Supplementary Information for

Nitrogen isotopic composition of tooth enamel organic matter records trophic position in modern and fossil ecosystems

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Supplementary Information

Tooth Formation

To reconstruct adult diet, and avoid the isotopic effect of breast milk consumption [1-4], the teeth that mineralize latest in life were targeted in this study whenever possible (Tab. 1). In most mammals, the latest forming tooth is the third permanent molar. In this study only elephants, felids (lions and leopards), canids (African wild dogs) and hyenas, differ in their tooth formation.

Elephants have a total of six successively developing molars (M1 – M6) in each dental quadrant which are shed throughout their lifetime as wear. For this study we sampled M4 or later forming molars, (i.e., 7 years of age and older [5]) which erupt after the individuals are fully weaned [6]. One juvenile elephant was also sampled, and was included in $\delta^{13}C_{bone\text{-}collagen}$ *versus* $\delta^{13}C_{enamel}$ correlation (Fig. S4), but was otherwise excluded from our analyses. For this specimen the M1 or M2 was sampled, which develop between 0 and 2 years of age [5]. This individual would have still relied heavily on breastmilk at the time that it died (weaning in African elephants occurs between 3.5 to 6 years of age[6]), thus its $\delta^{15}N_{enamel}$ value likely incorporates a weaning signal. In this case, tooth enamel and mandibular bone collagen would have formed during the same time, and this is reflected in similar $\delta^{15}N$ values ($\delta^{15}N_{enamel}$ = 10.7 ‰; $\delta^{15}N_{collagen}$ = 10.2 ‰).

Felids have only one molar (M1), which is the latest forming tooth and was therefore sampled for this study. Lions are usually weaned at ca. 6 to 7 months, and first enamel mineralization does not initiate until 9 to11 months, and is concluded by 28 to 36 months [7-9]. Little information is available regarding the rate of tooth enamel mineralization in modern leopards, but canines, molars, and premolars do not erupt until 8 to12 months, about 5 months after weaning [10]. Thus, the stable isotope data reported for felids should reflect adult diet.

African wild dogs are generally weaned at a younger age (35 days) than are most other carnivores, thus their permanent molars mineralize when he animal is consuming an adult diet [11].

In spotted hyenas, the changeover from deciduous to permanent dentition usually takes place between 12 and 14 months [12], with tooth mineralization taking place in the months before eruption (i.e., 11 to 13 months). Hyenas are usually weaned after 12 months, thus permanent teeth mineralize while cubs are still nursing [12]. In this study, hyena $\delta^{15}N_{enamel}$ values are significantly higher than those of other carnivores (p = 0.011), likely as a result of breastmilk consumption during enamel mineralization. In contrast, hyena $\delta^{15}N_{collagen}$ values do not differ from those of the other carnivores (p = 0.990) indicating that death occurred after weaning, when individuals were consuming an adult diet. If hyenas are excluded completely from the dataset the correlation between $\delta^{15}N_{enamel}$ and $\delta^{15}N_{bone\text{-}collagen}$ increases to 0.78.

In conclusion, adult diet is reflected for nearly all taxa in this study (with the exception of the juvenile elephant and hyenas).

Nitrogen isotope variability in tooth enamel

The $\delta^{15}N$ values of herbivore body tissues are believed to be determined primarily by the isotopic composition of their diet [13-18], which is in turn controlled by abiotic factors specific to each ecosystem. It has been well demonstrated, for instance, that a negative relationship between plant $\delta^{15}N$ values and rainfall exists at both global and regional scales [19-21]. Plants growing in arid regions tend to have elevated $\delta^{15}N$ values relative to plants growing in regions that

experience greater rainfall. The $\delta^{15}N$ values of plants are in turn passed along to the herbivores that consume them.

