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► **To cite this version:**

Maria Ana Correia, Robert Foley, Tamsin C O'Connell, Fernando Ramírez-Rozzi, Marta Mirazón Lahr. Carbon and nitrogen isotopic signatures of hair, nail, and breath from tropical African human populations. *Rapid Communications in Mass Spectrometry*, 2019, 10.1002/rcm.8524 . hal-02359632

HAL Id: hal-02359632

<https://hal.science/hal-02359632>

Submitted on 19 Nov 2019

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1 **TITLE** CARBON AND NITROGEN ISOTOPIC SIGNATURES OF HAIR, NAIL, AND BREATH FROM
2 TROPICAL AFRICAN HUMAN POPULATIONS

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11 **ABSTRACT**

12 *Rationale:* Stable isotopic analyses are increasingly used to study the diets of past and present
13 human populations. Yet, the carbon and nitrogen isotopic signals of modern human diets
14 collected so far are biased towards Europe and North America ([Hülsemann et al. 2015](#)). Here,
15 we address this gap by reporting on the dietary isotopic signatures of six tropical African
16 communities: El Molo, Turkana (Kerio), Luhya (Webuye), Luhya (Port Victoria), and
17 Luo (Port Victoria) from Kenya, and Baka from Cameroon; representing four subsistence
18 strategies: fishing, pastoralism, agriculturalism, and hunter-gatherer.

19 *Methods:* We ~~analysed~~ [measured](#) the carbon and nitrogen isotopic signals of hair ($n = 134$)
20 and nail ($n = 80$), and the carbon isotopic signal of breath ($n = 184$) from these communities,
21 as well as the carbon and nitrogen isotopic signals of some food samples from the Kenyan
22 communities.

23 *Results:* We expand on the known range of $\delta^{13}\text{C}$ values in human hair through the hunter-
24 gatherer Baka, with a diet based on C_3 plants, and through the agriculturalist
25 Luhya (Webuye), with a diet based on C_4 plants. In addition, we found that the consumption
26 of fish from East African lakes is difficult to detect isotopically due to the combined effects of
27 high nitrogen isotopic ~~ratios~~ [values](#) of plants and the low nitrogen isotopic ~~ratios~~ [values](#) of fish.
28 Finally, we found that some of the communities studied are markedly changing their diets
29 through increasing sedentism and urbanization.

30 *Conclusion:* Our findings contribute substantially to the understanding of the environmental,
31 demographic and economic dynamics that affect the dietary landscape of different tropical
32 populations of Africa. These [results](#) highlight the importance of [studying](#) a broader sample of

- 1 human populations and their diet, with a focus on their precise context [– both from an isotopic](#)
- 2 [perspective, as well as from a more general anthropological perspective.](#)
- 3 **Keywords** food transitions; stable isotopic analysis; East Africa; Central Africa; subsistence
- 4 strategies

1 **INTRODUCTION**

2 Africa is central to both prehistoric and contemporary human evolution and biology. As the
3 place where humans evolved, it is the cornerstone to research on who we are and how we
4 came to be. Today, Africa continues to be a place of great change due to ongoing political,
5 economic, social, and environmental shifts in the continent ^{1,2}. However, we still lack focused
6 research on the biology of human activities in both time frames. For instance, there is a
7 surprising lack of fossil and chronologically-controlled archaeological evidence of the events
8 that took place in Africa between the appearance of *Homo sapiens*, 200 000 years ago (200
9 Ka), until the present day ³. At the same time, a lot of research into current human behaviours
10 relies on sampling of WEIRD populations (Western, educated, industrialized, rich, and
11 democratic) ⁴.

12 As a component of the ecological niche that people occupy, diet is a useful lens when
13 studying *both* present and past human populations. Dietary assessment allows for a
14 comprehensive grasp of human social structures, mobility patterns, activities, and overall
15 health ⁵⁻⁸. The methods most often used for assessment of *present* diets still rely on dietary
16 reporting (e.g. food frequency questionnaires and 24-hour recalls), although recent
17 developments have led to the emergence of biomarkers as dietary trackers (e.g. analyses of
18 double labelled water, stable isotope ratios, and gut microbiota) ⁹. Methods for assessing *past*
19 diets are numerous – they include the study of craniomandibular biomechanics, of dental
20 macro- and microwear, of coprolites, of microfossils, of stable isotope ratios, of parasite
21 relationships, of gut microbiota, and of genomic adaptations ^{reviewed in 7}. Clearly, dietary
22 assessment in either of these time frames presents its own set of challenges: present
23 populations are rarely accurate when reporting diet and biochemical approaches can be
24 invasive or laborious, whereas the diet of past populations can only be inferred from proxies,
25 all of which have their limitations. In this context, one of the few methods that has been used
26 to great effect to assess both present and past diets is stable isotope analysis. For instance, in
27 present populations, stable isotope analyses have been successfully used to study associations
28 between diet and diseases ^{e.g. 10,11} and to track food transitions ^{for a review, see 12}. In past
29 populations, stable isotope analyses were first applied to detect the consumption of maize
30 among prehistoric North American groups ¹³, and have since provided ample evidence for
31 specific dietary adaptations, such as the high meat consumption among Neanderthals ¹⁴, or the
32 consumption of C₄ foods by some *Australopithecus* *sps.* ¹⁵.

1 Here, we investigate the degree to which we can use carbon and nitrogen isotopic data to
2 inform us about the diet of different groups living in different environments in Central and
3 East Africa. We compare the isotopic data from different samples, to see if:

- 4 1. we can observe carbon and nitrogen isotopic differences between groups that are
5 known to have different diets;
- 6 2. we can identify dietary factors that result in carbon and nitrogen isotopic changes in
7 hair, nail and breath.

8 Through this work, we aim to further validate the use of stable isotope analysis as a tool of
9 dietary assessment, to expand our knowledge on the isotopic landscape of present diets, and to
10 contribute to the interpretation of past events in tropical Africa.

11

12 **SCIENTIFIC BACKGROUND**

13 Stable isotope analysis is one of the few scientific methods that directly quantifies the diet
14 that an organism consumes throughout its life. This approach is based on the principle that
15 ‘we are what we eat’, i.e. that the chemical components of ingested food find their way into
16 an organism’s tissues in a measurable fashion ¹⁶⁻¹⁸. [However, one must always consider that](#)
17 [other factors, such as metabolism and environment, also influence stable isotopic](#)
18 [signatures](#) ¹⁹⁻²¹. The most common elements used in diet assessment are carbon and nitrogen.

19 In simple terms, carbon isotope analyses distinguish between the types of plants (C₃ or C₄)
20 that are at base of the food chain, while nitrogen isotope analyses track an organism’s position
21 in the food chain ²²⁻²⁵. Within archaeology, stable isotope studies are more often performed
22 on bone collagen and bioapatite. However, the technique is applicable to other tissues
23 containing carbon and nitrogen, including hair, nails, skin, and muscle ^{26,27}.

24 Stable isotope ratios have been validated for use as dietary biomarkers based on three types of
25 work. First, controlled feeding studies, mostly conducted in animals ²⁸, but in some cases also
26 in humans ^{29,30}; second, observational studies in free-living populations ^{10,31-34}, and finally,
27 large-scale global surveys ^{35,36}.

