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Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies

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Abstract The isotope enrichment ϵ^* of ^{13}C between tooth enamel of large ruminant mammals and their diet is $14.1 \pm 0.5\text{‰}$. This value was obtained by analyzing both the dental enamel of a variety of wild and captive mammals and the vegetation that comprised their foodstuffs. This isotope enrichment factor applies to a wide variety of ruminant mammals. Non-ruminant ungulates have a similar isotope enrichment, although our data cannot determine if it is significantly different. We also found a ^{13}C isotope enrichment ϵ^* of $3.1 \pm 0.7\text{‰}$ for horn relative to diet, and $11.1 \pm 0.8\text{‰}$ for enamel relative to horn for ruminant mammals. Tooth enamel is a faithful recorder of diet. Its isotopic composition can be used to track changes in the isotopic composition of the atmosphere, determine the fraction of C_3 or C_4 biomass in diets of modern or fossil mammals, distinguish between mammals using different subpathways of C_4 photosynthesis, and identify those mammals whose diet is derived from closed-canopy habitats.

Key words Isotope fractionation · Enamel · Diet · Carbon isotopes

Introduction

The stable isotopic composition of mammalian tooth enamel is directly related to the isotopic composition of mammalian diet (Lee-Thorp and van der Merwe 1987;

Cerling et al. 1997). The principal reason for the $\delta^{13}\text{C}$ difference in plants is because the C_3 and C_4 photosynthetic pathways produce greatly different $\delta^{13}\text{C}$ values, averaging about -27‰ and -13‰ , respectively (Bender 1971). The ability to reconstruct animal diets using stable isotopes was first demonstrated using collagen (DeNiro and Epstein 1978) and has been used in many modern and archeological settings (e.g., van der Merwe and Vogel 1978; Ambrose and DeNiro 1986a, 1986b; Schwarcz 1991; Bocherens et al. 1994; Cormie et al. 1994; Iacumin et al. 1996). Recently, it was shown that tooth enamel is a faithful recorder of diets in the geological record (Lee-Thorp and van der Merwe 1987) and that it is not susceptible to diagenesis (Quade et al. 1992; Wang and Cerling 1994; Koch et al. 1997). The isotopic composition of tooth enamel has important implications with respect to modern ecology and the reconstruction of modern mammalian diets (e.g., van der Merwe et al. 1990; Vogel et al. 1990) as well as for interpretation of fossil mammalian diets (Lee-Thorp and van der Merwe 1987; Lee-Thorp et al. 1989a, 1989b; Bocherens et al. 1996; MacFadden and Cerling 1996; Cerling et al. 1997).

Several different values have been proposed for the ^{13}C enrichment between plant resources and tooth enamel, ranging from about 9‰ (DeNiro and Epstein 1978; Ambrose and Norr 1993; Tieszen and Fagre 1993), to 12‰ (Krueger and Sullivan 1984) and 14‰ (Bocherens and Mariotti 1992; Cerling et al. 1997). An isotopic difference between diet and bioapatite of 12‰ , 12.5‰ , or $12\text{--}13\text{‰}$ is widely quoted and attributed to Lee-Thorp and van der Merwe (1987) (e.g., Lee-Thorp et al. 1989a, 1989b; Koch et al. 1994, 1995, 1999; Quade et al. 1995; Bocherens et al. 1996). However, although Lee-Thorp and van der Merwe (1987) report $\delta^{13}\text{C}$ values of -0.5 and -14.5‰ for presumed grazers and browsers, respectively, they do not specifically report any $\delta^{13}\text{C}$ values for the diets of the animals sampled, nor do they explicitly state an isotope enrichment factor in that paper. However, average $\delta^{13}\text{C}$ values for C_4 and C_3 plants are widely quoted to be -12.5 and -26.5‰ (e.g., van der Merwe 1991),

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respectively, and seemingly lend support to an isotopic enrichment in ^{13}C of 12‰ between diet and bioapatite.

In this paper, we examine the relationship between $\delta^{13}\text{C}$ of diet and tooth enamel in a variety of mammals from different habitats by measuring $\delta^{13}\text{C}$ values of both the diet and enamel. We find that the enrichment in ^{13}C for tooth enamel compared to diet is about 14‰ for ungulate mammals ranging in size from elephants to diminutive antelopes. We show that the isotopic difference between the NADP-me versus the NAD-me or PEP-ck C_4 subpathways is recorded in tooth enamel by examining mammals from regions dominated by these different C_4 ecosystems. By studying enamel from species collected from the same region in 1968 and in 1997 we show that the atmospheric $\delta^{13}\text{C}$ shift is recorded in mammalian tooth enamel. Further, we demonstrate differences in the isotopic composition of C_3 plants from different ecosystems and suggest these may be used to indicate subtle dietary differences in those mammals feeding only from C_3 plants.

Materials and methods

We analyzed plant parts and teeth from each of the localities reported here. In most localities, plants were collected only once, but for the Turkana Basin they were collected at several different times. Teeth were collected over a period of years for some localities, and during one field season for others. For a few samples, we also collected horn for isotope analysis. Details about the collection at each site, local vegetation, climate, and dietary preferences for different mammals are given below.

Plant samples were combusted in a Carlo-Erba system, analyzed on a GC-IRMS, and results are reported relative to the isotope standard PDB using the notation

$$\delta^{13}\text{C} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ ratios of the sample and the standard, respectively. Replicate analyses are reproducible to 0.1‰. Horn samples were also combusted using a Carlo-Erba system and analyzed on a GC-IRMS.

Enamel samples were physically separated from dentine and cementum by grinding with a diamond or tungsten grinder. Enamel was treated for 18 h in 5% H_2O_2 followed by reaction with 0.1 M acetic acid for 18 h. The treated enamel was then reacted in 100% H_3PO_4 for 36 h at 25°C and purified cryogenically. Because we have previously identified SO_2 as an occasional contaminant in both fossil and modern tooth enamel, we sealed the CO_2 reaction product in a closed glass tube with silver wool and reacted it at 50°C for at least 24 h before analysis on a mass spectrometer. Replicate analyses using this procedure are within 0.2‰ for $\delta^{13}\text{C}$.

Some attention is given here to terminology used to discuss isotope fractionation and enrichment factors. This is necessary because of the confusion resulting from conflicting definitions and because the processes involved in going from diet to bioapatite are not reversible reactions. The formal definition of the fractionation factor involves isotope equilibrium of reversible reactions. In this case, the process involves digestion of isotopically distinct compounds, production of CO_2 in the Krebs cycle, transport and diffusion of CO_2 in body fluids, and fixation of carbon in bioapatite. Therefore, because the relationship between the source diet and the product enamel is not reversible, the entire process is treated as an "apparent fractionation factor" α^* , where:

$$\alpha_{\text{enamel-diet}}^* = (1000 + \delta^{13}\text{C}_{\text{enamel}})/(1000 + \delta^{13}\text{C}_{\text{diet}})$$

Following Craig (1954), the isotope enrichment is given as ϵ^* where:

$$\epsilon^* = (\alpha^* - 1)$$

and the units are reported as ‰. The superscript "*" is used to indicate that isotopic equilibrium is not assumed. This isotope enrichment factor is similar to the "discrimination factor" used in biological science (Farquhar et al. 1982) except that the symbol " Δ " is used in biology. Unfortunately, the symbol " Δ " has been long used in the geological sciences as the numerical difference between two δ values. To avoid confusion in the following discussion we will refer to that difference as $\delta_{\text{enamel}} - \delta_{\text{diet}}$, where:

$$\delta_{\text{enamel}} - \delta_{\text{diet}} = \delta^{13}\text{C}_{\text{enamel}} - \delta^{13}\text{C}_{\text{diet}}$$

Isotopic uncertainties are calculated using the 1σ values for both the enamel and for the diet based on samples with at least three analyses for both diet and enamel.

In this paper, we make the distinction between grazers and hypergrazers, and between browsers and hyperbrowsers. Grazers and browsers have diets that are dominated by, but not exclusively restricted to, grass or browse. Hypergrazers and hyperbrowsers, on the other hand, are those mammals thought to feed exclusively on grass or browse, respectively. Wildebeest and hartebeest are considered to be hypergrazers and have <2% browse in their diet (Lamprey 1963; Casebeer and Koss 1970; Hofmann and Stewart 1972), likewise the African buffalo (McNaughton and Georgiadis 1986). Zebras are considered to be grazers based on the observations that they have 5–15% browse in their diets (Lamprey 1963; Kingdon 1979) although we note that Casebeer and Koss (1970) did not find herbs or browse in zebra dung or stomach content samples. McNaughton and Georgiadis (1986) consider the zebra to be a hypergrazer. The dikdik and giraffe are examples of hyperbrowsers (McNaughton and Georgiadis 1986).

Study areas: maximizing the range of $\delta^{13}\text{C}$ in isotope ecology

We studied a number of different localities to maximize the range of $\delta^{13}\text{C}$ in the diet and therefore tooth enamel, and chose a variety of habitats where the local mammals would use different photosynthetic pathways or subpathways, or where there would be a large difference in the $\delta^{13}\text{C}$ of the C_3 pathway because of environmental effects. Hattersley (1982, 1992) showed that the isotopic composition of C_4 grasses using the NADP-me (hereafter NADP) subpathway were systematically enriched in ^{13}C by about 1–2‰ compared to those using the NAD-me or the PEP-ck (hereafter NAD or PCK, respectively), and that NADP C_4 plants favored mesic environments while the NAD and PCK C_4 grasses were found in more xeric localities. Variation in C_3 plants is due to several factors: although the average $\delta^{13}\text{C}$ value is about -27‰, C_3 plants in xeric sites tend to be enriched in ^{13}C and can have values as high as -22‰, whereas C_3 plants growing under closed canopies are depleted in $\delta^{13}\text{C}$ and can have values as negative as -36‰, or lower (van der Merwe and Medina 1989).