In general, the $\delta^{15}N$ values of herbivore body tissues also correlate negatively with rainfall [17,22-26]. However, data from early studies of African mammals recorded unexpectedly high $\delta^{15}N$ values for herbivores living in hot and arid environments, often exceeding the expected degree of trophic ^{15}N enrichment based on rainfall amounts and plant $\delta^{15}N$ values. These studies noted that when the same taxa occurred in different habitats, $\delta^{15}N$ values were greater (by 1 to 3 ‰) in the tissues of individuals living in open and dry habitats (i.e., savannas) than in more closed, wet habitats (i.e., forests) [17,22-25,27]. This enrichment effect has been hypothesized to be the result of physiological adaptations for water conservation. Proposed mechanisms include increased protein catabolism in drought-tolerant taxa [17], increased reliance on amino acids produced by symbiotic gastrointestinal bacteria in arid regions where plant nitrogen content is low [23], and greater utilization of amino acids from hydrolyzed urea [28]. However, when herbivorous taxa in this study were grouped according to water dependence (high, low, and none; after [29]), we found no statistically significant differences in $\delta^{15}N_{enamel}$ (Fig. S5) between groups, suggesting that water dependence does not drive the observed variation in $\delta^{15}N_{enamel}$.

Variation in $\delta^{13}C$ values in tooth enamel

We measured the carbon isotope composition OF tooth enamel bioapatite (i.e. structurally bound carbonate; $\delta^{13}C_{enamel}$) in the same aliquot of tooth enamel powder used to measure $\delta^{15}N_{enamel}$ using the 'cold trap method' of Vonhof et al. [30], which permits high precision analysis of very small (50–100 µg) amounts of enamel. Carbon isotopes are widely used to reconstruct the type of vegetation (C_3 *versus* C_4 plants) consumed by animals (and subsequently by the predators that feed on them)[31-34] Uno et al., 2018. The ability to measure paired carbon and nitrogen isotopic values in a single aliquot of tooth enamel is an important step forward for paleodietary studies.

<u>$\delta^{13}C_{enamel}$ variation in modern African mammals</u>

Herbivores:

As anticipated, browsing and grazing herbivores are separable by their $\delta^{13}C_{enamel}$ values, reflecting the consumption of C_3 and C_4 plants, respectively, with mixed-feeders falling in between. Gorillas (*Gorilla gorilla*) have the lowest $\delta^{13}C_{enamel}$ values, along with duikers (*Philantomba monticola*) and the black rhino (*Diceros bicornis*), reflecting heavy C_3 consumption and possibly a small canopy effect for the gorillas and duikers [35]. Two grazers, the hippopotamus (*Hippopotamus amphibius*) and one of the blue wildebeest (*Connochaetes taurinus*), show $\delta^{13}C$ values typical for mixed feeders, probably due to the consumption of C_3 grasses near water sources. For mixed-feeders, $\delta^{13}C_{enamel}$ values indicate a predominantly C_3-based diet for elephants (*Loxodonta africana*) and springbok (*Antidorcas marsupialis*), and a more C_4-based diet for the impala (*Aepyceros melampus*).

Omnivores:

Existing carbon isotope data indicates that, overall, the typical baboon diet is comprised predominantly of C_3-foods and some C_4-foods (but that the consumption of C_4-based foods is

quite variable between environments), thus $\delta^{13}C_{enamel}$ values for baboons (*Papio*) in this study are consistent with previously published data.

Carnivores:

Isotopic spacing in $\delta^{13}C$ between enamel and collagen (i.e., $\Delta^{13}C_{enamel\text{-}bone\ collagen}$) was, as expected, greater in herbivores compared to carnivores. An offset between the two tissue types occurs because $\delta^{13}C_{collagen}$ reflects the protein component of diet only, whereas $\delta^{13}C_{enamel}$ reflects the whole diet (e.g., protein, carbohydrates, and fats [36]). Thus carnivores, which consume a protein-rich diet, have lower $\Delta^{13}C_{enamel\text{-}bone\ collagen}$ values (4.3 to 4.8 ‰) compared to herbivores (6.8 to 7.6 ‰), whose plant-based diet typically contains less crude protein and greater proportions of carbohydrates [37,38]. The $\Delta^{13}C_{enamel\text{-}bone\ collagen}$ values we observed in this study are therefore in line with the offsets documented in the literature.

Fig. S1. Map of Africa with sampling localities for modern mammals analyzed for their enamel and bone collagen nitrogen isotope composition. For information about the localities (vegetation, climate, altitude), see Table S1.