28 [Notwithstanding](#) [Nevertheless](#), additional validation studies are necessary if stable isotope
29 biomarkers are to reach their full potential. On the one hand, new controlled feeding studies in
30 humans may clarify aspects of the isotopic metabolism, such as diet-issue fractionation, and
31 macronutrient routing. On the other [hand](#), observational studies in diverse populations could

1 evaluate the effect of different diets on isotopic signals, and contribute to our understanding
2 of global variation in the chemical uptake of different elements in different human groups ¹².

3 Only a handful of studies have investigated the carbon and nitrogen isotopic signals of
4 modern groups in Africa ³⁵. Among these, we find different types of work: (1) forensic studies
5 using isotopic signals to allocate geographical origin to unknown individuals, with very few
6 samples of African origin ^{37,38}, (2) archaeological studies investigating the diets of historic
7 and prehistoric populations in East and South Africa ³⁹⁻⁴², and (3) one observational study that
8 analysed three living populations in the eastern margin of Lake Turkana ⁴³, one of which
9 (El Molo) overlaps with the present study. This paper contributes to our knowledge of the
10 dietary isotopic signature of present-day African populations by targeting groups who have
11 had traditionally different diets, all of whom are undergoing marked changes in subsistence
12 strategy, and focusing on inter-, rather than intra-population dietary changes.

13

14 **EXPERIMENTAL**

15 ETHNIC GROUPS, SUBJECTS, AND SAMPLES

16 The subjects sampled for this study come from six communities and five ethnic groups with
17 different traditional diets and living in different environmental settings across tropical Africa
18 (Table 1, [and Supplementary Section- S1.1. Supporting Information](#)). These groups were
19 chosen because each maintains relatively traditional subsistence strategies that, combined,
20 represent a high dietary diversity – agriculturalists, pastoralists, hunter gatherers, and fishers.
21 The communities studied include: (1) the El Molo fishers from the south-eastern margin of
22 Lake Turkana, Kenya; (2) the Turkana pastoralists from the Kerio Valley, Turkana County,
23 Kenya; (3) the Luhya agriculturalists from Webuye, Kenya; (4) the Luhya fishers from Lake
24 Victoria, Kenya; (5) the Luo fishers from the northern margin of Lake Victoria, Kenya; and
25 (6) the Baka hunter gatherers from the south-eastern rainforest of Cameroon.

26

27 **Table 1.** Summary table on main characteristics of study ethnic groups: ecology, livelihood,
28 and main staples of the traditional diet.

29

30 Fieldwork took place between April and September 2015. Samples were collected in as non-
31 invasive manner as possible. Hair and nail were collected to characterise the protein part of
32 the diet, while breath was collected to characterise the overall diet ^{17,18,44-47}.

1 The participants recruited were in general good health, and did not suffer from any of the
2 diseases known to lead to isotopic fractionation (e.g. [diabetes/liver cirrhosis](#))¹⁹. Sampling
3 aimed at a balanced female/male ratio of adult participants, but this was not always possible
4 ([Supplementary- Table S11, Supporting Information](#)). Breath was sampled around 11 am each
5 morning, or at least three hours after an individual's last meal in order to minimise any
6 diurnal variation or post-prandial effects^{45,48}. Plant and fish foods were also sampled in the
7 field to provide baseline isotopic data against which to compare participants' data.

9 FIELDWORK AND LABORATORY METHODOLOGY

10 The protocols used [were based on standard methods of stable isotope ratio measurements for](#)
11 [each type of sample](#) for hair 46, and 49, for breath 50, for fish collagen 51 ~~for hair and nail collection and~~
12 ~~analysis were based on and O'Connell et al. (2001), the protocols for breath were based on~~
13 ~~Slater, Preston, & Weaver (2004), and the protocols for fish collagen were based on Richards~~
14 ~~& Hedges (1999). Notably Furthermore,~~ two of the fish samples (*Dagaa* and *Ofulu*) were
15 whole fish, and not just the bone. Therefore, these samples were analysed twice: whole, and
16 just the bone (post-dissection).

18 *SAMPLE COLLECTION*

19 For hair collection, 20-30 hairs of at least 2 centimetres (cm) length were cut at the nape of
20 the head⁴⁹. Nail samples were collected by clipping the distal edge of a fingernail⁴⁶. Breath
21 was sampled by having the subject blow through a straw into a 12 millilitre (mL) evacuated
22 Exetainer vial (Labco, High Wycombe, United Kingdom)⁵⁰. For food samples, each item was
23 placed in a 50 ml plastic container, with silica gel added to fish samples for better
24 preservation.

26 *SAMPLE PREPARATION*

27 Each hair sample was cleaned by two successive immersions in a 2:1 mixture of methanol and
28 chloroform (MeOH:CHCl₃) for 30 minutes (min) each, followed by two 30 min rinses in
29 distilled water. After being freeze-dried, 0.8 ± 0.1 milligrams (mg) of sample was weighed
30 into tin capsules for analysis. Each nail sample was cleaned by sandblasting, followed by one
31 30 min rinse in distilled water, one 30 min immersion in 2:1 mixture of MeOH:CHCl₃, and
32 another 30 min rinse in distilled water, with all three steps taking place in an ultra-sonic bath.

1 Samples were then freeze dried and 0.8 ± 0.1 mg were weighed into tin capsules. Breath
2 samples required no preparation prior to analysis.

3 Extraction of collagen from fish bone was carried out in four steps: defatting;
4 demineralisation; gelatinisation; and freeze-drying⁵¹. For defatting, fish bones were soaked in
5 200 ml of 2:1 MeOH:CHCl₃ for 30 min in an ultra-sonic bath, and then left standing
6 overnight in the fume hood. If any fat was left, samples were soaked in new solution, and the
7 procedure was repeated. Once fat was removed, samples were cleaned by two 30 min rinse in
8 distilled water in an ultra-sonic bath. They were then placed in 8 ml 0.5 mole (M)
9 hydrochloric acid (HCl) at 4 °C for several days for demineralisation. During this period, the
10 samples were shaken twice a day and acid was replaced every two to four days. Once
11 demineralised, samples were rinsed three times in distilled water and gelatinised in acidic
12 water (pH 3.0) at 75 °C for 48 hours. The solution was then filtered into tubes using an Eezee
13 filter (8 µm) and freeze-dried. Finally, 0.8 ± 0.1 mg of the resulting collagen was weighed
14 into tin capsules for analysis.

15 Plant samples were dried, ground until homogeneous using a percussion mortar, and then
16 weighed into tin capsules for analysis.