We examined mammals from the same locality over time to check on the isotopic shift due to changing ^{13}C in the atmosphere, which has changed from the pre-industrial value of -6.5‰ to -8‰ for the current atmosphere.

We also examined a variety of mammals to see if there was a measurable difference in the fractionation factor for different mammals. This study includes only ungulate mammals, mostly ruminants, and ranges from very large individuals such as elephants (ca 4000 kg) and rhinoceros (ca 1500 kg), to large bovids such as wildebeest and topi (ca. 200 kg), to the diminutive dikdik antelope (ca 5 kg).

We included in our study ecosystems that were dominated by C_3 plants so that browsers or grazers had only the opportunity to eat C_3 plants. We also examined a variety of mammals from mixed ecosystems where both C_3 and C_4 vegetation was present: we include only those mammals thought to be hypergrazers or hyper-

browsers. For example, Casebeer and Koss (1970) report that zebras consume on the order of 5–15% forbs and herbs; therefore, they are not a good choice to determine the isotope fractionation factor in wild populations in mixed C₃/C₄ ecosystems. On the other hand, other workers claim them to be hypergrazers (Gwynne and Bell 1968; McNaughton and Georgiadis 1986). We decided not to use data from zebras for this analysis (but see discussion below).

Results

C₃ grazers

Northern Mongolia

Northern Mongolia is dominated by C₃ grasslands. Domestic horses were sampled in September 1996 in Arhangai, Bulgan, and Hovsgul Provinces which are between 48 and 50°N latitude, and between about 1500 and 2000 m elevation. The climate is highly seasonal with summer temperatures averaging 15–18°C, but with winter temperatures as low as –25 to –30°C. Rainfall occurs predominantly in the summer, but the mean annual precipitation is less than 300 mm in the valleys, and somewhat higher in the mountains. All samples probably died in the previous year (1995 or 1996) as most of the skeletons showed little weathering. Grasses and sedges, the dominant food of horses in this region, were also sampled on this transect.

The average δ¹³C value of five different grasses and one sedge was –25.3 ± 1.8‰, with a range from –23.6 to –27.6‰ (Appendix 1). Six different teeth from five different horses in the same transect varied from –11.2 to –12.1‰ (Appendix 2). Taken together, these samples from a pure C₃ ecosystem indicate an isotope enrichment

factor ε* between tooth enamel and diet of 13.8 ± 1.9 (Table 1).

Tierra del Fuego, Argentina

The grasses of Tierra del Fuego use the C₃ photosynthetic pathway. Samples of grass and teeth from guanaco were collected on Isla Grande between 53 and 55°S latitude. The climate of Tierra del Fuego is modified by its proximity to the ocean; at low elevations, the summer monthly temperatures are about 12°C and winter monthly temperatures are near 2°C. Annual precipitation varies from about 40 cm/year near Rio Grande to about 75 cm/year at Ushuaia. Samples of grasses were collected in 1998, and additional grasses were analyzed from the herbarium collection at CADIC-CONICET. Taken together, 24 grass samples collected between 1982 and 1998 had an average δ¹³C of –27.6 ± 1.9‰. The guanaco, *Llama guanaco*, is a grazer and had an average δ¹³C of –15.2‰ on Tierra del Fuego. This gives an isotope enrichment factor ε* between tooth enamel and diet of 12.9 ± 1.9‰ (Table 1).

Hogle Zoo, Salt Lake City, Utah

Hogle Zoo in Salt Lake City, Utah, USA, was an important source for a variety of large mammals with known diet in this study. All of the animals were born at Hogle Zoo or were imported when they were very young so that their enamel record of diet is restricted to the interval when they lived at Hogle Zoo. All animals died between 1982 and 1995 and included zebra, elephant,

Table 1 Summary of α*, ε*, and δ_{enamel} – δ_{diet} between enamel and diet for a wide variety of large mammals

Mammal	n	Region	δ ¹³ C _{enamel}	δ ¹³ C _{diet}	Diet	α* _{enamel–diet}	ε* _{enamel–diet}	δ _{enamel} – δ _{diet}
Ruminants								
Okapi	4	Ituri	–20.8 ± 1.0	–34.1 ± 1.7	C ₃ dicot	1.0138 ± 0.0020	13.8	13.3
Guanaco	6	Tierra del Fuego	–15.2 ± 0.4	–27.6 ± 1.9	C ₃ grass	1.0129 ± 0.0019	12.9	12.5
Dik-dik	5	Koobi Fora	–13.5 ± 1.1	–27.2 ± 1.5	C ₃ dicot	1.0140 ± 0.0018	14.0	13.7
Giraffe	9	E. Africa	–13.4 ± 1.4	–27.0 ± 1.7	C ₃ dicot	1.0141 ± 0.0022	14.1	13.7
Camel	3	Hogle Zoo	–13.3 ± 0.4	–26.6 ± 1.3	C ₃ dicot/C ₃ grass	1.0136 ± 0.0013	13.6	13.3
Other	3	Hogle Zoo	–12.8 ± 1.2	–26.6 ± 1.3	C ₃ dicot/C ₃ grass	1.0142 ± 0.0017	14.2	13.8
Wildebeest ^a	5	Amboseli	0.6 ± 1.0	–13.5 ± 0.7	NAD+PCK C ₄ grass	1.0143 ± 0.0012	14.3	14.1
Topi	3	Koobi Fora	1.3 ± 0.3	–12.8 ± 0.8	NAD+PCK C ₄ grass	1.0143 ± 0.0008	14.3	14.1
Buffalo	3	Lewa	1.8 ± 0.1	–12.8 ± 0.8	NAD+PCK C ₄ grass	1.0148 ± 0.0008	14.8	14.6
Wildebeest	10	Nairobi (1997)	2.5 ± 0.5	–11.7 ± 0.7	NADP C ₄ grass	1.0144 ± 0.0008	14.4	14.2
Hartebeest	3	Nairobi (1997)	2.8 ± 0.3	–11.7 ± 0.7	NADP C ₄ grass	1.0147 ± 0.0007	14.7	14.5
Wildebeest	5	Nairobi (1969)	3.5 ± 0.5	–10.6 ± 0.5	NADP C ₄ grass	1.0143 ± 0.0007	14.3	14.1
Hartebeest	5	Nairobi (1969)	3.0 ± 0.7	–10.6 ± 0.5	NADP C ₄ grass	1.0137 ± 0.0009	13.7	13.6
Non-ruminants								
Rhino	7	E. Africa	–13.4 ± 0.4	–27.4 ± 1.5	C ₃ dicot	1.0144 ± 0.0016	14.4	14.0
Zebra	4	Hogle Zoo	–12.2 ± 0.2	–26.6 ± 1.3	C ₃ dicot/C ₃ grass	1.0148 ± 0.0013	14.8	14.4
Other	4	Hogle Zoo	–12.6 ± 0.4	–26.6 ± 1.3	C ₃ dicot/C ₃ grass	1.0144 ± 0.0013	14.4	14.0
Horse	6	Mongolia	–11.9 ± 0.3	–25.3 ± 1.8	C ₃ grass	1.0138 ± 0.0019	13.8	13.4
Mean						1.0141 ± 0.0005	14.1 ± 0.5	13.8 ± 0.6

^a Data from Koch et al. (1991) and Bocherens et al. (1996)

bactrian camel, pigmy hippopotamus, fallow deer, and dall sheep. For most species, only one individual was sampled, except for zebra where two different individuals were sampled. However, in some cases, different teeth were sampled from a single individual so that the diet recorded is from different periods of the animal's life. The diet of all the animals in the zoo was a mixture of grass hay, meadow hay, alfalfa hay, and alfalfa pellets. We sampled these different foods several times between 1991 and 1996 to characterize the isotopic composition of the diet at Hogle Zoo. All of the hay is grown locally, so that there is no C_4 component in the grass or meadow hay over the period of these animals' lives.

The average $\delta^{13}C$ of the diet was $-26.6 \pm 1.3\text{‰}$ for seven samples and the average $\delta^{13}C$ for 15 different teeth averages $-12.7 \pm 0.7\text{‰}$ (Appendix 1, 2). For all these mammals, this gives an average ϵ^* of 14.3 ± 1.4 , and gives an ϵ^* of 13.6 ± 1.3 and 14.8 ± 1.3 for the bactrian camel (*Camelus bactrianus*) and zebra (*Equus burchelli*), respectively, the only species with at least three different analyses (Table 1). The camel and zebras died in the 1980s so that their enamel formed about 10 years before the vegetation was sampled. A correction of around -0.3‰ may be needed for these samples because of the negative trend in the $\delta^{13}C$ of the atmosphere over the last 150 years due to fossil fuel burning (see Discussion) – this would make the ϵ^* s slightly lower (about 13.3 and 14.5, respectively).

Savanna browsers: giraffes, rhinoceros, Kenya

We have a number of individual giraffes (*Giraffa camelopardalis*) and black rhinoceros (*Diceros bicornis*) collected over the period from about 1956 to 1997. The older samples came from the National Museums of Kenya Osteology Department. These individuals lived in a variety of habitats, including the arid Turkana Basin in northern Kenya, the more mesic highlands in the Nairobi region, the shrublands of Laikipia to Lewa in northern Kenya, and the rift valley. In addition several rhinoceros were from the Aberdares highlands. Because of the variety of ages and localities, we calculate a $\delta^{13}C$ value of the tooth enamel corrected to 1997 based on observed changes in the $\delta^{13}C$ of the atmosphere from about -7 to -8‰ between 1956 and 1997 (Keeling et al. 1979; Francey et al. 1995). We then compared those values to Kenyan vegetation samples collected in 1996 and 1997.

We collected a variety of plants in 1997. Most of them were collected after the rainy season although the plants collected in the Turkana Basin in January 1997 were collected after a prolonged drought (see Discussion).

