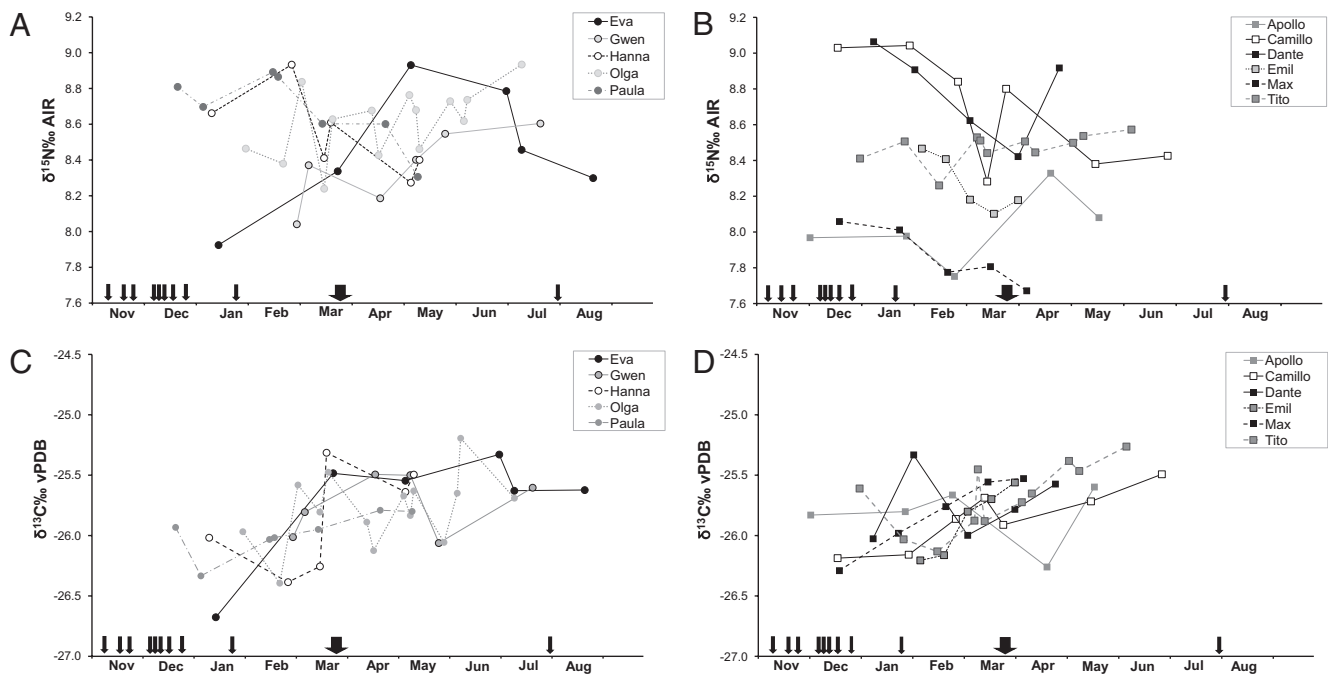
Fig. 3. Individual bonobo hair isotope ratios plotted chronologically (December 2008–August 2009). The variation in $\delta^{15}N$ for females (*A*) and males (*B*) is shown, as is the variation in $\delta^{13}C$ for females (*C*) and males (*D*). Each hair sample was cut into sections, and each data point represents the mean point in time of the respective hair section. For 10 mm of sectioned hair, we calculated 28 d; a month here represents 30.5 d. Each arrow represents an observed event of faunivory (mammals, birds, and caterpillars), and its thickness indicates the relative amount of consumed vertebrate and nonvertebrate protein.

dominant source of dietary protein for bonobos. However, the overall variation in hair keratin $\delta^{15}N$ values is strikingly low (Table S3). This may reflect low temporal fluctuation of nutrient supply in the bonobo diet. The impression of low isotopic variability in bonobo hair remains when comparing different sections of an individual hair sample, representing different points in time (Fig. 3 *A* and *B*). It is remarkable that the large isotopic variation in food plants known to be consumed by the Salonga bonobos (42) is not reflected in the hair isotope values. This can be explained by the low range in $\delta^{15}N$ in dominant food plants, which were identified in feeding observations (Table S4). Despite the wide range of potential food plants (7–20 species) per month, the main plant foods are commonly restricted to less than five species. These, with a mean $\delta^{15}N$ value of 5.5% ± 0.9% (1σ), appear to be quite stable in terms of isotopic variation throughout the study period. From November to March, Dialium fruits (5.1% $\delta^{15}N$) were nearly always consumed when the bonobos were observed feeding, alternated by Irvingia (6.0% $\delta^{15}N$), Gambeya (6.6% $\delta^{15}N$), and the leaves of an unidentified tree from April to July. Although feeding observations are incomplete and not all plant species could be identified, we found no evidence for seasonal isotopic fluctuation in food plants.