17

18 *ISOTOPIC ANALYSIS*

19 The isotopic analyses of hair, nail, fish collagen, and plant samples were carried out at [the](#)
20 [Godwin Laboratory, Department of Earth Sciences, University of Cambridge](#)~~(removed for~~
21 ~~blind review)~~, using a Costech [elemental analyser \(EA\)](#) coupled in continuous-flow mode to a
22 Thermo-Finnigan Delta V mass spectrometer. Hair and nail samples were analysed in
23 triplicate, with carbon and nitrogen isotopic ~~values-ratios~~ measured on each run. Carbon and
24 nitrogen results are reported as δ values in parts per mil (‰). Due to the high and variable
25 C/N ratio of plant samples, their carbon isotopic ~~ratios-values~~ were measured on a first run
26 using a sample mass of 1 ± 0.1 mg, then again using a mass calculated from the C/N ratio that
27 was obtained in the first analysis to measure $\delta^{15}\text{N}$. Carbon and nitrogen isotopic analyses were
28 measured relative to international standards, VPDB (Vienna Peedee Belemnite) and AIR
29 (atmospheric N₂) respectively,~~and were based on replicate analysis of international and in-~~
30 ~~house standards. Repeated measurements on international and in-house standards showed that~~
31 ~~the analytical error was less than 0.2‰ for both elements. The international isotopic standard~~
32 ~~used was caffeine ($\delta^{13}\text{C}$: -27.5‰ ; $\delta^{15}\text{N}$: $+1.0\text{‰}$, IAEA-600, IAEA, Vienna, Austria), whereas~~
33 ~~the in- house standards were nylon (size standard, Nylon 6, Sigma- Aldrich, Gillingham,~~

1 [United Kingdom](#)), alanine ($\delta^{13}\text{C}$: -26.9% ; $\delta^{15}\text{N}$: -1.4% , L- alanine, Honeywell Fluka,
2 [Bucharest, Romania](#)), protein 2 ($\delta^{13}\text{C}$: -27.0% ; $\delta^{15}\text{N}$: $+6.0\%$, Protein standard OAS,
3 [Elemental Microanalysis, Okehampton, United Kingdom](#)) and again caffeine ($\delta^{13}\text{C}$: -35.9% ;
4 $\delta^{15}\text{N}$: -2.6% , [Elemental Microanalysis, Okehampton, United Kingdom](#)). Analytical errors
5 were less than to 0.2% for both elements.

6 Isotopic analyses of breath were carried out [at Iso-Analytical Limited \(Crewe, United](#)
7 [Kingdom\)](#) ~~at by (removed for blind review)~~ using gas chromatography (GC) coupled in
8 continuous flow with a Europa Scientific Hydra 20-20 mass spectrometer. These analyses
9 were measured relative to a reference gas ($\delta^{13}\text{C}$: -34.56% , [IA-R060, traceable to NBS-19,](#)
10 [which is distributed by the International Atomic Energy Agency, Vienna](#)) diluted to 3.3%
11 CO_2 and were based on replicate analysis of in-house standards. Analytical errors were less
12 than 0.2% for ~~both elements~~ [carbon](#).

14 STATISTICAL ANALYSIS

15 Statistical analyses and figure drawing were performed on the R platform (version 3.3.1) ⁵².
16 The normality of the data was checked graphically using histograms or quantile-quantile
17 plots, and formally using Shapiro-Wilk tests, while the equality of variances was tested using
18 Levene's test. Inferential tests were adapted to the specific statistical question, but as a rule,
19 when the assumptions of the test were not met, robust versions of the tests were used.
20 Whenever possible, we report the effect sizes of the tests ^{53(p57)}.

22 ETHICS

23 Fieldwork data collection in Kenya was carried out under [the IN-AFRICA Project permit](#)
24 [granted to Prof. Marta Mirazón Lahr by the Government of the Republic of Kenya](#)
25 [\(NACOSTI/P/15/2669/4758\)](#) ~~(removed for blind review)~~ permit granted by the Government of
26 the Republic of Kenya. An exploration licence was also obtained from the National Museums
27 of Kenya that specifically includes the present work. During fieldwork, all Kenyan
28 participants signed a consent form, or, if illiterate, had the consent form read out to them in
29 their language, and a thumb print was taken instead. Fieldwork in Cameroon was approved by
30 [the Centre National de la Recherche Scientifique \(CNRS\), Agence National de la Recherche](#)
31 [\(ANR\) and Institut de Recherche et Développement \(IRD\) and was carried out as part of the](#)
32 [international agreement between the IRD and the Ministry of Scientific Research and](#)

1 [Technology of Cameroon](#).(removed for blind review). Consent from participants in Cameroon
2 was obtained orally.

3

4 **RESULTS**

5 ASSESSMENT OF QUALITY OF RESULTS

6 A total of 134 hair samples and 82 nail samples produced reliable results on the basis of a C/N
7 ratio in the range of 3.0 to 3.8 ^{46,49} and low replicate measurement errors (<0.3 ‰ for $\delta^{13}\text{C}$ and
8 <0.4 ‰ for $\delta^{15}\text{N}$). Similarly, a total of 184 breath samples were considered reliable on the
9 basis of CO_2 concentrations greater than 3 ‰. Assessment of the quality of fish (collagen)
10 samples was based on a C/N ratio in the range of 2.9 to 3.6 ⁵⁴ and the same replicate
11 measurement errors as those of hair and nail (Supplementary Section S1-2.1, [Supporting](#)
12 [Information](#)).

13

14 COMPARISON WITHIN AND BETWEEN POPULATIONS

15 Variation in the isotopic signal of all body pools within populations was explored in terms of
16 the potential effects of sex and age. No statistically significant associations with age and sex
17 were observed, nor with pregnancy or breastfeeding (Supplementary Section S1-2.2, [and](#)
18 [Supplementary Tables S14-6, Supporting Information](#)).

19 Variation in the isotopic signal of carbon and nitrogen between the sampled populations was
20 explored separately in each of the sample body pools. The statistical results obtained for
21 between-group variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each body pool are presented below. Figure 1
22 and Table 2 illustrate and summarise the human isotopic results for all body pools.

23

24 **Figure 1.** Stable isotopic results of the body pools analysed, by livelihood and population: (A)
25 carbon and nitrogen isotopic ratios of hair; (B) carbon and nitrogen isotopic ratios of nail
26 (shaded areas in the hair and nail plots represent bagplots – two dimensional boxplots – that
27 contain 50% of the data distribution); (C) carbon isotopic ratios of breath according to time of
28 collection (in hours).

29 **Table 2.** Summary measures of carbon and nitrogen isotopic results, by body pool and by
30 population.

1

2 *HAIR DATA*

3 Robust analysis of variance (rANOVA) found a significant effect of population on both hair
4 $\delta^{13}\text{C}$, $F_t = 481.5$, $p < 0.001$, $\zeta = 0.95$, and hair $\delta^{15}\text{N}$, $F_t = 42.8$, $p < 0.001$, $\zeta = 0.79$
5 (Supplementary Section- SI-2.2, Supporting Information). Based Table 3 informs on the
6 ~~robust~~ *post hoc* tests that followed (Table 3)-Taken together, the hair isotopic results show
7 that the Baka hunter gatherers have the lowest carbon and the highest nitrogen isotopic
8 signals, and are thus, the most distinct group. Among the Kenyan populations, the Webuye
9 Luhya agriculturalists have the highest carbon isotopic signal, while the remaining four
10 groups overlap considerably in both carbon and nitrogen isotopic signals. Among these latter
11 four groups, the Turkana (Kerio) pastoralist have the lowest carbon isotopic signal and the
12 widest nitrogen isotopic range. The three remaining groups (the Luo, Lake Victoria Luhya
13 and the El Molo) are all fishers and expected to share a dietary isotopic signature, although
14 they do not present the expected ^{15}N enrichment associated with a high trophic position ¹⁷.
15 Nevertheless, the hair isotopic results of the El Molo are closer to those of the Turkana
16 (Kerio) than to the two fishing groups from Port Victoria.

17

18 **Table 3.** Robust *post hoc* results for hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (with 20% trimmed means, 5000
19 bootstrap samples, and an FDR correction). The cells above the diagonal represent the
20 pairwise comparisons between groups for hair $\delta^{15}\text{N}$, whereas the cells below the diagonal
21 represent the pairwise comparisons between groups for hair $\delta^{13}\text{C}$. Values in each cell are the
22 robust effect size (ζ) for each pairwise comparison. Shaded cells are significant comparisons
23 ($p < 0.05$).