Giraffes are hyperbrowsers (Hofmann and Stewart 1972; Kingdon 1979). To estimate the $\delta^{13}C$ of the diet of giraffes we used the average $\delta^{13}C$ of acacia leaves, their dominant dietary resource which had an average $\delta^{13}C$ value of $-27.0 \pm 1.7\text{‰}$ for 19 samples (range: from

-23.7 to -29.7‰). The average $\delta^{13}C$ value for giraffes, after correction to 1997, was $-13.4 \pm 1.4\text{‰}$ indicating an isotope enrichment ϵ^* of $14.1 \pm 2.2\text{‰}$.

For black rhinoceros, we used the average $\delta^{13}C$ of all C_3 plants from Kenya because the diet of black rhinos is much more varied than that of the giraffe. However, although black rhinoceros are probably hyperbrowsers, their reported dietary preferences include *Aloe*, *Blepharis*, *Euphorbia*, *Sansevieria*, and *Suaeda* (Kingdon 1979) which are C_4 or crassulacean acid metabolism (CAM) dicots (Sage et al. 1999). The $\delta^{13}C$ values for individual plants are given in Appendix 1, and had an average of $-27.4 \pm 1.5\text{‰}$ for 63 C_3 dicots, collected primarily in the Turkana Basin, the Nairobi region, the Laikipia-Lewa-Mpala region, and the Aberdares. Two individuals from arid regions, where C_4 dicots and CAM plants are more abundant had $\delta^{13}C$ values of -10.2‰ (Appendix 2). Such samples were excluded from the average discussed below because they were so far outside the $\delta^{13}C$ values for other hyperbrowsers, and because they came from regions with known abundances of C_4 dicots. We note that the rhinoceros from the Amboseli region (Bocherens et al. 1996), have enriched $\delta^{13}C$ values which probably indicate that they ingest a significant fraction of C_4 dicots or CAM plants which are abundant in this semi-arid setting. The $\delta^{13}C$ for rhino enamel averaged $-13.4 \pm 0.4\text{‰}$ for five individuals. The calculated enrichment factor ϵ^* is $14.4 \pm 1.6\text{‰}$ for these rhinoceros.

Dwarf desert shrubland hyperbrowsers, Turkana Basin, northern Kenya

Here we consider one hyperbrowser, the diminutive dikdik (*Madoqua kirki*) which is found in the Turkana Basin in northern Kenya, an arid dwarf shrubland. It has a mean annual temperature of $29^\circ C$ and a mean rainfall of 180 mm (East African Meteorological Department 1975), and elevations ranging from about 400 to 700 m. Samples were collected during field seasons in the Turkana Basin beginning in 1992, although most of the samples were collected from 1995 to 1997. The dikdik is the smallest mammal of this study with an average mass of about 5 kg.

M.G. Leakey made two plant collections in the Turkana Basin, one in January 1997 and one in July 1997. The January collection was made after a prolonged drought and had an average $\delta^{13}C$ of $-26.6 \pm 1.7\text{‰}$ while the July collection had an average $\delta^{13}C$ value of $-27.9 \pm 0.8\text{‰}$. The differences in $\delta^{13}C$ values during different seasons illustrate the problem in evaluating the enamel–diet fractionation factor, and provides a good reason why many species from different regions should be examined. The average $\delta^{13}C$ for the 40 C_3 dicots of the Turkana Basin was $-27.2 \pm 1.5\text{‰}$.

Seven different dikdik individuals had an average $\delta^{13}C$ value for tooth enamel of $-13.5 \pm 1.1\text{‰}$ indicating an enrichment factor ϵ^* of about $14.0 \pm 1.8\text{‰}$. We

excluded the results from one individual that was $>2\sigma$ outside the mean of the other seven samples.

Closed canopy browsers: Ituri Forest,
Democratic Republic of the Congo (formerly Zaire)

The most negative $\delta^{13}\text{C}$ values in modern plants are found in plants growing below the canopy of closed-canopy tropical forests (e.g., Medina and Minchin 1980; Medina et al. 1986; van der Merwe and Medina 1989). The Ituri Forest is in the Ituri River Basin in eastern Democratic Republic of the Congo (formerly Zaire), between about $0\text{--}3^\circ\text{N}$ latitude and $27\text{--}30^\circ\text{E}$ longitude. The Epulu area is near the center of the Ituri Forest ($1^\circ23'\text{N}$, $28^\circ35'\text{E}$), and is at an elevation of between about 700 and 850 m. It is in the transition zone between two rainforest types: the mixed moist evergreen forest and a mosaic of monodominant forest where *Gibbertiodendron dewevrei* makes up most ($>70\%$) of the large trees (Hart et al. 1996). Mean annual rainfall is about 1700 mm with a distinct dry season from January to March. Mean annual temperature is 25°C with little seasonal variation.

Plants growing beneath the closed canopy in the Ituri region had an average $\delta^{13}\text{C}$ value of $-34.1 \pm 1.7\text{‰}$. The okapi (*Okapia johnstoni*) is an elusive forest dweller that feeds on leaves from the subcanopy. We sampled two individuals, one of whose age was unknown but was pre-1980 and from the eastern Zaire region. The other came from Epulu; for this specimen we analyzed three different teeth: the upper P2, P3, and P4. Because these form at different times in the life of an animal, each tooth represents a somewhat different diet. The four different teeth of okapi had an average $\delta^{13}\text{C}$ value of $-20.8 \pm 1.0\text{‰}$, giving an isotope enrichment factor of $13.8 \pm 2.0\text{‰}$.

C_4 (NAD-PCK) grazers

Northern Kenya

In northern Kenya the grasses are dominated by those using the NAD and PCK C_4 subpathways which is in keeping with the observation that NADP grasses are more common in mesic environments and NAD or PCK grasses are found in more xeric environments (Hattersley 1992). NAD and PCK grasses were collected primarily in the Laikipia region although samples also came from other parts of Kenya. Most of the NAD grazers of this study were from the Turkana Basin although we also present data from the Laikipia region. The average temperature and rainfall in the Turkana region is 29°C and 180 mm/year, while data from Mpala in Laikipia indicate a mean annual temperature and mean annual precipitation of 20°C and 500 mm. The Mpala Ranch is at about 1700 m elevation and grasses using the NAD and PCK subpathways dominate the

local vegetation. Lewa is at about the same elevation, but is somewhat warmer and drier than Mpala. The Samburu Game Reserve is significant lower in elevation at about 900 m and has a mean temperature of about 26°C and receives about 400 mm rainfall each year. NAD and PCK grasses dominate the lower Laikipia region at elevations less than about 1900 m, although NADP grasses can be found in riparian settings.

The average $\delta^{13}\text{C}$ of 27 NAD and PCK grasses collected in 1997 was $-12.8 \pm 0.8\text{‰}$. In general, seeds were enriched in ^{13}C by about 0.5‰ compared to blades of grass. Topi (*Damaliscus lunatus*) sampled from near Koobi Fora in the Turkana Basin had an average $\delta^{13}\text{C}$ value of $+1.3 \pm 0.3\text{‰}$. These data yield an isotope enrichment factor of $14.3 \pm 0.8\text{‰}$ for topi. Buffalo (*Syncerus caffer*) from the Laikipia region had an average $\delta^{13}\text{C}$ value of $1.8 \pm 0.3\text{‰}$, giving an enrichment factor ϵ^* of $14.8 \pm 0.8\text{‰}$. A single Jackson's hartebeest (*Alcelaphus buselaphus jacksoni*) from the Mpala region had a $\delta^{13}\text{C}$ value of $+1.7$ which is compatible with these enrichment factors.

Southern Kenya

NAD and PCK C_4 grasses are the dominant grasses in the Amboseli region studied by Koch et al. (1991) and Bocherens et al. (1996). Koch reported that the average $\delta^{13}\text{C}$ of grasses in the Amboseli region (1990) was $-13.7 \pm 0.7\text{‰}$ and the average $\delta^{13}\text{C}$ for Amboseli wildebeest was $0.6 \pm 1.0\text{‰}$ (Bocherens et al. 1996). These data indicate an enrichment factor of $14.3 \pm 1.2\text{‰}$.

C_4 (NADP) grazers: Athi plains region, Kenya

The Athi plains region near Nairobi is an extensive grassland with riparian forests. In the following discussion we consider the Athi plains, the nearby Nairobi Game Park, and Kitengela to be part of the same ecosystem. Nairobi has a mean annual temperature and precipitation of 18°C and 980 mm, respectively, and the elevation ranges from about 1500 to 1900 m. The vegetation is dominated by *Themeda triandra*, *Hyparrhenia* sp., and other C_4 grasses, most of which use the NADP C_4 subpathway. Hattersley (1992) and others have shown that NADP grasses are favored in mesic environments, whereas NAD and PCK grasses are favored in arid environments. Of particular interest is the observation (Hattersley 1982) that the NADP grasses have a different isotopic composition than NAD and PCK grasses. We analyzed 21 samples of NADP grasses collected in the Kenya highlands in 1997 and found a $\delta^{13}\text{C}$ value of -11.7 ± 0.7 .

The white-bearded wildebeest (*Connochaetes taurinus albojutus*) is a hypergrazer that in the Athi Plains region consumes almost exclusively NADP grasses. Casebeer and Koss (1970) studied wildebeest diets by examining stomach contents and feces and found that it consisted

of >97% grass. The diet through 1 year was dominated (ca 70%) by three species of grass (*T. triandra*, *Pennisetum mezianum*, and *Digitaria macroblephara*) all of which are NADP C₄ grasses. Hofmann and Stewart (1972) also showed that dicots are an insignificant part of the diet of *C. taurinus*. We analyzed teeth from five different individuals from the Nairobi Game Park, all collected in 1997 and all being very recent kills. We analyzed nine different teeth, and from one tooth separately analyzed the base and top of a tooth, giving a total of ten different diets recorded in the enamel. The average $\delta^{13}\text{C}$ for these samples was $+2.4 \pm 0.5\text{‰}$ giving an isotopic enrichment factor of $14.4 \pm 0.8\text{‰}$ for enamel compared to diet.