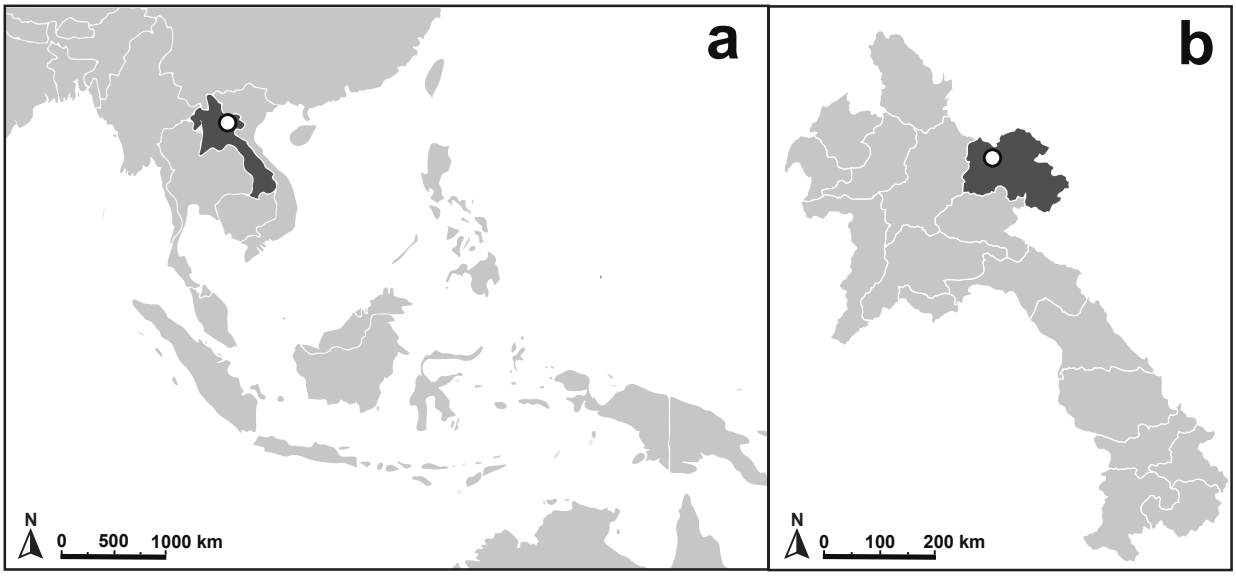


Fig. S2. Map indicating location of Tam Hay Marklot (THM) in southeast Asia (A) and in the Hua Pan Province in Laos (B). This cave locality yielded the Late Pleistocene mammalian teeth analyzed in this study. For further information about geological context, sedimentary deposits, cave filling history, faunal description, chronology, ecology and dating, see [39].