24

25 *NAIL DATA*

26 A standard ANOVA found a significant effect of population on nail $\delta^{13}\text{C}$, $F(4, 77) = 38.5$,
27 $p < 0.001$, $\omega^2 = 0.65$, as did the robust ANOVA on nail $\delta^{15}\text{N}$, $F_t = 7.48$, $p < 0.01$, $\zeta = 0.50$
28 (Supplementary Section- SI-2.2, Supporting Information). Based on Table 4 reports the
29 ~~standard~~ *post hoc* tests that followed ~~for carbon isotopic results and on the robust *post hoc*~~
30 ~~tests that followed for nitrogen nail isotopic results~~(Table 4)-Overall, the nail carbon isotopic
31 results show a similar pattern to those of hair data, where the Turkana (Kerio) and the
32 El Molo are more depleted in ^{13}C , followed by the Luo and Luhya from Port Victoria

1 (although these two groups are only significantly different from the Turkana, and not from the
2 El Molo), and finally by the Luhya (Webuye), more enriched in ^{13}C . The *post hoc* analyses of
3 nail found fewer significant comparisons than those of hair, possibly because of the lower
4 sample size available for nail statistical tests. Contrary to the carbon isotopic results, the
5 pattern in nitrogen isotopic signal of nail differs from that of hair. The Luhya (Webuye) are
6 more depleted in ^{15}N than all other groups, who have similar values. Therefore, while hair
7 nitrogen isotopes fail to discriminate the Luhya (Webuye) from both the El Molo and the
8 Turkana (Kerio), $\delta^{15}\text{N}$ on nail does. This discrepancy in hair and nail $\delta^{15}\text{N}$ values could
9 indicate a metabolic difference between the two tissues ⁴⁶, as discussed in the section
10 Comparison between Body Pools.

11
12 **Table 4.** *Post hoc* results for nail: standard for $\delta^{13}\text{C}$ and robust for $\delta^{15}\text{N}$ (with 20% trimmed
13 means, 5000 bootstrap samples, and an FDR correction). The cells above the diagonal
14 represent the pairwise comparisons between groups for nail $\delta^{15}\text{N}$, whereas the cells below the
15 diagonal represent the pairwise comparisons between groups for nail $\delta^{13}\text{C}$. Values in each cell
16 for carbon pairwise comparisons are the standard effect size, r , while values for nitrogen
17 comparisons are the robust effect size, ζ . Shaded cells are significant comparisons ($p < 0.05$).

18
19 *BREATH DATA*

20 Before examining inter-population differences in breath $\delta^{13}\text{C}$, an analysis of covariance
21 (ANCOVA) with time of collection as covariate was performed to test for potential residual
22 effects of diurnal variation. The results show that time of collection was not significantly
23 related to breath $\delta^{13}\text{C}$, $F(1, 176) = 0.46$, $p = 0.5$, partial $\omega^2 = 0.00$, suggesting that the
24 collection standard (sampling around 11 am) was kept to an adequate level. Hence, a standard
25 ANOVA was applied instead, which found a significant effect of population on breath $\delta^{13}\text{C}$,
26 $F(5, 178) = 71.5$, $p < 0.001$, $\omega^2 = 0.66$.

27 ~~Based on Table 5 reports the standard *post hoc* tests that followed (Table 5) for breath $\delta^{13}\text{C}$.~~
28 ~~Overall, the breath carbon isotopic results find three groups: one significantly depleted in ^{13}C~~
29 ~~represented by the Baka; a second group, also depleted in ^{13}C but to a lesser extent than the~~
30 ~~Baka, which includes the three fishing populations (El Molo, the Luo, and the Luhya from~~
31 ~~Port Victoria) and the Turkana (Kerio); and a group comparatively enriched in ^{13}C , the Luhya~~
32 ~~farmers from Webuye.~~

1

2 **Table 5.** Standard Post hoc results for breath $\delta^{13}\text{C}$. Values in each cell for carbon pairwise
3 comparisons are the standard effect size, r . Shaded cells are significant comparisons
4 ($p < 0.05$).

5

6 Breath $\delta^{13}\text{C}$ varies more within groups than either nail or hair $\delta^{13}\text{C}$ (Table 2), so that fewer
7 statistically significant differences among groups were observed, and the differences found
8 overlapped with observations already made for $\delta^{13}\text{C}$ in hair and nail. The body isotope pools
9 act as buffers against the effects of short-term fluctuations in diet on the $\delta^{13}\text{C}$ of hair and nail.
10 These buffering mechanisms do not include breath, which therefore, shows a faster response
11 to dietary changes in isotopic signal that results in greater variation in breath $\delta^{13}\text{C}$ among
12 individuals^{55,56}.

13

14 *FOOD DATA*

15 Although this work includes a relatively small portion of the range of plants and animals
16 consumed as food by the groups being studied, a few compelling patterns are observed in
17 their isotopic signals (Figure 2, Table 6).

18

19 **Figure 2.** Carbon and nitrogen isotope ratios for individual food samples.

20 **Table 6.** Carbon and nitrogen isotope ratios for individual food samples.

21

22 Carbon isotopic ~~ratios~~ ~~values~~ clearly distinguish between the three food categories: C_3 foods,
23 C_4 foods, and fish. For plants, these ~~values~~ ~~isotopic ratios~~ fall within the expected ranges²⁵,
24 while the ~~values~~ ~~ratios~~ of the fish samples that we tested span the entire isotopic range
25 between the C_3 and C_4 foods analysed, most likely tracing the plant diet at the base of the
26 food chain^{18,57}.

27 The $\delta^{15}\text{N}$ plant ~~values~~ ~~isotopic ratios~~ varied more than is suggested for either leguminous or
28 non-leguminous plants in the literature^{17,58}. This finding is understandable since many factors
29 affect the $\delta^{15}\text{N}$ values of plants⁵⁹. In particular, high nitrification rates in soil, within a wet

1 agriculture context^{59,60}, [use of animal-derived fertilisers](#)^{21,35,61} and low precipitation and high
2 temperatures^{20,21,35} could explain the high $\delta^{15}\text{N}$ values observed^{20,21,35}. In addition, although
3 the overall dispersion of nitrogen isotopic [ratios/values](#) observed in fish is smaller than that of
4 plants, we observe two clusters among fish analysed, one around +5 ‰ and one around
5 +10 ‰, which may correspond to a trophic level difference ([Supplementary Section S1-2.2,](#)
6 [Supporting Information](#)). No clear trophic shift is detectable between the fish foods and the
7 plants analysed. Different and not mutually exclusive effects may contribute to this: it could
8 be that the analysed plants are enriched in ^{15}N , as discussed before, that the food chains in
9 these lakes are short, and that the base of the food chain in the two lakes (Turkana and
10 Victoria) is depleted in ^{15}N ⁶².

11 Finally, we also observe that food samples from Webuye have relatively low nitrogen isotopic
12 [ratios/values](#). Given the very small sample size, this finding is tentative; nevertheless, it may
13 explain the lower nitrogen isotopic [ratios/values](#) of the Luhya (Webuye).