Three teeth from hartebeest (or kongoni) (*A. b. cokei*) had an average $\delta^{13}\text{C}$ of $2.8 \pm 0.3\text{‰}$, giving an enrichment factor of $14.7 \pm 0.0.7\text{‰}$. The work of Casebeer and Koss (1970) showed that hartebeest is also a hypergrazer with the three grasses *T. triandra*, *P. mezianum*, and *D. macroblephara* ranging from about 70–90% of the identifiable grass species in the diet of hartebeest, and with herbs and browse making up less than 1% of their diet.

The atmospheric $\delta^{13}\text{C}$ shift and changes in the $\delta^{13}\text{C}$ of tooth enamel

The isotopic composition of the atmosphere has changed as a result of fossil fuel burning during the last two centuries. Keeling et al. (1979) and Francey et al. (1995) have documented this trend and find that the $\delta^{13}\text{C}$ of the atmosphere has changed from about -7‰ in 1956 to -8‰ in 1997. It is of interest to examine plants and animals that lived and died when the isotopic composition of the atmosphere was different. In 1968, several herds of wildebeest, Coke's hartebeest, *A. b. cokei*, and zebra were killed in the Kitengela region and some of the material is archived in the National Museum of Kenya. We examined five different wildebeest and five different hartebeest from this collection and found that the $\delta^{13}\text{C}$ values of these species averaged 3.5 ± 0.5 and $3.0 \pm 0.7\text{‰}$, respectively. However, one of the hartebeest samples had a $\delta^{13}\text{C}$ value $>2 \sigma$ outside the mean of the other four individuals, which had an average $\delta^{13}\text{C}$ value of $3.3 \pm 0.4\text{‰}$.

Six samples of *T. triandra* or *Hyparrhenia* (NADP grasses) collected between 1962 and 1966 in southern and central Kenya had average $\delta^{13}\text{C}$ values of $10.2 \pm 0.2\text{‰}$ (Table 1), which is 1.4‰ enriched in ^{13}C compared to the NADP C₄ grasses collected in 1997. This is compatible with the known change in the isotopic composition of the atmosphere from 1965 to 1997 of 0.9‰ . Based on the 1997 grass data and using the known change in the isotopic composition of the atmosphere, the calculated $\delta^{13}\text{C}$ for NADP grasses in 1968 should be -11‰ . Thus, we have two estimates of the $\delta^{13}\text{C}$ of the 1960s diet: that based on the known shift in the atmosphere and that based on a relatively small number of

herbarium samples. Taking the average of the two methods, we estimate the diet of these wildebeest and hartebeest to have been about $-10.6 \pm 0.5\text{‰}$.

Using the samples of NADP C₄ grasses collected in the 1960s from Kenya, and the samples of wildebeest and hartebeest from the 1968 Kitengela herds, enrichment factors of $14.3 \pm 0.7\text{‰}$ and $13.7 \pm 0.9\text{‰}$ were calculated, respectively. (With the exclusion of the anomalous hartebeest sample discussed above, the isotope enrichment factor becomes $14.0 \pm 0.6\text{‰}$.) These are indistinguishable from the enrichment factors determined for wildebeest and hartebeest in 1997 from the same region (Table 1).

Isotope enrichment between horn and diet, and between enamel and horn

We analyzed horn sheath, which is composed of keratin, from several of the individuals for which we have data for the $\delta^{13}\text{C}$ of tooth enamel plus $\delta^{13}\text{C}$ estimates of their diet. In addition, for one zoo animal, we analyzed keratin from hoof and hair. Table 2 shows the results of these analyses and calculated isotope enrichment factors for $\epsilon^*_{\text{horn-diet}}$ and $\epsilon^*_{\text{enamel-horn}}$. For two samples from the Aberdare forest, a bongo (*Boocercus eurycerus*) and a bushbuck (*Tragelaphus scriptus*), the diet was estimated using the $\delta^{13}\text{C}$ values from the Aberdare Forest dicots (Appendix 1). A buffalo (*S. caffer*) from the alpine zone of the Aberdares (K97-222) had a C₃-dominated diet, which is to be expected from the predominance of C₃ grasses above 3000 m in that region (Tieszen et al. 1979). No $\delta^{13}\text{C}$ estimate was made for the diet of that individual because both C₃ and C₄ grasses are present there. A bighorn sheep (*Ovis canadensis*) from the Hogle Zoo contributed hoof and hair which had indistinguishable $\delta^{13}\text{C}$ values (within 0.1‰). The diet and tooth enamel estimates for this individual were taken to be the average for the Hogle Zoo population (Tables 1, 2). Oryx (*Oryx beisa*) and waterbuck (*Kobus ellipsiprymnus*) have a component of C₃ forbs or browse in their diets so no diet estimate was used for those individuals. Taken together, the estimated $\epsilon^*_{\text{horn-diet}}$ and $\epsilon^*_{\text{enamel-horn}}$ values were $3.1 \pm 0.7\text{‰}$ and $11.1 \pm 0.8\text{‰}$, respectively.

Discussion and implications for ecology and paleoecology

Fractionation factor and isotope enrichment between enamel–diet in large ungulate mammals

Taken together, we analyzed a wide variety of wild and captive large mammals from Africa, Asia, and North America and found that the apparent isotope fractionation factor $\alpha^*_{\text{diet-enamel}}$ is 1.0141 ± 0.0005 corresponding to an isotope enrichment of $14.1 \pm 0.5\text{‰}$ (Table 1). Figure 1 shows the relationship between

Table 2 $\delta^{13}\text{C}$ values for keratin (horn, hoof, and hair; $\delta^{13}\text{C}_h$) from wild animals in Kenya and from the Hogle Zoo, Utah, along with $\delta^{13}\text{C}_{\text{enamel}}$ and the estimated $\delta^{13}\text{C}_{\text{diet}}$. $\delta_h - \delta_d$, α_{e-h} , ϵ_{e-h} , and $\delta_e - \delta_h$, and are calculated and tabulated from this data. These results suggest an isotope enrichment of 3.1‰ for horn relative to diet, and 11.1‰ for enamel relative to horn. See text for details

Sample	Material	Common name	Scientific name	Region	Horn $\delta^{13}\text{C}_h$	Enamel $\delta^{13}\text{C}_{\text{enamel}}$	Diet $\delta^{13}\text{C}_{\text{diet}}$		Horn-diet		Enamel-horn		
							α_{h-d}	ϵ_{h-d}	$\delta_h - \delta_d$	ϵ_{e-h}	α_{e-h}	$\delta_e - \delta_h$	
OM-1628	Horn	Bongo	<i>Boocercus eurycercus</i>	Aberdares	-25.1	-15.1	-27.8	1.0027	2.7	2.7	1.0103	10.3	10.0
K97-208	Horn	Bushbuck	<i>Tragelaphus scriptus</i>	Aberdares	-23.6		-27.8	1.0043	4.3	4.2			
K97-228	Horn	Buffalo	<i>Syncerus caffer</i>	Aberdares	-23.3	-11.5					1.0122	12.2	11.9
H1/98.bhs	Hoof	Bighorn sheep	<i>Ovis canadensis</i>	Hogle Zoo	-23.2	-12.7 ^a	-26.6	1.0035	3.5	3.4	1.0107	10.7	10.5
H1/98.bhs	Hair	Bighorn sheep	<i>O. canadensis</i>	Hogle Zoo	-23.1	-12.7 ^a	-26.6	1.0036	3.6	3.5	1.0106	10.6	10.4
K97-389	Horn	Buffalo	<i>S. caffer</i>	Lewa	-11.1	1.9	-12.8	1.0017	1.7	1.7	1.0131	13.1	13.0
OM 1530	Horn	Oryx	<i>Oryx beisa</i>	Turkana	-9.9	0.4					1.0104	10.4	10.3
K97-393	Horn	Waterbuck	<i>Kobus ellipsiprymnus</i>	Lewa	-9.5	0.7					1.0103	10.3	10.2
K97-263C ^b	Horn	Wildebeest	<i>Connochaetes taurinus</i>	Nairobi	-8.7	2.7	-11.6	1.0030	3.0	2.9	1.0115	11.5	11.4
K97-263E ^b	Horn	Wildebeest	<i>C. taurinus</i>	Nairobi	-8.5	2.7	-11.6	1.0032	3.2	3.1	1.0113	11.3	11.2
K97-264C ^b	Horn	Hartebeest	<i>Alcelaphus buselaphus</i>	Nairobi	-8.9	2.9	-11.6	1.0028	2.8	2.7	1.0119	11.9	11.8
K97-264D ^b	Horn	Hartebeest	<i>A. b. cokei</i>	Nairobi	-8.1	2.9	-11.6	1.0036	3.6	3.5	1.0111	11.1	11.0
OM 1529	Horn	Oryx	<i>O. beisa</i>	Nanyuki	-7.9	2.2					1.0102	10.2	10.1
OM-58	Horn	Wildebeest	<i>C. taurinus</i>	Nairobi	-7.3	3.7	-10.6	1.0033	3.3	3.3	1.0111	11.1	11.0
OM-57	Horn	Wildebeest	<i>C. taurinus</i>	Nairobi	-7.1	3.9	-10.6	1.0036	3.6	3.5	1.0110	11.0	10.9
Mean								1.0031 ±	3.1 ±	3.1 ±	1.0111 ±	11.1 ±	11.0 ±
								0.0007	0.7	0.7	0.0008	0.8	0.8

^a The $\delta^{13}\text{C}$ value is the average for all large mammals from Hogle Zoo (see Table 1)

^b K97-263C and E, and K97-264C and D are different segments of the same horn sheath (37 and 13 cm apart, respectively)

$\delta^{13}\text{C}_{\text{enamel}}$ and $\delta^{13}\text{C}_{\text{diet}}$. This value is larger than most previous estimates, which ranged from about 9‰ (Ambrose and Norr 1993; Tieszen and Fagre 1993) to about 12.5‰ (Lee-Thorp and van der Merwe 1987) to the recent report of 14‰ (Cerling et al. 1997). We find that the apparent fractionation factor is indistinguishable for a variety of large ruminant mammals, including camelids, giraffids, and both large and small bovids. Analyses from an elephant, horses, and rhinocerotids are compatible with this isotope enrichment factor, although the data set is not as robust (see below).