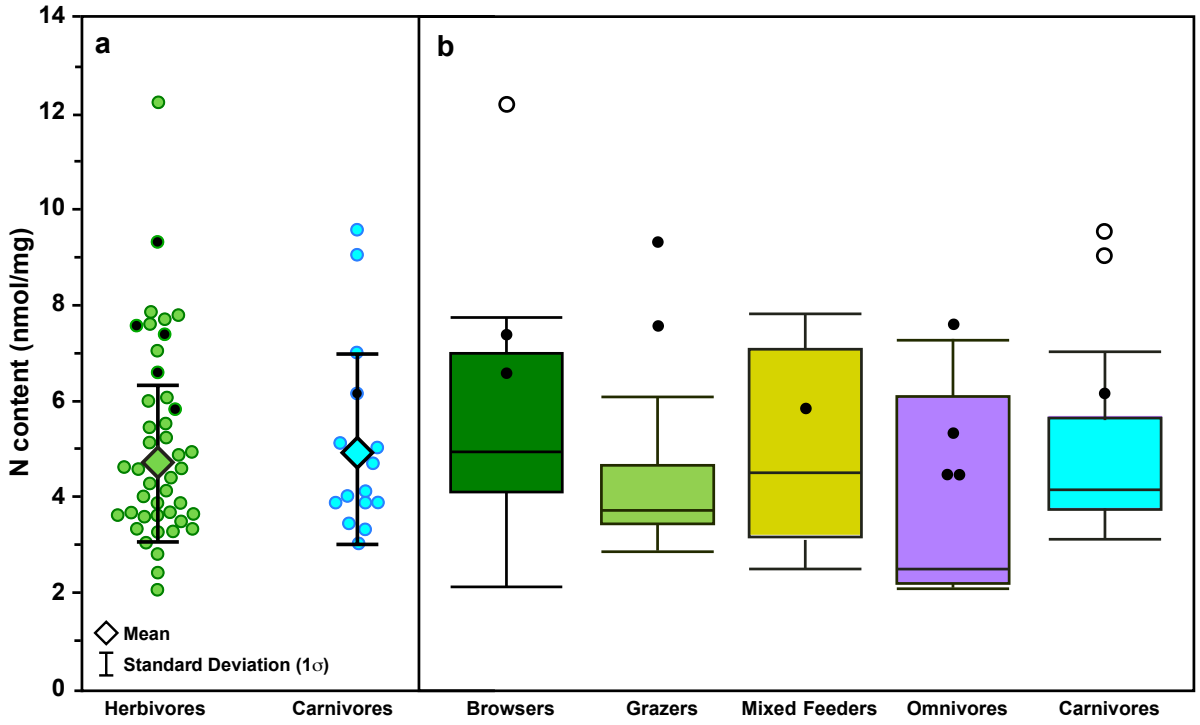


Fig. S3. Nitrogen contents for all enamel samples analyzed in this study. Colored circles and box plots refer to modern African mammal data, filled black circles indicate fossil THM specimens. Fossil data is excluded from calculations for box plots, means, and standard deviations. Open white circles denote outliers Modern and fossil tooth enamel N content fall in the same range and no differences in N content were observed between dietary groups.

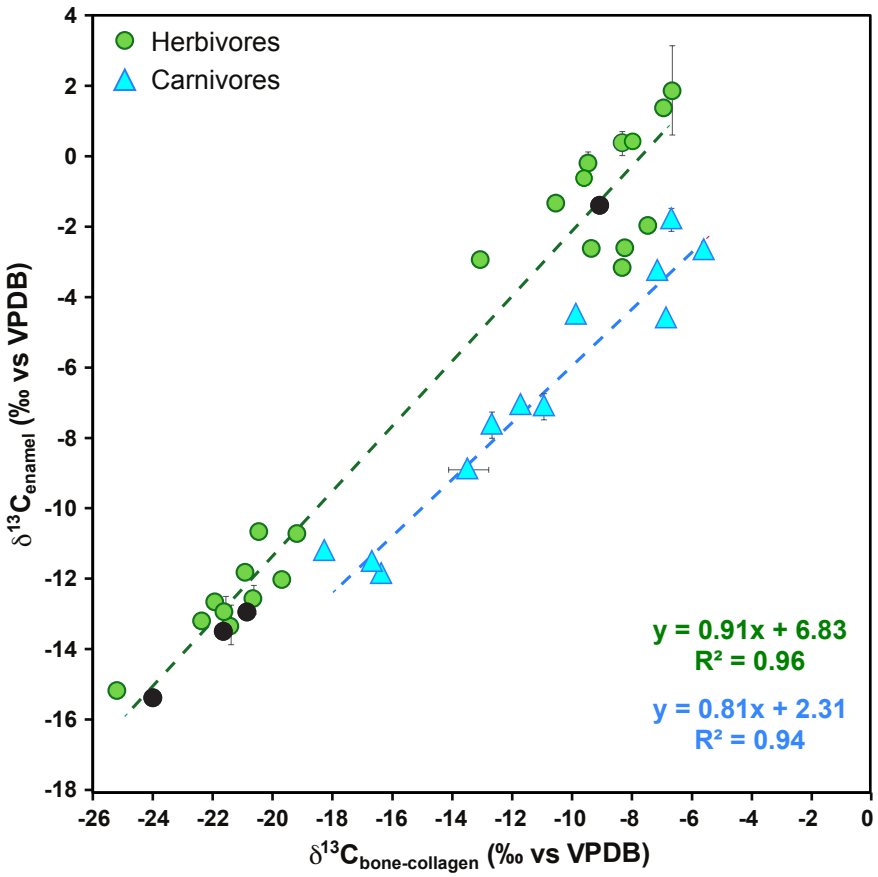


Fig. S4. Regression of paired $\delta^{13}C_{bone\text{-}collagen}$ *versus* $\delta^{13}C_{enamel}$ values ($\bar{x} \pm 1\sigma$) for all modern African mammals (colored symbols; $n = 34$) and THM fossils (black symbols, $n = 4$;$\delta^{13}C_{dentin\text{-}collagen}$). The dashed lines and equations indicate the regression between the two variables for modern herbivores (green) and carnivores (blue). Note the positive correlation between bone collagen and enamel values within each diet group, as well as the higher $\delta^{13}C_{bone\text{-}collagen}$ values for the carnivores compared to the herbivores.