14

15 COMPARISON BETWEEN BODY POOLS

16 The present work also considered how the different body pools relate to each other
17 isotopically ([Supplementary Section S2.3, Supporting Information](#)). [Here, we must consider](#)
18 [the different time scale of growth and sampling for each body pool: 1 cm of hair represents](#)
19 [one-month growth](#)⁶³, [1 cm of nail represents three months' growth](#)⁶⁴, [and breath will signal a](#)
20 [diet change after only three hours, simply associated with digestion time](#)⁵⁵, [whereas hair](#)
21 [sampling is much closer to the time of formation than nail sampling. Therefore, it is possible](#)
22 [that a changing diet associated with seasonality could explain the differences between the](#)
23 [sampled body pools. However, none of the participants reported substantial changes in diet in](#)
24 [the months prior to sampling, suggesting other factors may play a role. The results are](#)
25 [summarised here, and detailed analyses can be found in Suppl. SI 2.3.](#)

26 We found that hair is slightly enriched in ^{13}C in relation to nail, but this enrichment is
27 negligible, as [previously suggested](#)⁴⁶ [by O'Connell et al. \(2001\)](#). This slight enrichment may
28 be explained by differences in the amino acid composition of the two tissues – hair is richer in
29 cysteine and serine than nail⁴⁶ – combined with the enrichment in ^{13}C observed in cysteine
30 and serine⁶⁵.

31 We found that hair is depleted in ^{15}N in relation to nail, which is also consistent with previous
32 studies^{35,46}. However, we believe that this relationship cannot be modelled with a simple

1 fixed offset⁴⁶. It is possible that the intracellular turnover of amino acids differs between the
2 hair follicle and the nail matrix⁴⁶. This explanation is untested but supported by the stronger
3 effect of metabolism on the composition of nitrogen isotopes (through the de- and
4 transamination of amino acids)^{29,49}, and by the lack of constant offset between the $\delta^{15}\text{N}$ of
5 different tissues and their corresponding pools of free amino acids⁶⁶. ~~Notwithstanding the
6 underlying model that explains the depletion of hair ^{15}N in relation to nail, this finding
7 clarifies the differences found between hair and nail in the $\delta^{15}\text{N}$ of each population studied.~~

8 Finally, we found that it was not possible to model accurately the isotopic relationship
9 between breath $\delta^{13}\text{C}$ and hair or nail $\delta^{13}\text{C}$, because breath $\delta^{13}\text{C}$ is extremely variable due to
10 the rapid response of this body pool to dietary intake, and because hair ~~and nail~~ ~~and versus~~
11 breath record diet differently – hair ~~and nail~~ records the protein part of the diet preferentially,
12 while breath records the overall diet. Thus, this relationship will depend on the type of protein
13 source that the populations consume (e.g. C_3/C_4 -based or marine)^{67,68}. Indeed, the best fitting
14 model was obtained when considering each diet separately. When dealing with mixed diets
15 and complex systems, a simple model fails to explain the relationship between the isotopic
16 signal of different tissues.

18 DISCUSSION

19 The results of this study show that stable isotope analyses distinguish between traditional
20 diets in tropical Africa, although not always in the way expected. Our results can be grouped
21 into those that reveal isotopic patterns that are particular to the tropical African environment,
22 those that uncover recent changes to traditional diets, and (to a lesser extent) those that hint at
23 the complex innerworkings of the human isotope metabolism. These results will be discussed
24 separately, and in order to frame them in the wider context of isotopic research in modern
25 diets, the discussion compares our findings to other isotopic studies on human hair and nail.

27 ISOTOPIC PATTERNS OF THE TROPICAL AFRICAN ENVIRONMENT

28 Our study found that the inclusion of freshwater fish in the diets of tropical African groups is
29 difficult to detect through the analysis of nitrogen isotopic results, since we detected no
30 signals of a clear trophic shift between fisher (El Molo, Luhya and Luo from Port Victoria)
31 and non-fisher populations (Turkana from Kerio, Luhya from Webuye, and Baka). This
32 observation is likely to result from the combined effects of high nitrogen isotopic ~~ratios~~ ~~values~~

1 in local plants and the low nitrogen isotopic [ratios/values](#) in the lacustrine fish sampled. As
2 discussed earlier, a wet agriculture context ^{59,60}, [use of animal-derived fertilisers^{21,35,61}](#), and
3 low precipitation and high temperatures ^{20,21,35} could explain the high $\delta^{15}\text{N}$ values observed in
4 plants, whereas the low $\delta^{15}\text{N}$ values of fish could result from short food chains in these lakes
5 or from a ^{15}N -depleted baseline ^{62,69}. The last two explanations are not mutually exclusive, as
6 there is evidence that food chains in Lake Victoria are short ⁷⁰ ([Campbell, Hecky, and
7 Wandera 2003](#)) but also that nitrogen-fixing cyanobacteria contribute to ^{15}N depletion at the
8 baseline in both lakes ^{24,43,69,71–73}. Worth noting, the nitrogen isotopic [ratios/values](#) of fish
9 obtained in this study are close to those found by other isotopic studies on the aquatic fauna of
10 these two lakes (Lake Turkana and Lake Victoria) ^{43,62,70} ([Kiura 2005, 292; Gownaris et al.
11 2015; Campbell, Hecky, and Wandera 2003](#)). As such, these findings suggest that lake fish
12 consumption is hard to detect in an East African context, which could be relevant to the
13 interpretation of archaeological isotopic events. However, one must consider that shortening
14 of food webs and proliferation of cyanobacteria in Lake Turkana and Lake Victoria are at
15 least partially the result of recent human activity through the introduction of invasive species
16 (e.g. Nile Perch in Lake Victoria) and pollution ^{62,70,72}.

17 The hunter gatherer Baka have a very distinct isotopic signal characterised by low carbon and
18 high nitrogen isotopic signals. On the one hand, the forest environment where they live,
19 dominated by C_3 plants, easily clarifies the first result, although the “canopy effect” might
20 also contribute to the lowering of carbon isotopic [ratios/values](#) ⁷⁴. On the other hand, the high
21 nitrogen isotopic signal cannot be easily explained by high meat or fish consumption, [or by
22 any of the factors that explain the high nitrogen isotopic ratios of plants in Kenya \(wet
23 agriculture context, use of animal-derived fertilisers, combined low precipitation and high
24 temperatures\), since none of these factors are present in the hunter gatherer forest
25 environment. ~~and~~ instead, the \$^{15}\text{N}\$ enrichment](#) might result from the complex pathways of
26 nitrogen isotopic fixation in tropical forests. This explanation is supported by isotopic
27 analyses of primate hair in West African forests, which also report relatively high $\delta^{15}\text{N}$ values
28 ^{75–77}.

29

30 RECENT CHANGES TO TRADITIONAL DIETS

31 The agriculturalists Luhya in Webuye have the highest carbon isotopic signal, which probably
32 derives from a high consumption of C_4 plant foods. In fact, the carbon isotopic signal of hair
33 and nail among the Luhya (Webuye) is very close to the values obtained for C_4 plant foods in

1 that region, suggesting that the protein component of this group's diet is entirely based on C₄
2 plants. Therefore, the lower nitrogen isotopic signal of this group might arise from ¹⁵N
3 depleted staples (Figure 2), and not from a lower consumption of animal and fish foods. Also
4 relevant, the Luhya from Webuye are known to have traditionally supplemented their diet
5 with termites ⁷⁸. However, almost all participants in this study declared they did not eat
6 termites or consumed them in negligible quantities. Furthermore, previous studies ^{79,80} did not
7 find that insects had particularly enriched-high nitrogen isotopic signatures.