This isotope enrichment factor ϵ^* is constant for any fractionation factor, but isotopic differences (i.e., $\delta_{\text{enamel}} - \delta_{\text{diet}}$) are not constant across a large range of $\delta^{13}\text{C}$ values for a single fractionation factor (Table 1). This is illustrated in Fig. 2 which shows that the difference between ϵ^* and $\delta_{\text{enamel}} - \delta_{\text{diet}}$ approaches 0.1‰ for C_4 grazers, but is nearly 0.5‰ for closed-canopy C_3 eco-

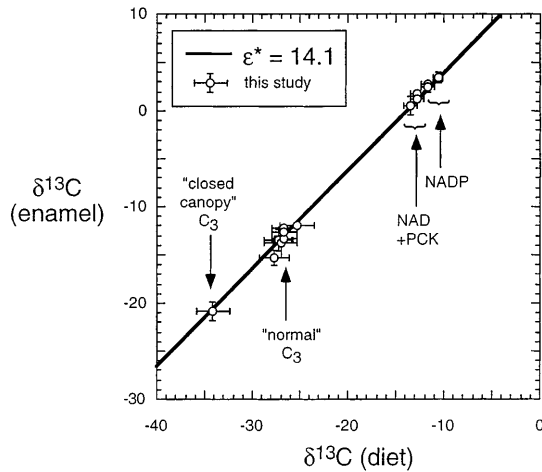


Fig. 1 Relationship between $\delta^{13}\text{C}$ values of estimated diet and measured tooth enamel for the animal populations of this study. The solid line represents the ^{13}C enrichment of 14.1‰ between diet and enamel

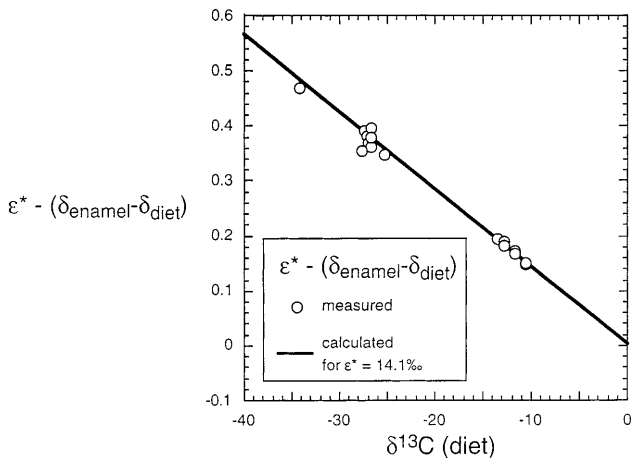


Fig. 2 Difference between ϵ^* and $(\delta_{\text{enamel}} - \delta_{\text{diet}})$ for the samples of this study. Solid line is that predicted for $\epsilon^* = 14.1\text{‰}$

systems. Therefore, isotopic enrichment factors should be used rather than absolute differences between tissue and diet.

In this study, we characterized the isotopic composition of vegetation in natural communities, which was not done in previous studies, and used hypergrazers to characterize C_4 diets in regions where mixed C_3/C_4 ecosystems were present. Most, but not all, of the animals studied were ruminants and so our results may be more applicable to ruminants than to non-ruminants. Metges et al. (1990) showed that ruminant methane has very negative $\delta^{13}\text{C}$ values, and it is possible that animals that produce large quantities of methane may have a different isotope enrichment factor than those producing minor amounts of methane. Ruminants have much higher production rates of methane than other mammals; Crutzen et al. (1986) estimated methane production rates of 6 and 1 moles/kg per year for ruminants and non-ruminants, respectively, from the Serengeti in Tanzania. It is possible that high rates of methane production will affect the total isotope fractionation between diet and enamel. DeNiro and Epstein (1978), Ambrose and Norr (1993), and Tieszen and Fagre (1993) used small rodents in their studies; isotope fractionation and enrichment factors reported here might not be valid for mammals having significantly different physiologies.

Whether or not hypergrazers are used in these types of studies is very important. For example, the zebra (*E. burchelli*) is a grazer according to Lamprey (1963) with about 10% browse in its diet, yet Casebeer and Koss (1970) did not find any browse in the stomach contents of zebra. Gwynne and Bell (1968) also reported that zebra have essentially 100% grass in their diet and McNaughton and Georgiadis (1986) also consider the zebra to be a hypergrazer. So, is the zebra a hypergrazer, in which case it is useful for this study, or is it merely a grazer? Figure 3 shows the isotope relationship between zebras and sympatric confirmed hypergrazers (buffalo, wildebeest, hartebeest, topi). Zebras are consistently 1–2‰ depleted in ^{13}C compared to hypergrazers. Is this due to their consumption of 10% browse, or could it be that zebras have a slightly different isotope enrichment than the ruminant bovids to which they are compared? The range in $\delta^{13}\text{C}$ values for 42 analyses from Burchell's zebra is 4.1‰, whereas the range in $\delta^{13}\text{C}$ values for topi, hartebeest, and wildebeest (28 analyses) is 2.7‰. Thus, there is greater variability in Burchell's zebra than in three species of alcelaphine bovids and so it seems likely that at least some zebra are not hypergrazers. However, without additional data our results are compatible with either interpretation, and may have a bearing on the difference between our conclusions and those of Lee-Thorp and van der Merwe (1987) as discussed below.

The difference between an isotope enrichment of 12‰ (Lee-Thorp and van der Merwe 1987) versus 14‰ (this study) is significant, and may be due to several factors. Lee-Thorp and van der Merwe assumed that zebras were grazers. Their data show that zebras are 1–2‰ depleted

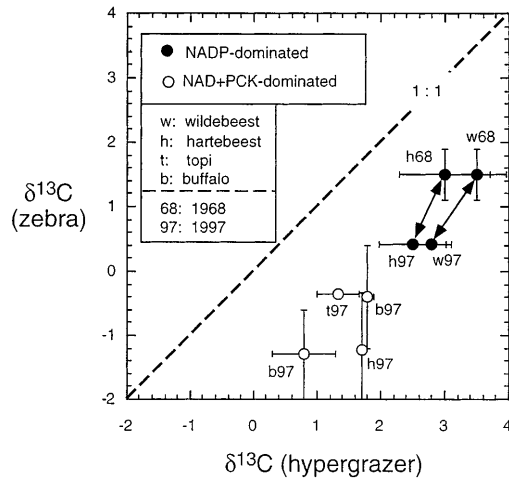


Fig. 3 $\delta^{13}\text{C}$ values for sympatric zebra and known hypergrazers (buffalo, hartebeest, topi, wildebeest) from Kenya. Zebras are consistently depleted in ^{13}C compared to coexisting ruminant hypergrazers. This is compatible with zebras having a small (5–15%) component of C_3 biomass in their diet, or with their being hypergrazers and having a slightly different isotope enrichment factor than ruminants. Both ruminant hypergrazers (wildebeest and hartebeest) and zebras became about 1‰ more negative between 1968 and 1997

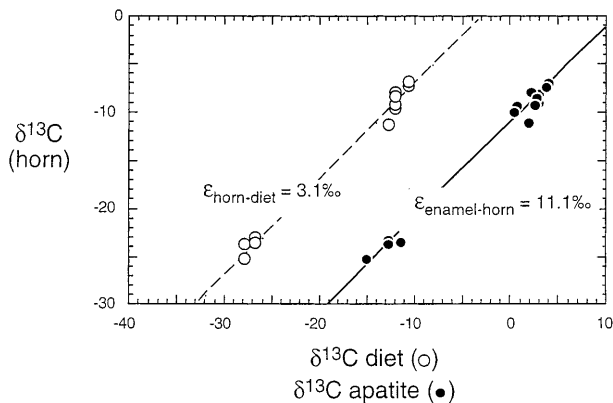


Fig. 4 Relationship between $\delta^{13}\text{C}$ values of keratin (horn, hoof, hair) and estimated diet, and between keratin and tooth enamel. Isotope enrichment factors $\epsilon_{\text{horn-diet}}^*$ and $\epsilon_{\text{enamel-horn}}^*$ of 3.1‰ and 11.1‰, respectively, are also plotted

in ^{13}C compared to wildebeest from the same region – a difference compatible with the observation that zebras have a significant non-grass component to their diet (Lamprey 1963). On the other hand, if zebras are hypergrazers (Casebeer and Koss 1970; Gwynne and Bell 1968), then Lee-Thorp and van der Merwe's (1987) results and our results (Fig. 3) are compatible with an ϵ^* of $13 \pm 1\%$ for equids. Lee-Thorp and van der Merwe (1987) do not report $\delta^{13}\text{C}$ values for local vegetation and so it is difficult to extract exact isotope enrichment factors for grazers and browsers from their data.

This paper does not close the story on isotope enrichment factors between diet and tooth enamel. More studies are needed to clarify the issues of species effects,

habitat effects, experimental conditions, physiology, and other factors. However, in summary, we have found an isotope enrichment of 14.1‰ between diet and bioapatite for wild, large (> 5 kg) ruminant mammals from a variety of environments. Ruminants produce more methane than other mammals. Other large ungulate mammals may have a slightly smaller isotope enrichment, possibly 12–13‰; our data are not yet sufficient to establish that relationship. These isotope enrichment factors may not apply to all mammals; smaller mammals (e.g., rodents) and those that differ significantly in their physiology may result in other isotopic enrichment factors.