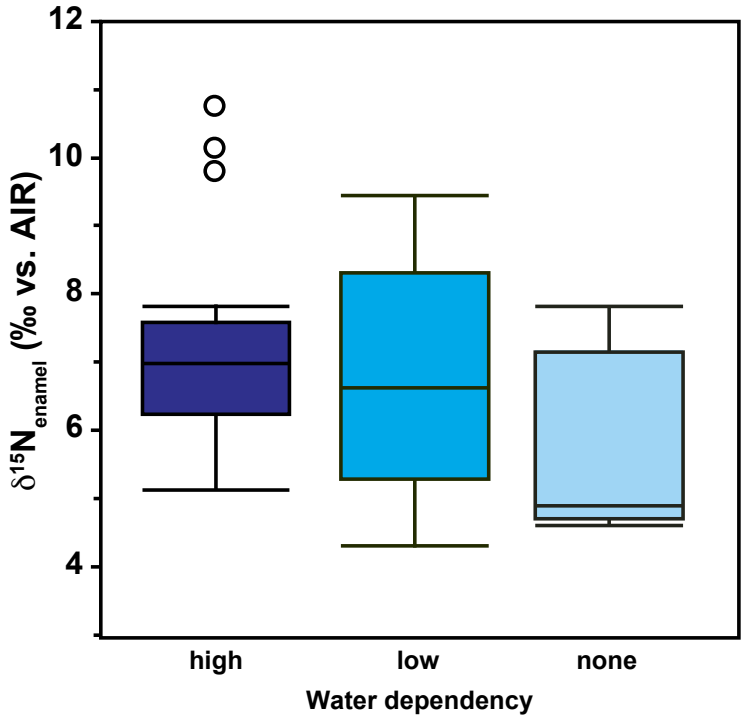
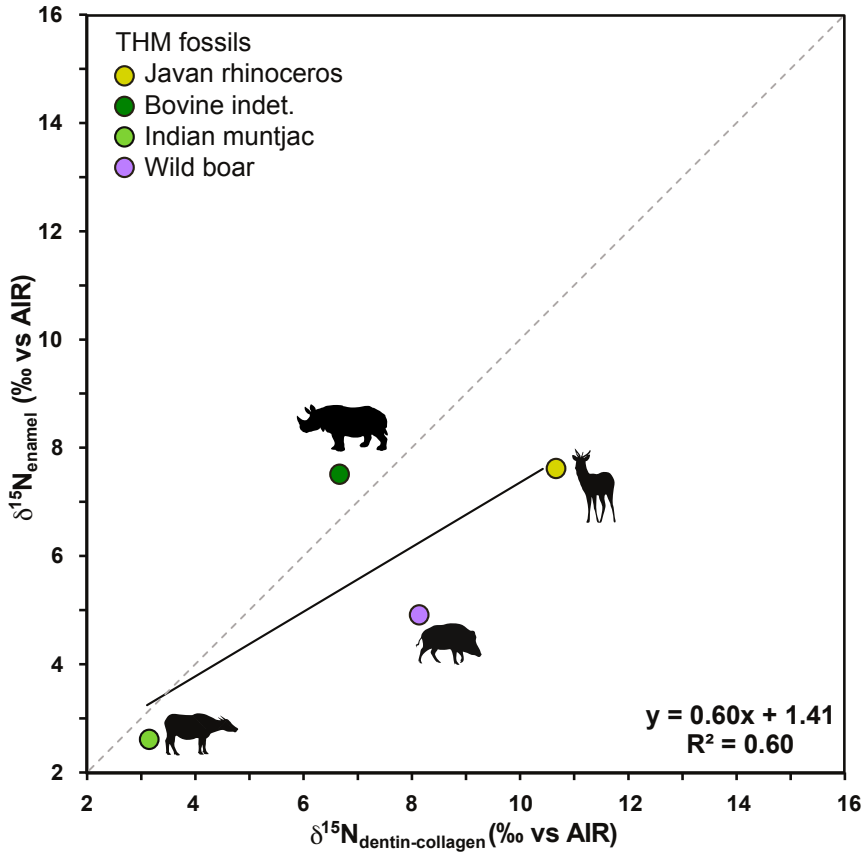


Fig. S5. $\delta^{15}N_{enamel}$ values for modern African herbivores grouped according to their water dependency in decreasing order (categories high, low, none after [29,40-42] do not show statistically significant differences ($\chi^2(2) = 3.78$, $p = 0.151$; see Table S4 for pairwise comparisons). Open white circles denote outliers.