8 The Turkana were chosen as a representative of traditional pastoralists of Kenya. However,
9 the isotopic analyses indicate that the particular community of Turkana from the Kerio Valley
10 has replaced animal foods with C₄ plant foods, probably due to an ongoing sedentarisation
11 process ^{81,82}. Notwithstanding, this was the population with the wider variability in nitrogen
12 isotopic ratios-values, which indicates that individuals with very different diets might be
13 present within the group. The effects of recent changes in diet are also visible to some extent
14 in the other Kenyan groups, most notably in the Luhya (Webuye). Although some reliance on
15 C₄ plants is expected given the global distribution of such staples, the very high carbon
16 isotopic values-ratios detected in this study indicate an over-reliance on these foods. This is
17 not consistent with traditional diets – instead, it concurs with famine relief programmes in the
18 case of the Turkana, which often supply maize as nutritional support to populations, and
19 through the increasing participation in market economies in the case of the Luhya (Webuye)
20 ⁸³⁻⁸⁷.

21

22 ISOTOPIC DIFFERENCES BETWEEN HUMAN BODY POOLS

23 Isotopic differences between sampled body pools may represent a changing diet recorded by
24 the different time scale of growth and sampling for each body pool, with nail representing the
25 longest time span and breath the shortest. However, we found no strong indication this is the
26 case in this study. Instead, this study confirmed that hair is slightly ¹³C enriched in relation
27 to nail, possibly due to disparate amino acid compositions, but that this difference is not
28 significant^{35,46}. We also found that a simple offset did not accurately model the relationship
29 in the nitrogen isotopic signal of hair and nail, which can be explained by differences in the
30 intracellular turnover of amino acids. Similarly, it was not possible to model accurately the
31 isotopic relationship between breath $\delta^{13}\text{C}$ and hair or nail $\delta^{13}\text{C}$, possibly due to the high
32 variability in breath $\delta^{13}\text{C}$, which itself is a result of the rapid response of this body pool to

1 dietary intake, but also to the complex relationship between these body pools in the context of
2 mixed diets.

3

4 COMPARATIVE FRAMEWORK

5 When comparing these results to 16 previous isotopic studies on [contemporary](#) human hair
6 and nail, totalling over 2000 individual hair and nail samples ([Supplementary Section- S1-3,](#)
7 [Supporting Information](#)), we find that both the highest and the lowest carbon isotopic ~~values~~
8 [ratios](#) recorded were obtained by the present study – the Luhya (Webuye) and the Baka,
9 respectively. Regarding nitrogen isotopic signals, our results are consistent with previous
10 studies that have shown that samples of African origin have a higher nitrogen isotopic signal
11 than European ones, even though they originate from populations with a relatively lower
12 consumption of meat and fish. This outcome has been explained by the ^{15}N enrichment
13 observed in hot and arid environments ³⁵. However, this relationship between
14 rainfall/humidity and $\delta^{15}\text{N}$ values has been shown to derive from denitrification processes in
15 the soil that directly affect plants ^{20,88}, rather than through physiological responses at the
16 consumer level, as previously suggested ⁸⁹⁻⁹². Our results are consistent with the plant
17 denitrification hypothesis – variation in the $\delta^{15}\text{N}$ values of the human populations roughly
18 tracks the values of plant staples, i.e. most plant staples are ^{15}N enriched as are most of the
19 populations, while the staples from Webuye have lower $\delta^{15}\text{N}$ values, just as the corresponding
20 human group.

21 Two earlier isotopic studies included one of the populations sampled in our work, so that we
22 can directly compare the results. The first is that of Kiura⁴³ ([2005](#)), who compared multiple
23 aspects of the diet of three populations of northern Kenya who live along the eastern shores of
24 Lake Turkana – two pastoralist groups (Dassanech and Gabra), and the El Molo fishers who
25 also participated in the present study. Kiura ~~analysed-determined~~ the carbon and nitrogen
26 isotopic signals of [eight](#) human hair samples, as well as of the staples consumed directly and
27 indirectly. She reports higher $\delta^{13}\text{C}$ (~~mean~~ $= -14.3 \pm 0.7 \text{‰}$, ~~n~~ $= 8$) and lower $\delta^{15}\text{N}$
28 (~~mean~~ $= +8.0 \pm 0.6 \text{‰}$, ~~n~~ $= 8$) isotopic signals in the El Molo than the present work ($\delta^{13}\text{C}$:
29 $-16.8 \pm 1 \text{‰}$; $\delta^{15}\text{N}$: $+9.0 \pm 0.8 \text{‰}$) ^{43(pp312-313)}. Several factors may contribute to the
30 differences between the two studies, including samples size and constitution, and short-term
31 differences in diet. The latter may reflect the fact that there was a severe drought in the area
32 during 1999-2001 followed by erratic rains in 2002, which elicited emergency food aid rich in
33 C_4 foods ^{93,94}, and that the population has since decreased the consumption of C_4 foods and

1 increased the consumption of animal foods. In addition, Kiura (~~2005~~) found that the
2 agropastoralists Dassanech had higher nitrogen isotopic ~~ratios~~ values than the Gabra
3 pastoralists, whom in turn had higher ~~values~~ isotopic ratios than those of the Turkana people
4 in the present study. Kiura attributes the higher Dassanech ~~values~~ isotopic ratios to the
5 combined consumption of animal and plant products with high $\delta^{15}\text{N}$ (e.g. sorghum) ^{43(p381)}.
6 This interpretation is consistent with the high nitrogen isotopic ~~ratios~~ values obtained here for
7 the plant samples, but also with the hypothesis that the low nitrogen isotopic ~~ratios~~ values of
8 the Turkana communities of the Kerio Valley included in this study reflect a sedentarisation
9 process and decreased consumption of animal products.

10 The second study is that of Ambrose ~~and~~ DeNiro³⁹ (~~1986~~), who studied the isotopic signals
11 from the bone collagen of 97 archaeological humans from South and East Africa. Relevant to
12 the present work, they found that 7 bone samples from historic Turkana and Dassanech
13 (combined) had lower $\delta^{13}\text{C}$ levels (~~mean~~ -14.6 ± 2.9 ‰) and higher $\delta^{15}\text{N}$ levels
14 (~~mean~~ $+13.8 \pm 1.3$ ‰) than those reported here for either hair and nail samples among 27
15 Turkana³⁹. This further endorses the view that there has been a significant recent change in
16 the diet of the Turkana communities living along the Kerio Valley; the differences may also
17 partly reflect the fact that the data for the two populations (Turkana and Dassanech) in
18 ~~Ambrose & DeNiro's study (1986)~~ this study was combined, as suggested by the
19 comparatively much larger standard deviations of the reported mean values.

20 The changes in diet detected in these two studies highlight the variation observed not only
21 horizontally within a population, but also vertically through time, which emphasizes the
22 ability of individuals to adjust to new conditions and environments. This is consistent with the
23 differences we observed between the declared diets of the individuals who participated in our
24 study and those traditionally attributed to their communities on a historical basis. For
25 example, not only different Luhya communities focus on different staple diets in Webuye and
26 Port Victoria, but many individuals from the Webuye community can no longer be described
27 as traditional farmers since they take full part in the regional market economy. Similarly,
28 while traditional nomadic pastoralism was the main subsistence strategy amongst most
29 Turkana communities historically, most groups today, including those from the Kerio Valley
30 who participated in our study, have become largely sedentary, increasingly depending on a
31 maize-based diet^{81,82,95} (~~B. Campbell et al. 1999; McCabe 1990; Ellis et al. 1987~~).