Differences in $\delta^{15}N$ were expected in comparison with the savanna or woodland chimpanzees from Ugalla, Ishasha, and Fongoli, which have significantly lower $\delta^{15}N$ values. In Ugalla and Fongoli, low mean $\delta^{15}N$ values of 2.3 ± 0.8%, and 2.9 ± 0.3%, respectively, are the result of intense legume consumption (28, 29). For Ishasha, values with a mean of 5.9 ± 0.9% (1σ) were reported (two potentially breastfed individuals excluded), whereas the mean value for the Kibale chimpanzee sample was 6.4 ± 1.2% 1σ (28, 31). The nitrogen isotope ecology of the Salonga rainforest therefore differs significantly from other ape habitats.

Compared with the values obtained from sympatric animals and plant foods, bonobo isotope ratios were remarkably similar within and between individuals (Fig. 3 and Fig. 4). Moreover, on a community level, there was little evidence for ^{15}N-enrichment that could be related to the consumption of fauna. We attempted

to correlate observed incidences of faunivory—specifically the consumption of insects such as caterpillars—with increased hair nitrogen isotope values. Five faunivory events were observed in December 2008 and initially appear to be recorded as slightly elevated $\delta^{15}N$ values (8.8–9.1%) in the hair of some individuals (e.g., Paula, Camillo, Dante). The female Eva had the lowest $\delta^{15}N$ value in this time period, and she was not observed to be a primary consumer of vertebrate meat. Eva's isotope values show the strongest fluctuation in the group. Her $\delta^{15}N$ values increased after a period of intense consumption of caterpillars in March 2009. Given the elevated $\delta^{15}N$ values of 8.3% for the caterpillars, we suggest that the female Eva possibly shows a response to this significant intake of invertebrate protein (Fig. 3*A*).
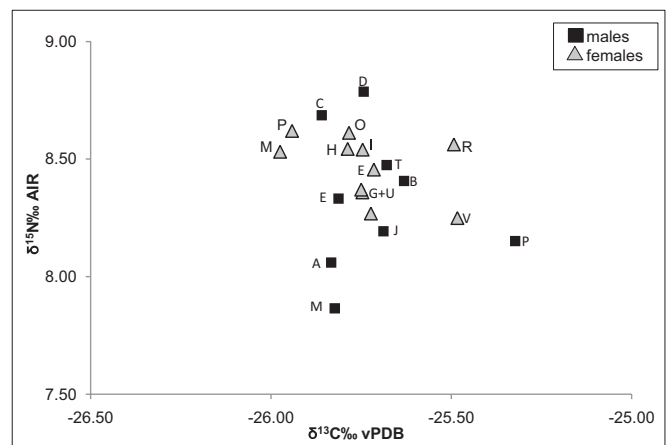
Fig. 4. Mean isotope values (1σ SD) of hair samples for each individual bonobo of the study community. The initial next to each data point refers to the individual name of each male (square) and female (triangle). See Table S3 for further details. Analytical error is <0.2%.

A similar pattern could be observed in the male Camillo. His $\delta^{15}N$ values rose in the time he was observed eating caterpillars repeatedly (Fig. 3B). However, the isotope data of other individuals did not show the same increase, although they were also observed consuming insects (e.g., Dante, Tito). We found no evidence of isotopic fluctuation in the bonobos main plant diet, which might explain these short-term variations in the nitrogen isotope values in hair keratin; therefore, these could be related to faunivory events. However, the increase in nitrogen isotope values is very slight and not observed in all individuals. One limitation of our study derives from the unknown rate of hair growth in bonobos, which reduces our ability to align observed events of meat consumption to the hair. In addition, assessment of the amount of meat consumed by each individual is difficult and prone to errors. Finally, discontinuity of direct observations renders our knowledge of diet composition incomplete. However, despite these limitations, detecting peaks of faunivory or insectivory through the measurement of temporarily elevated $\delta^{15}N$ values in small hair sections is likely and remains a promising approach, although it did not provide definitive results here.