Isotope enrichment between horn and diet, and between enamel and horn in ruminants

Our results of 3.1‰ ^{13}C enrichment in horn or hair compared to diet is similar to that found by Nakamura et al. (1982) and by Froment and Ambrose (1995), but is higher than found by DeNiro and Epstein (1978) in their study of mice. We found a consistent enrichment of 11.1‰ in enamel relative to horn for these samples. Table 2 and Fig. 4 shows the $\delta^{13}\text{C}$ relationships between horn and diet and between horn and enamel.

Implications for diets of browsers and grazers

This result has important implications for both modern ecological studies and for paleoecological studies. The significance to modern ecological studies is that tooth enamel can be used to closely characterize the total diet of mammals. This is important in determining whether modern mammals have changed their diets due to increasing competition with humans for scarce resources in different regions of the world. Samples archived in museums can be used to reconstruct diets of mammals that have been dead for many years.

While field observations of the feeding behavior of extant mammals captures much of the diversity in dietary preferences, such studies sometimes miss the mark. For example, observations of elephant feeding behavior in Africa have concentrated on a few localities where elephants had a high grass component in their diet (e.g., Laws et al. 1974). As a result, it is generally believed that savanna elephants eat a significant amount of grass whereas the diet of forest elephants is dominated by browse (e.g., Kingdon 1979; Tanglely 1997). However, isotope surveys done in a variety of places (van der Merwe et al. 1990; Vogel et al. 1990; Koch et al. 1995), many of them areas where direct observation is difficult, show that most savanna elephants are predominantly browsers (Cerling et al. 1999).

Closed-canopy habitats and $\delta^{13}\text{C}$

The closed-canopy effect causing ^{13}C depletion in C_3 plants is well known (Medina and Minchin 1980; van

der Merwe and Medina 1989). This ^{13}C depletion is passed along to the consumer (Ambrose and DeNiro 1986b; van der Merwe and Medina 1991) as was illustrated above with the forest-dwelling okapi having $\delta^{13}\text{C}$ values as negative as -22‰ .

Animal diets and the carbon isotopic composition of the atmosphere

The isotopic composition of the atmosphere became about 0.8‰ more negative between the mid to late 1960s and 1997. We analyzed NADP grasses harvested in the mid 1960s and in 1997 and observed a 1.4‰ negative shift over that time. Meanwhile, the $\delta^{13}\text{C}$ component of the tooth enamel of wildebeest and hartebeest in the Athi Plains region changed by about the same amount: from $+3.5\text{‰}$ for wildebeest that died in 1968 to $+2.5\text{‰}$ for those that died in 1997, and from $+3.3$ to $+2.8\text{‰}$ for hartebeest during the same time span. Therefore, diets of mammals track changes in the $\delta^{13}\text{C}$ value of atmosphere via changes in the $\delta^{13}\text{C}$ of plants. Likewise, the $\delta^{13}\text{C}$ of horn changed by a similar amount between 1968 and 1997.

Previously, several studies (Thackeray et al. 1990; Koch et al. 1995) have suggested that extreme variations in the isotopic composition of tooth enamel indicate changes in the isotopic composition of the atmosphere. Our results concur with their conclusions, and it is interesting to speculate that it may be possible to find other excursions in the isotopic composition of the atmosphere using tooth enamel.

The distinction between NADP C_4 plants and NAD or PCK C_4 plants

NADP and NAD or PCK C_4 plants have different water requirements. NADP grasses are better suited to mesic conditions whereas NAD grasses, in particular, are better adapted to more xeric environments (Hattersley 1992). Greenhouse experiments also indicate that they have different $\delta^{13}\text{C}$ values. In 1997, we collected and analyzed NADP, NAD, and PCK grasses from different parts of Kenya and found that the NADP grasses had $\delta^{13}\text{C}$ values of $-11.8 \pm 0.7\text{‰}$ whereas NAD and PCK grasses had $\delta^{13}\text{C}$ values of $-12.8 \pm 0.8\text{‰}$.

We found that the isotopic difference between NADP and NAD + PCK C_4 grasses is recorded in the tooth enamel of hypergrazers. Alcelaphine bovids, such as hartebeest, wildebeest, and topi, are hypergrazers, as are buffalo. In 1997, the wildebeest and hartebeest in the NADP-dominated grasslands near Nairobi had $\delta^{13}\text{C}$ values of 2.5 and 2.8‰ . In contrast, buffalo and topi from Lewa and the Turkana region, where NAD + PCK dominate the grasses, had $\delta^{13}\text{C}$ values of 1.8 and 1.3‰ , respectively. This separation of about 1‰ reflects the difference in $\delta^{13}\text{C}$ between NADP grasses and NAD + PCK grasses (Appendix 1).

Equids also have ^{13}C values that are different in NADP-dominated or NAD + PCK-dominated ecosystems. This observation is independent of whether they are grazers or hypergrazers (see discussion above). Sixteen different zebras (*E. burchelli*) from the 1968 Kitengela population had an average $\delta^{13}\text{C}$ value of $+1.5 \pm 0.4\text{‰}$ with a total range from 0.3 to 2.1‰ , which is about 1.5 – 2.0‰ more negative than sympatric kongoni and wildebeest, respectively (Appendix 2), which are hypergrazers. Zebra (*E. burchelli*) from the Lake Turkana region, which is dominated by NAD and PCK grasses, had $\delta^{13}\text{C}$ values of about -1 to 0‰ , about 1.5‰ more negative than the hypergrazer topi in the same region. Equids are consistently 1 – 2‰ lower in ^{13}C than sympatric hypergrazer ruminants (Fig. 3). Ten equids from the Turkana Basin with ages between 6 and 1 million years ago had an average $\delta^{13}\text{C}$ value of $-0.8 \pm 0.7\text{‰}$, indicating that the grasses in the Turkana Basin during this interval were most likely dominated by NAD or PCK grasses. Analyses of more than 100 bovids, equids, rhinocerotids, hippopotamids, suids, and proboscideans from the Turkana Basin during the last 8 million-year interval, when C_4 plants are known to have been in the region (Cerling et al. 1997), show that none had $\delta^{13}\text{C}$ values as high as 1.0‰ , compatible with all of these animals living in an environment dominated by NAD or PCK grasses. On the other hand, Bocherens et al. (1996) reported $\delta^{13}\text{C}$ values as high as $+3\text{‰}$ for fossil wildebeest in Ethiopia during this time, indicating that in that region, NADP grasses, not NAD or PCK grasses, were the most abundant grasses.

The modeling work of Ehleringer et al. (1997) suggests that the NADP grasses should have been better suited to early C_4 biomass expansion because they have somewhat higher quantum yield than do NAD or PCK C_4 grasses. It will be interesting, and challenging to see if stable isotopes in the fossil record can contribute to demonstrating the early spread of NADP versus NAD or PCK C_4 grasses.

Conclusions

This study has shown that the fractionation factor between the tooth enamel of ruminant mammals compared to their diet is 1.0141 ± 0.0005 , or an isotope enrichment ϵ^* of $14.1 \pm 0.5\text{‰}$. The isotope enrichment ϵ^* between horn (keratin) compared to diet is $3.1 \pm 0.7\text{‰}$, and the isotope enrichment ϵ^* between enamel compared to horn is $11.1 \pm 0.8\text{‰}$. These results were obtained by analyzing both captive and wild mammals and their respective dietary material. This is true for ruminant mammals with either a C_3 or a C_4 diet. Non-ruminants have a similar isotope enrichment in enamel compared to diet, but our studies are not sufficient to determine if, in fact, it is different than the value for ruminants. It is likely that variations from this value will be found as we understand better the differences between isotope fractionation and digestive strategies.

The study of tooth enamel has important implications for investigating both modern and fossil mammals. The close relationship between the $\delta^{13}\text{C}$ of diet and tooth enamel means that accurate reconstruction of the fraction of C_4 biomass can be made in mammals whose habits are not easy to observe or characterize. For example, we have shown that savanna elephants have less grass in their diets than conventional wisdom dictated. Likewise, diets in closed-canopy habitats can be recognized by the extreme depletion in the $\delta^{13}\text{C}$ of tooth enamel.

We were able to distinguish a fraction of 10% browse in the diets of C_4 -grazing mammals. This distinction should allow the characterization of dietary strategies in the fossil record. In addition, we were able to distinguish mammals using NADP C_4 grasses from those using NAD or PCK C_4 grasses. This has important paleoecological implications because NADP grasses are better suited for mesic conditions, and NAD and PCK grasses are better suited to xeric environments. We give an ex-

ample of the Turkana Basin, which seems to have been dominated by NAD or PCK C_4 grasses for all of the last 6 million years, or longer.

The $\delta^{13}\text{C}$ composition of plants changes because of changes in the $\delta^{13}\text{C}$ of the atmosphere. This change is recorded in mammalian tooth enamel and it may be possible to use data from fossil teeth as a measure of the $\delta^{13}\text{C}$ of the ancient atmosphere.