32 Overall, this work provides novel data on the isotopic signatures of tropical African
33 populations. It extends the known range of $\delta^{13}\text{C}$ values in human hair by providing evidence

1 on the strongly C₃ plant-based diet of the hunter gatherer Baka, and on the strongly C₄ plant-
2 based diet of the agriculturalist Luhya (Webuye). It also shows that, within an East African
3 context, the consumption of lacustrine fish might be difficult to detect isotopically due to the
4 high nitrogen isotopic content of plants and the low nitrogen isotopic content of fish.
5 Furthermore, among the ethnic groups for whom dietary information is available at different
6 points during the last 50 years – the El Molo, and the Turkana – we find evidence of relatively
7 recent changes in diet. Taken together, these findings reinforce the view that the dietary
8 diversity of different populations today remains poorly understood, and that stable isotopic
9 analyses are a useful tool for tracking the dynamics of food transitions, such as those
10 associated with urbanisation or with food aid interventions. Finally, this work corroborates
11 that in order to achieve a more complete picture of the isotopic signal of a targeted organism,
12 we should include different types of body pools and all components of the food web in the
13 analyses.

14

15 **CONCLUSION**

16 In summary, we found that the hunter gatherer Baka have low carbon and high nitrogen
17 isotopic signals, consistent with the tropical forest environment they inhabit. In contrast, the
18 Luhya from Webuye and the Turkana have high carbon and relatively low nitrogen isotopic
19 signals, indicating they have diverged from a traditional agriculturalist and pastoralist diet,
20 respectively. We also found that the consumption of fish from Lake Victoria and Lake
21 Turkana does not lead to a trophic shift between fisher (El Molo, Luhya and Luo from Port
22 Victoria) and non-fisher populations (Turkana from Kerio, Luhya from Webuye, and Baka).
23 Finally, we confirmed that hair is very slightly ¹³C enriched in relation to nail, but that the
24 relationship between the δ¹⁵N of hair and nail is more complex, as is the one between breath
25 δ¹³C and hair or nail δ¹³C. Thus, this study addresses a gap in our knowledge of the isotopic
26 signals of tropical African populations with well-known traditional diets, which in some cases
27 are rapidly changing through increasing sedentism and inclusion in market economies.

28 This study also highlights the need of more information at both population and individual
29 levels. At the population level, it is necessary to collect more data on the isotopic variation of
30 traditional diets across the world. As Western diets or even famine relief foods expand their
31 reach, a lot of the diversity of human diet is being lost, and with it, the opportunity to
32 understand the significance of such subsistence strategies in a past and present context. At the
33 individual level, it is necessary to better understand the processes that determine isotopic

1 signals through controlled studies on the isotopic metabolism of the individual. We believe
2 that such knowledge will enable a more effective use of isotopic analyses to track dietary
3 changes, allowing us to better design dietary interventions and to preserve dietary diversity.

4
5 [Acknowledgements We would like to thank all the participants that agreed to take part in this](#)
6 [project and put up with our puzzling requests with grace and patience. The authors are also](#)
7 [grateful to Catherine Kneale and James Rolfe \(University of Cambridge\) for their help with](#)
8 [isotopic analysis and to Prof. Jonathon Grey for helpful advice on fish webs in East African](#)
9 [lakes. M.A.C. is grateful to Luis A. Vasconcelos \(Josie\) for support throughout the writing](#)
10 [process. All authors wish to thank the European Research Council \(ERC 295907\) for financial](#)
11 [support. We are also grateful to the two anonymous reviewers for their useful comments on](#)
12 [the manuscript.](#)

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Table 1

Summary table on main characteristics of study ethnic groups: ecology, livelihood, and main staples of the traditional diet.

	El Molo	Turkana	Luhya	Luo	Baka
Field site	Layeni 02°49'36"N, 36°41'50"E	Nakurio 02°52'23"N, 36°08'30"E	Webuye 0°35'57"N, 34°46'47"E	Port Victoria 0°5'47"N, 33°58'42"E	Moangé-Le-Bosquet 3°4'34"N, 13°31'47"E
	Komote 02°51'19"N, 36°41'33"E	Lotukomo 02°46'57"N, 36°12'17"E	Port Victoria 0°5'47"N, 33°58'42"E		
Population size	~ 600	~ 900 000	>5 000 000	>4 000 000	>30 000
Ecology	semi-arid	semi-arid	sub-humid	sub-humid	humid
<i>Temperature</i>	28°C	29°C	20°C	22°C	23°C
<i>Rainfall</i>	<200 mm	~200 mm	>1600 mm	700-1300 mm	>1600 mm
Traditional livelihood	fishers	pastoralists	agriculturalists	fishers and agriculturalists	hunter gatherers
Main staples described in the literature	lake fish, goat, chicken and other lake birds; maize, rice, beans, tea, sugar ⁸⁶	milk and blood, meat on special occasions; sorghum, maize, wild plants (e.g. doum palm fruit) ⁹⁶	chicken, sheep, goats, beef, fish if close to water bodies; maize, beans, finger millet, sweet potatoes, bananas ^{83,84,97}	fish, beef, chicken, sheep, and goats; maize, sorghum, and beans, but also cassava and sweet potatoes ^{85,97}	small fish, wild game, and insects; wild yam, mushrooms, crops like cassava, plantain, taro, and okra ^{98,99}

Table 2
[Summary measures of carbon and nitrogen isotopic results, by body pool and by population.](#)

POPULATION	HAIR			NAIL			BREATH	
	<i>N</i>	$\delta^{13}\text{C}/\text{‰}$	$\delta^{15}\text{N}/\text{‰}$	<i>N</i>	$\delta^{13}\text{C}/\text{‰}$	$\delta^{15}\text{N}/\text{‰}$	<i>N</i>	$\delta^{13}\text{C}/\text{‰}$
El Molo	27	-16.8 (1.0)	+9.0 (0.9)	9	-16.6 (0.5)	+10.2 (0.9)	29	-19.8 (1.9)
Turkana	21	-17.5 (1.0)	+8.9 (1.3)	20	-17.5 (1.1)	+10.4 (1.1)	32	-18.9 (2.5)
Luhya (Webuye)	17	-13.6 (1.0)	+8.5 (0.5)	15	-13.1 (1.2)	+9.5 (0.5)	32	-15.5 (2.2)
Luhya (Port Victoria)	18	-16.1 (1.8)	+9.7 (0.8)	17	-15.7 (0.9)	+10.6 (0.9)	30	-19.1 (2.5)
Luo (Port Victoria)	18	-15.6 (1.2)	+9.7 (0.6)	21	-15.8 (1.2)	+10.3 (0.4)	29	-19.3 (1.8)
Baka	33	-23.1 (0.6)	11.4 (0.9)	—	—	—	32	-25.5 (1.6)

Note. Values are mean (standard deviation). Robust measures of central tendency and dispersion are found in [Supplementary- Table S42 \(Supporting Information\)](#). Values in **bold** indicate a sampling distribution that deviates significantly from normality (Shapiro Wilk test, $p < 0.05$, [Supplementary- Table- S43, Supporting Information](#)).