153 **Fig. S6.** Regression of paired $\delta^{15}N_{dentin\text{-}collagen}$ *versus* $\delta^{15}N_{enamel}$ values ($\bar{x} \pm 1\sigma$) for the fossil Tam
154 Hay Marklot tooth specimens ($n = 4$). The dashed line represents the 1:1 correlation between
155 dentin collagen and enamel values. The solid line indicates the true regression. A positive
156 relationship between measured $\delta^{15}N_{dentin\text{-}collagen}$ and $\delta^{15}N_{enamel}$ is present (see also Fig. 2).

Table S1: Table with modern African mammal locality information (see Figure S1 for map), including altitude in meters above sea level, mean annual precipitation (MAP) in mm/year, mean annual temperature (MAT) in °C (data from WorldClim Version 2.1 bioclimatic variables[43] and dominate vegetation type [44-48].

Country	Locality	Altitude (m)	MAP (mm/year)	MAT (°C)	Dominant vegetation type
Angola	Cambembe	1127	1204	21	Angolan Miombo Woodlands
Angola	Capelongo	1449	968	21	Angolan Miombo Woodlands
Angola	Capolopoppo	526	213	24	Namibian Savanna Woodlands
Angola	Chana	1183	494	22	Angolan Mopane Woodlands, Zambezian Baikiaea Woodlands
Angola	Chitado	846	312	23	Angolan Mopane Woodlands, Zambezian Baikiaea Woodlands
Angola	Cubal	919	957	22	Angolan Scarp Savanna and Woodlands
Angola	Cunene	1425	674	23	Angolan Mopane Woodlands, Zambezian Baikiaea Woodlands
Angola	Dirico	1239	651	22	Zambezian Baikiaea Woodlands
Angola	Dondo	73	701	25	Angolan miombo woodlands and Angolan mopane woodlands
Angola	Luati	1196	933	20	Zambezian Baikiaea Woodlands: Brachystegia, Berlinia, Monotes
Angola	Rio Caporello	1695	1390	20	Angolan Miombo woodlands
Angola	Ruacana	865	338	23	Savanna with thorn trees and broad deciduous trees (Combretaceae), often forest-like, also *Copaifera mopane*
Angola	Secadiva	1591	840	20	Angolan miombo woodlands and Angolan mopane woodlands
Angola	Taka Region	1173	502	21	Angolan miombo woodlands and Angolan mopane woodlands
Cameroon	Yaoundé	722	1604	24	Submontane (900-1500 m) and Montane (>1500 m) forest
Congo	Brazzaville	389	1482	25	Humid tropical forest
Congo	Sanga	678	1614	24	Rain forest, riverine forest, swamp forest, monospecific forest of Limbali (*Gilbertiodendron dewevrei*)
Gabon	Gabon	118	2079	23	Montane forest
Kenya	Aberdare	3419	1491	9	Mountain rainforest
Kenya	Kajiado	1734	554	19	Savanna with thorn trees
Kenya	Lake Baringo	983	659	23	Acacia and Commiphora species with little undergrowth
Kenya	Nanyuki	1944	851	16	Savanna with thorn trees
Kenya	Narok/Maasai-Mara	1852	784	17	Savanna with thorn trees
Kenya	Wamba	1297	795	20	Savanna with thorn trees
Namibia	Etosha Pan	1186	422	23	Dry savanna with broad deciduous trees (Combretaceae), often forest-like, also *Copaifera mopane*
South Africa	Hluhluwe Reservation	348	1031	20	Savanna with thorn trees, subtropical rainforest
South Africa	Umfolozi Reservation	138	969	21	Savanna with thorn trees, subtropical rainforest
Tanzania	Kirawira/Serengeti	1469	842	21	Savanna with thorn and broad-leaved trees
Tanzania	Koma, Mara Region	1134	1043	21	Wet tropical savanna
Tanzania	Makania National Park	824	693	23	Grasslands and woody savanna mosaic
Uganda	Virunga National Park	1278	1239	21	Evergreen tropical rainforest

Table S2: Results of post-hoc Tukey-Howell pairwise comparisons of $\delta^{15}N$ values from enamel bound organic matter and bone collagen for modern African mammals.