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Appendix 1 $\delta^{13}\text{C}$ values for vegetation

Family	Species	$\delta^{13}\text{C}$	Date	Region
Mongolia, C_3 grasses and sedges, 1996				
Cyperaceae	<i>Carex rhynchophysa</i>	-27.6	September 1996	
Gramineae	<i>Agrostis trinii</i>	-27.4	September 1996	
Gramineae	<i>Lasiagrostis splendens</i>	-23.6	September 1996	
Gramineae	<i>Lemus chenensis</i>	-25.3	September 1996	
Gramineae	<i>Ptilogrostis mongolica</i>	-24.2	September 1996	
Gramineae	<i>Stipa krylovii</i>	-23.6	September 1996	
		Mean: -25.3 \pm 1.8		
Tierra del Fuego, Argentina, C_3 grasses, 1982–1996				
Gramineae	<i>Agropyron antarcticum</i>	-25.4	January 1984	E. M. Behety
Gramineae	<i>Agrostis magellanica</i>	-27.0	February 1985	Bahia Brien
Gramineae	<i>Agrostis meyenii</i>	-27.7	January 1982	E. Sara
Gramineae	<i>Agrostis</i> sp.	-26.7	March 1998	Harberton
Gramineae	<i>Agrostis</i> sp.	-26.3	March 1998	Ensenada Bay
Gramineae	<i>Agrostis stolonifera</i>	-27.3	January 1982	Harberton
Gramineae	<i>Agrostis tenuis</i>	-27.6	January 1982	Harberton
Gramineae	<i>Alopecurus magellanicus</i>	-26.9	February 1982	E. S. Vidal
Gramineae	<i>Bromus araucanus</i>	-28.4	February 1985	Bahia Valentia
Gramineae	<i>Bromus coloratus</i>	-27.8	February 1983	C. San Sebastian
Gramineae	<i>Bromus pellitus</i>	-30.5	February 1983	Cabo E. Santo
Gramineae	<i>Dactylis glomerata</i>	-28.8	February 1982	Lago Fagnano
Gramineae	<i>Deschampsia flexuosa</i>	-26.1	December 1982	E. M. Christina
Gramineae	<i>Elymus antarcticus</i>	-28.1	January 1984	E. S. Salvador
Gramineae	<i>Festuca rubra</i>	-29.2	January 1982	Harberton
Gramineae	<i>Festuca</i> sp.	-26.5	March 1998	E. Sara
Gramineae	<i>Festuca</i> sp.	-27.8	March 1998	Harberton
Gramineae	<i>Festuca</i> sp.	-27.1	March 1998	Ensenada Bay
Gramineae	<i>Hordeum</i> cf. <i>comosum</i>	-24.4	March 1998	Ensenada Bay
Gramineae	<i>Hordeum pubiflorum</i>	-27.6	January 83	Canodon tortuga
Gramineae	<i>Poa pungionifolia</i>	-26.4	January 1982	N. Isla Grande
Gramineae	<i>Poa trivialis</i>	-33.9	January 1982	Harberton
Gramineae	<i>Trisetum phleoides</i>	-28.5	December 1982	E. M. Christina
Gramineae	<i>Trisetum spicatum</i>	-26.8	December 1982	Cabo E. Santo
		Mean: -27.6 \pm 1.8		
Hogle Zoo, Utah, large-animal feed				
	Meadow Hay	-26.8	1991	N. Utah
	Alfalfa pellets	-27.0	1991	N. Utah
	Alfalfa hay	-27.9	1996	N. Utah

Appendix 1. (Contd.)

Family	Species	$\delta^{13}\text{C}$	Date	Region
	Hay cube	-27.9	1996	N. Utah
	Grass hay	-25.4	1991	N. Utah
	Grass hay	-26.7	1993	N. Utah
	Grass hay	-24.5	1996	N. Utah
		Mean: -26.6 ± 1.3		
Ituri Forest, Zaire (subcanopy browse)				
Connaraceae	<i>Agelaea paradoxa</i>	-34.5	1996	Epulu
Rubiaceae	<i>Aidia micrantha</i>	-33.0	1996	Epulu
Maranthaceae	<i>Ataenidia conferta</i>	-36.5	1996	Epulu
Euphorbiaceae	<i>Alchornea floribunda</i>	-33.4	1996	Epulu
Caesalpiniaceae	<i>Anthonotha macrophylla</i>	-31.0	1996	Epulu
Caesalpiniaceae	<i>Cynometra alexandri</i>	-33.7	1996	Epulu
Ebenaceae	<i>Diospyros bipendensis</i>	-32.1	1996	Epulu
Flacourtiaceae	<i>Homalium africana</i>	-35.4	1996	Epulu
Flacourtiaceae	<i>Homalium africana</i>	-34.3	1996	Epulu
Gramineae	<i>Leptaspis zeylanica</i>	-32.2	1996	Epulu
Maranthaceae	<i>Megaphrynium macrostachyum</i>	-36.2	1996	Epulu
Violaceae	<i>Rinorea</i> sp.	-34.4	1996	Epulu
Sterculiaceae	<i>Scaphopetalum dewevrei</i>	-36.0	1996	Epulu
Urticaceae	<i>Urea cameroonensis</i>	-34.9	1996	Epulu
		Mean: -34.1 ± 1.7		
Kenya, C ₃ dicots and monocots				
Malvaceae	<i>Abutilon longicuspa</i>	-28.1	July 1997	Abardares
Leguminosae	<i>Acacia depanolobium</i>	-25.0	July 1997	Mpala
Leguminosae	<i>Acacia elatior</i>	-26.2	January 1997	Turkana Basin
Leguminosae	<i>Acacia etbaica</i>	-27.9	July 1997	Mpala
Leguminosae	<i>Acacia horrida</i>	-23.3	July 1997	Samburu
Leguminosae	<i>Acacia mellifera</i>	-28.2	July 1997	Athi Plains
Leguminosae	<i>Acacia nunica</i>	-28.7	July 1997	Turkana Basin
Leguminosae	<i>Acacia reficiens</i>	-26.7	July 1997	Turkana Basin
Leguminosae	<i>Acacia senegal</i>	-27.4	July 1997	Turkana Basin
Leguminosae	<i>Acacia seyal</i> var. <i>fistula</i>	-28.4	July 1997	Mpala
Leguminosae	<i>Acacia tortilis</i>	-25.3	January 1997	Turkana Basin
Leguminosae	<i>Acacia tortilis</i>	-24.6	January 1997	Turkana Basin
Leguminosae	<i>Acacia tortilis</i>	-29.2	July 1997	Turkana Basin
Leguminosae	<i>Acacia tortilis</i>	-27.9	July 1997	Turkana Basin
Leguminosae	<i>Acacia tortilis</i>	-27.4	July 1997	Samburu
Leguminosae	<i>Acacia xanthophloea</i>	-28.2	July 1997	Athi Plains
Leguminosae	<i>Acacia xanthophloea</i>	-28.1	July 1997	Athi Plains
Balinitaceae	<i>Balanites orbicularis</i>	-29.2	January 1997	Turkana Basin
Balinitaceae	<i>Balanites orbicularis</i>	-28.0	July 1997	Turkana Basin
Acanthaceae	<i>Barleria acanthoides</i>	-27.0	January 1997	Turkana Basin
Capparaceae	<i>Boscia coriacea</i>	-28.4	July 1997	Turkana Basin
Capparaceae	<i>Boscia coriacea</i>	-26.1	January 1997	Turkana Basin
Capparaceae	<i>Cadaba rotundifolia</i>	-30.5	January 1997	Turkana Basin
Combretaceae	<i>Combretum denhardtiorum</i>	-25.9	January 1997	Turkana Basin
Burseraceae	<i>Commiphora schimperi</i>	-27.4	July 1997	Turkana Basin
Burseraceae	<i>Commiphora</i> sp.	-27.8	July 1997	Samburu
Burseraceae	<i>Commiphora</i> sp.	-30.9	July 1997	Athi Plains
Rubiaceae	<i>Conostyomium kenienne</i>	-27.9	July 1997	Turkana Basin
Boraginaceae	<i>Cordia gharaf</i>	-24.9	1984	Turkana Basin
Boraginaceae	<i>Cordia sinensis</i>	-26.1	January 1997	Turkana Basin
Papilionaceae	<i>Crotalaria agatufolia</i>	-28.6	July 1997	Abardares
Cucurbitaceae	<i>Cucumis</i> sp.	-27.5	July 1997	Turkana Basin
Salvadoraceae	<i>Dobera glabra</i>	-25.4	1995	Turkana Basin
Salvadoraceae	<i>Dobera glabra</i>	-27.6	July 1997	Turkana Basin
Flacourtiaceae	<i>Dovyalis abyssinica</i>	-26.3	July 1997	Abardares
Asclepiadaceae	<i>Dregea abyssinica</i>	-28.1	July 1997	Turkana Basin
Euphorbiaceae	<i>Euphorbia cuneata</i>	-27.4	July 1997	Turkana Basin
Tiliaceae	<i>Grewia tembensis</i>	-27.5	January 1997	Turkana Basin
Palmae	<i>Hyphaene coriacea</i>	-24.8	January 1997	Turkana Basin
Palmae	<i>Hyphaene coriacea</i>	-27.0	July 1997	Turkana Basin
Bignoniaceae	<i>Kigelia africana</i>	-28.9	July 1997	Samburu
Euphorbiaceae	<i>Lawsonia inermis</i>	-27.1	January 1997	Turkana Basin
Capparaceae	<i>Maerua angolensis</i>	-25.7	January 1997	Turkana Basin
Labiatae	<i>Ocimum suave</i>	-28.3	July 1997	Abardares

Appendix 1. (Contd.)