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Table 3

Robust post hoc results for hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (with 20% trimmed means, 5000 bootstrap samples, and an FDR correction). The cells above the diagonal represent the pairwise comparisons between groups for hair $\delta^{15}\text{N}$, whereas the cells below the diagonal represent the pairwise comparisons between groups for hair $\delta^{13}\text{C}$. Values in each cell are the robust effect size (ζ) for each pairwise comparison. Shaded cells are significant comparisons ($p < 0.05$).

		HAIR $\delta^{15}\text{N}$					
		El Molo	Turkana	Luhya (Webuye)	Luhya (Port Vict.)	Luo (Port Vict.)	Baka
HAIR $\delta^{13}\text{C}$	El Molo	—	0.2	0.4	0.5	0.6	0.9
	Turkana	0.5	—	0.1	0.5	0.6	0.9
	Luhya (Webuye)	1.0	1.0	—	0.9	0.9	1.0
	Luhya (Port Vict.)	0.4	0.6	0.8	—	0.1	0.9
	Luo (Port Vict.)	0.7	0.9	0.9	0.3	—	0.9
	Baka	0.9	0.9	0.9	1.0	1.0	—

Notes. Interpretation of ζ : small = 0.15, medium = 0.35, and large = 0.50 ^{100(p169)}.

Table 4

Post hoc results for nail: standard for $\delta^{13}\text{C}$ and robust for $\delta^{15}\text{N}$ (with 20% trimmed means, 5000 bootstrap samples, and an FDR correction). The cells above the diagonal represent the pairwise comparisons between groups for nail $\delta^{15}\text{N}$, whereas the cells below the diagonal represent the pairwise comparisons between groups for nail $\delta^{13}\text{C}$. Values in each cell for carbon pairwise comparisons are the standard effect size, r , while values for nitrogen comparisons are the robust effect size, ζ . Shaded cells are significant comparisons ($p < 0.05$).

		NAIL $\delta^{15}\text{N}$				
		El Molo	Turkana	Luhya (Webuye)	Luhya (Port Vict.)	Luo (Port Vict.)
NAIL $\delta^{13}\text{C}$	El Molo	—	0.2	0.7	0.4	0.1
	Turkana	0.4	—	0.7	0.1	0.4
	Luhya (Webuye)	0.9	0.9	—	0.9	0.9
	Luhya (Port Vict.)	0.5	0.7	0.8	—	0.4
	Luo (Port Vict.)	0.3	0.6	0.7	0.1	—

Note. Interpretation of r : small = 0.10, medium = 0.30, and large = 0.50 ^{53(p58)};
Interpretation of ζ : small = 0.15, medium = 0.35, and large = 0.50 ^{100(p169)}.

Table 5

Standard Post hoc results for breath $\delta^{13}\text{C}$. Values in each cell for carbon pairwise comparisons are the standard effect size, r . Shaded cells are significant comparisons ($p < 0.05$).

	El Molo	Turkana	Luhya (Webuye)	Luhya (Port Vict.)	Luo (Port Vict.)	Baka
El Molo	—					
Turkana	0.2	—				
Luhya (Webuye)	0.7	0.6				
Luhya (Port Vict.)	0.2	0.0	0.6	—		
Luo (Port Vict.)	0.2	0.1	0.7	0.1	—	
Baka	0.8	0.8	0.9	0.8	0.9	—

Notes. Interpretation of r : small = 0.10, medium = 0.30, and large = 0.50^{53(p58)}.

Table 6
Carbon and nitrogen isotope ratios for individual food samples.

Location (Ethnic Group)	Sample	$\delta^{13}\text{C}/\text{‰}$	<i>n</i>	$\delta^{15}\text{N}/\text{‰}$	<i>n</i>
Layeni (El Molo)	Sorghum (<i>Sorghum bicolor</i>)	-12.1	2	+3.6	2
	Maize (<i>Zea mays</i>)	-11.3 (0.1)	3	+4.8 (0.1)	3
	Tilapia (<i>Oreochromis niloticus</i>)	-13.1 (0.0)	3	+3.8 (0.0)	3
	Golefish (<i>Hydrocynus forskahlii</i>)	-16.4 (0.0)	3	+9.3 (0.1)	3
	Flatfish (<i>Barbus turkanae</i>)	-24.0 (0.1)	3	+4.9 (0.1)	3
	Catfish (<i>Bagrus sp.</i>)	-21.9 (0.1)	3	+9.7 (0.1)	3
	Mudfish (<i>Clarias sp.</i>)	-12.9 (0.0)	3	+3.9 (0.1)	3
Nakurio (Turkana)	Doum palm fruit (<i>Hyphaene ventricosa</i>)	-25.9 (0.2)	3	+4.0	2
	Sorghum (<i>Sorghum bicolor</i>)	-12.1 (0.8)	3	+7.4	2
Webuye (Luhya)	Beans (<i>Phaseolus vulgaris</i>)	-30.5 (0.1)	3	+5.2	2
	Cow peas (<i>Vigna unguiculata</i>)	-27.6 (0.3)	3	+2.4	2
	Maize (<i>Zea mays</i>)	-12.0 (0.4)	3	+1.1	2
Port Victoria (Luhya and Luo)	Soya beans (<i>Glycine max</i>)	-28.8 (0.3)	3	+13.2	2
	Beans (<i>Phaseolus vulgaris</i>)	-26.6	2	+7.2 (1.5)	3
	Cassava (<i>Manihot esculenta</i>)	-24.1 (0.1)	3	—	—
	Rice (<i>Oryza sativa</i>)	-28.5 (0.1)	3	+15.7	2
	Cow peas (<i>Vigna unguiculata</i>)	-27.5 (0.3)	3	+10.2	2
	Green peas (<i>Pisum sativum</i>)	-26.5 (0.2)	3	+2.9 (1.0)	3
	Sorghum (<i>Sorghum bicolor</i>)	-12.2	2	+9.1 (1.2)	3
	Finger millet (<i>Eleusine coracana</i>)	-13.0 (0.1)	3	+7.7	2
	Yellow maize (<i>Zea mays</i>)	-11.9 (0.3)	3	+5.9	2
	Dagaa (<i>Rastrineobola argentea</i>)	-18.4	2	+9.4	2
	Dagaa (whole)	-19.4 (0.1)	3	+11.0 (0.1)	3
	Ofulu (<i>Haplochromis sp.</i>)	-17.7 (0.1)	3	+9.1 (0.1)	3
	Ofulu (whole)	-19.6 (0.0)	3	+9.8 (0.1)	3
	Nile perch (<i>Lates niloticus</i>)	-15.9 (0.1)	3	+8.8 (0.0)	3
	Helicopter fish (<i>Protopterus sp.</i>)	-18.2 (0.1)	3	+7.0 (0.0)	3
	Esebu (<i>Clarias sp.</i>)	-20.9 (0.0)	3	+5.6 (0.1)	3
Tilapia (<i>Oreochromis niloticus</i>)	-16.1 (0.1)	3	+4.9 (0.1)	3	

Notes. Values are mean (standard deviation) *n* = number of replicates.

^a Isotopic analysis to determine the $\delta^{15}\text{N}$ of cassava failed systematically, possibly as a result of its low nitrogen content. Consequently, this datum point is not plotted in Figure 2.

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