Pair	Difference	Lower CI	Upper CI	*p*-value	Significant
			$\delta^{15}N_{enamel}$		
Browser – Grazer	0.4629	-1.1351	2.061	0.9235	NS
Browser – Mixed Feeder	1.8495	-0.1858	3.8849	0.09145	NS
Browser – Omnivore	1.7317	-0.7705	4.2339	0.3015	NS
Browser – Carnivore	4.2352	2.5829	5.8876	2.19E-08	*
Grazer – Mixed Feeder	1.3866	-0.6284	3.4016	0.307	NS
Grazer – Omnivore	1.2687	-1.2169	3.7544	0.6031	NS
Grazer – Carnivore	3.7723	2.1451	5.3996	2.70E-07	*
Mixed Feeder – Omnivore	0.1179	-2.6691	2.9048	1	NS
Mixed Feeder – Carnivore	2.3857	0.3274	4.444	0.01552	*
Omnivore - Carnivore	2.5036	-0.01736	5.0245	0.05243	NS
			$\delta^{15}N_{bone\text{-}collagen}$		
Browser – Grazer	0.3192	-1.9777	2.616	0.9812	NS
Browser – Mixed Feeder	3.2283	-0.01989	6.4766	0.05188	NS
Browser – Carnivore	3.7917	1.4948	6.0885	0.000563	*
Grazer – Mixed Feeder	2.9092	-0.05604	5.8744	0.056	NS
Grazer – Carnivore	3.4725	1.5971	5.3479	0.000126	*
Mixed Feeder - Carnivore	0.5633	-2.4019	3.5285	0.9542	NS

Table S3: Results of pairwise comparisons of $\delta^{13}C$ values of enamel bioapatite and bone collagen using Dunn's post-hoc test with a Bonferroni correction for all measured modern African mammals.

Pair	Mean Rank Difference	Z	SE	*p*-value	Significant
		$\delta^{13}C_{enamel}$			
Browser – Grazer	-34.44	5.7756	5.9637	7.67E-09	*
Browser – Mixed Feeder	-9.163	1.2612	7.2646	0.2072	NS
Browser – Omnivore	-13.6	1.4565	9.3378	0.1453	NS
Browser – Carnivore	-19.1	3.0974	6.1664	0.001952	*
Grazer – Mixed Feeder	25.281	3.5185	7.1852	0.000434	*
Grazer – Omnivore	20.844	2.247	9.2761	0.02464	NS
Grazer – Carnivore	15.344	2.5267	6.0726	0.01151	NS
Mixed Feeder – Omnivore	-4.438	0.4367	10.162	0.6623	NS
Mixed Feeder – Carnivore	-9.938	1.3512	7.3543	0.1766	NS
Omnivore - Carnivore	-5.5	0.5846	9.4077	0.5588	NS
		$\delta^{13}C_{bone\text{-}collagen}$			
Browser – Grazer	-18.92	3.9136	4.8336	9.1E-05	*
Browser – Mixed Feeder	-1.5	0.2194	6.8357	0.8263	NS
Browser – Carnivore	-15.08	3.1205	4.8336	0.00181	*
Grazer – Mixed Feeder	17.417	2.7911	6.2401	0.00525	*
Grazer – Carnivore	3.8333	0.9713	3.9466	0.3314	NS
Mixed Feeder - Carnivore	-13.58	2.1768	6.2401	0.0295	NS

169 **Table S4**: Results of pairwise comparisons of $\delta^{15}N$ values of enamel and bone collagen according to water dependency (categories
170 high, low, none after [29,40,42,49]) using Dunn's post-hoc test with a Bonferroni correction for all measured modern African mammals.

Pair	Mean Rank Difference	Z	SE	*p*-value	Significant
		$\delta^{15}N_{enamel}$			
High – Low	3.5326	0.8708	4.0567	0.3839	NS
High – None	11.658	1.889	6.1714	0.0589	NS
Low – None	8.125	1.2353	6.5771	0.2167	NS
		$\delta^{15}N_{bone\text{-}collagen}$			
High – Low	2.1167	0.6413	3.3006	0.5213	NS
High – None	4.7917	1.3384	3.58	0.1808	NS
Low – None	2.675	0.6431	4.1596	0.5202	NS

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