No significant sex differences were detected in the isotope ratios measured in hair samples from female and male bonobos. This finding is in line with reports emphasizing the cohesiveness of community members and spatial associations of females and males (43) but contradicts reported sex differences in meat consumption. However, our data show that males differed: $\delta^{15}N$ values significantly increased with male dominance status and were higher in adult males compared with adolescent males (Fig. 4 and Table S5). Evidence suggests a relation between dominance status and age, but at this stage we are not able to distinguish the effect of the two parameters. Adolescent males are subordinate to adult females and to adult males and are more often the target of aggression than other group members (44), and probably this also applies to the context of food competition. As a result, they are often excluded from accessing high-quality food patches such as ripe fruit or meat. From this perspective, the positive correlation between rank and $\delta^{15}N$ can be explained by reduced feeding opportunities of subordinate males. Although the overall range of $\delta^{15}N$ values is relatively small (7.7–9.1%), the interindividual variation indicates differences in access to food from higher trophic levels in the male bonobos. Dominance relations among female group members were unknown at the time of sample collection, and further studies are needed to explore the relation between status and $\delta^{15}N$ in bonobos.

Conclusion

On the basis of the findings of this study, we conclude that overall, the amount of protein obtained from fauna does not make a significant contribution to the bonobo's tissue. Alternatively, it has been suggested that, rather than affecting the nutritional status, hunting and meat sharing may derive social rather than nutritional benefits (10, 45). Compared with the values obtained from sympatric animals and from plant foods, bonobo isotope ratios were remarkably similar within and between individuals. This finding is especially interesting for high-resolution carbon isotope studies on fossil hominins that found pronounced intra- and interindividual dietary variation (17). Even though physiological differences between the sample tissues of tooth enamel and hair should be taken into account, isotopic studies on extant apes can serve as a useful referential model for hominin paleoecological studies. Although direct evidence showed that

LuiKotale bonobos do hunt and consume the meat of other vertebrates, the isotopic evidence indicated that the majority of dietary protein was derived from plant foods, which mainly revealed unexpectedly constant $\delta^{15}N$ values. Although temporal changes in $\delta^{15}N$ in the samples of some individuals did correlate with events of meat consumption, other observed events of faunivory and insectivory did not show the same effect. Given the large variation in hunting and the relative amounts of animal protein consumption for *Pan* populations across the African continent, detection of seasonal changes in faunivory and insectivory by temporarily elevated $\delta^{15}N$ values in sectioned ape hair remains a promising approach.

Materials and Methods

Study Site and Subjects. Data were collected from an ongoing field study at LuiKotale, Democratic Republic of Congo (46). The site is located at the western border of Salonga National Park and consists of tropical lowland forest with a closed canopy and small patches of grassland. At the time of data collection, the studied community consisted of 33–35 individuals, including 5 adult and 4 adolescent males and 11 adult and 5 adolescent females. Dominance status of males was based on behavioral interactions as described by Surbeck et al. (44) and was consistent throughout the study period.

Sample Material. Hair samples from bonobos were collected systematically from fresh night nests. Samples of hair, feathers, and tissue from other animals were collected opportunistically whenever dead animals were found in the forest. It was not always possible to identify tissues on a species level so that some specimens are classified only as, e.g., bird or rodent. Plant samples were derived from an ongoing study (42). Observations of feeding behavior were recorded during focal scans and ad libitum (*SI Materials and Methods*). All samples were stored dry or were frozen. Dry matter of hair samples largely consists of protein (90–95%) and does not change its isotopic composition once it is formed (12, 36, 47). It therefore reflects the incorporated diet, however with a delay of ~6–12 d (48). Human scalp hair has an average growth rate of 0.35 mm/day and about 10 mm/month (49). Because data on hair growth in *Pan* are not available, we used the value from human hair to align hair segments to a given time period. Each of the hair samples used in this study for sectioning consisted of 3–10 bonobo hairs of 2–7 cm in length and had complete hair roots Hence, hair samples could be aligned at the roots to a initial chronological point. Sectioning the hair with a scalpel gained several time-reverse samples covering a period of up to 9 mo (November 2008 to August 2009). See *SI Materials and Methods* for more details on the procedure.

All samples were cleaned and purified before isotopic analysis. Hair samples were classified and selected under a microscope. Complete hairs of a sample were aligned at the roots under the microscope and cut into 0.5-cm (= 2 wk) to 2-cm (= 2 mo) sections with a scalpel (Table S3). Each section of hair (≥0.4 mg) was transferred into tin capsules for isotopic measurement. Bulk samples of hair, feathers, and insects (≥0.5 mg) were weighed into tin capsules for combustion. Plant items were freeze-dried and homogenized. Following this, ~2 mg of plant powder was weighed in for analysis (*SI Materials and Methods*). All measurements were performed in a Flash EA 2112 coupled to a DeltaXP mass spectrometer (Thermo-Finnigan) at the Max Planck-Institute for Evolutionary Anthropology in Leipzig, Germany. The analytical precision was better than 0.2% (1σ) for $\delta^{13}C$ and $\delta^{15}N$.

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