Family	Species	$\delta^{13}\text{C}$	Date	Region
Malvaceae	<i>Pavonia</i> sp.	-25.6	1984	Turkana Basin
Salvadoraceae	<i>Salvadora persica</i>	-26.5	January 1997	Turkana Basin
Salvadoraceae	<i>Salvadora persica</i>	-26.3	July 1997	Turkana Basin
Salvadoraceae	<i>Salvadora</i> sp.	-29.2	August 1997	Samburu
Salvadoraceae	<i>Salvadora</i> sp.	-27.9	July 1997	Samburu
Amaranthaceae	<i>Sericocomopsis pallida</i>	-29.9	January 1997	Turkana Basin
Pedaliaceae	<i>Sesamum alatum</i>	-28.1	July 1997	Turkana Basin
Solanaceae	<i>Solanum aculeastrum</i>	-27.9	July 1997	Abardares
Solanaceae	<i>Solanum incanum</i>	-27.1	July 1997	Abardares
Urticaceae	<i>Urtica masaica</i>	-28.2	July 1997	Abardares
Rhamnaceae	<i>Ziziphus mauritania</i>	-28.8	July 1997	Turkana Basin
Rhamnaceae	<i>Ziziphus mauritania</i>	-26.0	January 1997	Turkana Basin
		Dicot mean: -27.4 ± 1.5		
		<i>Acacia</i> mean: -27.0 ± 1.7		
		Turkana mean: -27.2 ± 1.5		
		Abardares mean: -27.8 ± 0.8		
Kenya. NADP grasses, 1997				
Gramineae	<i>Cenchrus ciliaris</i>	-11.7	July 1997	Mpala
Gramineae	<i>Cenchrus ciliaris</i>	-12.8	July 1997	Samburu
Gramineae	<i>Cenchrus ciliaris</i>	-12.2	July 1997	Samburu
Gramineae	<i>Digitaria nuda</i>	-11.1	July 1997	Athi Plains
Gramineae	<i>Digitaria mombasana</i>	-11.6	July 1997	Mpala
Gramineae	<i>Hyparrhenia diplandra</i>	-11.8	July 1997	Athi Plains
Gramineae	<i>Hyparrhenia hirta</i>	-12.0	July 1997	Athi Plains
Gramineae	<i>Hyparrhenia dregeana</i>	-12.9	July 1997	Timau
Gramineae	<i>Hyparrhenia dregeana</i>	-11.7	July 1997	Timau
Gramineae	<i>Hyparrhenia variabilis</i>	-12.3	July 1997	Athi Plains
Gramineae	<i>Pennisetum clandestinum</i>	-10.0	July 1997	Abardares
Gramineae	<i>Pennisetum schacelatum</i>	-11.7	July 1997	Samburu
Gramineae	<i>Pennisetum schacelatum</i>	-11.3	July 1997	Samburu
Gramineae	<i>Setaria incrasata</i>	-12.0	July 1997	Timau
Gramineae	<i>Themeda triandra</i>	-12.6	July 1997	Lewa
Gramineae	<i>Themeda triandra</i>	-12.0	July 1997	Athi Plains
Gramineae	<i>Themeda triandra</i>	-11.6	July 1997	Timau
Gramineae	<i>Themeda triandra</i>	-11.4	July 1997	Athi Plains
Gramineae	<i>Themeda triandra</i>	-11.4	July 1997	Athi Plains
Gramineae	<i>Themeda triandra</i>	-11.2	July 1997	Athi Plains
Gramineae	<i>Themeda triandra</i>	-10.9	July 1997	Timau
		Mean: -11.7 ± 0.7		
NAD C ₄ grasses, 1997				
Gramineae	<i>Cynodon dactylum</i>	-14.0	July 1997	Mpala
Gramineae	<i>Eragrostis racemosa</i>	-13.2	July 1997	Samburu
Gramineae	<i>Eragrostis schweinfurthii</i>	-13.3	July 1997	Lewa
Gramineae	<i>Eragrostis superba</i>	-13.4	July 1997	Mpala
Gramineae	<i>Eragrostis superba</i>	-11.9	July 1997	Athi Plains
Gramineae	<i>Eragrostis superba</i>	-11.8	July 1997	Athi Plains
Gramineae	<i>Eragrostis superba</i>	-13.4	July 1997	Mpala
Gramineae	<i>Eragrostis superba</i>	-12.9	July 1997	Mpala
Gramineae	<i>Eragrostis volkensii</i>	-11.0	July 1997	Abardares
Gramineae	<i>Eleusine jaegeri</i>	-12.3	July 1997	Abardares
Gramineae	<i>Eleusine jaegeri</i>	-13.1	July 1997	Abardares
Gramineae	<i>Harpachne schimperi</i>	-13.0	July 1997	Mpala
Gramineae	<i>Harpachne schimperi</i>	-12.6	July 1997	Mpala
Gramineae	<i>Sporobolus africanus</i>	-12.8	July 1997	Athi Plains
Gramineae	<i>Sporobolus ioclades</i>	-12.3	July 1997	Samburu
Gramineae	<i>Sporobolus spikatis</i>	-14.2	January 1997	Turkana Basin
Gramineae	<i>Sporobolus spikatis</i>	-13.8	January 1997	Turkana Basin
PCK C ₄ grasses, 1997				
Gramineae	<i>Chloris roxberghiana</i>	-13.2	July 1997	Mpala
Gramineae	<i>Chloris roxberghiana</i>	-12.7	July 1997	Mpala
Gramineae	<i>Chloris virgata</i>	-12.6	July 1997	Mpala
Gramineae	<i>Chloris virgata</i>	-11.3	July 1997	Mpala
Gramineae	<i>Chloris virgata</i>	-12.8	July 1997	Mpala
Gramineae	<i>Dactyloctenium aegyptium</i>	-13.2	July 1997	Mpala
Gramineae	<i>Dactyloctenium aegyptium</i>	-12.6	July 1997	Mpala
Gramineae	<i>Microchloa kunthii</i>	-12.7	July 1997	Mpala
Gramineae	<i>Microchloa kunthii</i>	-12.0	July 1997	Mpala

Appendix 1. (Contd.)

Family	Species	$\delta^{13}\text{C}$	Date	Region
Gramineae	<i>Rhynchelytrum repens</i>	-12.4	July 1997	Mpala
Gramineae	<i>Tragus berteronianus</i>	-13.7	July 1997	Mpala
		NAD+PCK mean: -12.8 \pm 0.8		
NADP C ₄ grasses, 1962–1964				
Gramineae	<i>Themeda triandra</i>	-10.2	1964	Nairobi
Gramineae	<i>Themeda triandra</i>	-10.3	1962	Nairobi
Gramineae	<i>Themeda triandra</i>	-10.1	1964	Tsavo
Gramineae	<i>Themeda triandra</i>	-10.0	1964	Tsavo
Gramineae	<i>Hyparrhenia nyassa</i>	-10.4	1964	Thika
Gramineae	<i>Hyparrhenia nyassa</i>	-10.4	1964	Thika
		Mean: -10.2 \pm 0.2		

Appendix 2 $\delta^{13}\text{C}$ of modern large mammals with restricted diets

Sample	$\delta^{13}\text{C}_e$	$\delta^{13}\text{C}^*$	Date	Region	Species	Tooth
Zoo mammals, Hogle Zoo, Utah, USA, C ₃ diet only						
HZ-1a	-12.8			Utah	<i>Loxodonta africana</i>	M3
HZ-1b	-12.7			Utah	<i>L. africana</i>	M3
HZ-4	-13.7		1982	Utah	<i>Camelus bactrianus</i>	M2
96-Bram	-13.4		1982	Utah	<i>C. bactrianus</i>	M3
No. ^b	-12.9		1982	Utah	<i>C. bactrianus</i>	M
11796a	-11.6		1990	Utah	<i>Ovis dalli dalli</i>	M3
10412a	-12.4		1986	Utah	<i>Equus burchelli</i>	M1
10412b	-12.3		1986	Utah	<i>E. burchelli</i>	M1
96-UT-209a	-12.0		1980	Utah	<i>E. burchelli</i>	M2
96-UT-209b	-12.0		1980	Utah	<i>E. burchelli</i>	M3
11797	-13.9		1990	Utah	<i>Dama dama</i>	M
HZ-2	-13.0		1989	Utah	<i>Giraffa camelopardalis</i>	M
HZ-3a	-12.8		1984	Utah	<i>Choeropsis liberensis</i>	I
HZ-3b	-12.0		1984	Utah	<i>C. liberensis</i>	I
		Mean: -12.7 \pm 0.7				
Northern Mongolia, C ₃ grazers, horses						
MG-515	-11.2		1995/6	Zaamar	<i>Equus caballus</i>	P2
MG-516	-12.1		1995/6	Zaamar	<i>E. caballus</i>	M3
MG-518	-12.1		1995/6	Magod	<i>E. caballus</i>	rM3
MG-549	-11.9		1995/6	Tunumal Nuur	<i>E. caballus</i>	M3
MG-572-IM3	-11.9		1995/6	Tsaagan Nuur	<i>E. caballus</i>	IM3
MG-572-rM3	-11.9		1995/6	Tsaagan Nuur	<i>E. caballus</i>	rM3
		Mean: -11.9 \pm 0.3				
Tierra del Fuego, C ₃ grazer, guanaco						
Arg98-48	-15.6		1998	Harberton	<i>Llama guanaco</i>	IM2
Arg98-56	-15.2		1997	Harberton	<i>L. guanaco</i>	M3
Arg98-56	-14.9		1997	Harberton	<i>L. guanaco</i>	M2
Arg98-57	-15.5		1996	Lago Blanco	<i>L. guanaco</i>	IM3
Arg98-57	-15.3		1996	Lago Blanco	<i>L. guanaco</i>	rM3
Arg98-58	-14.7		1996	Lago Blanco	<i>L. guanaco</i>	M3
		Mean: -15.2 \pm 0.4				
Zaire browser, okapi, closed-canopy rain forest						
JAH-A	-22.3		1992	Ituri Forest	<i>Okapia johnstoni</i>	P3
JAH-A-P4	-20.7		1992	Ituri Forest	<i>O. johnstoni</i>	P4
JAH-A-P2	-20.2		1992	Ituri Forest	<i>O. johnstoni</i>	P2
OM 2218	-20.0		?	Ituri Forest	<i>O. johnstoni</i>	P3
		Mean: -20.8 \pm 1.0				
Kenya browsers, dik-dik						
SU-2-M2	-12.4		1995	Turkana Basin	<i>Madoqua kirki</i>	M2
SU 3	-14.8		1995	Turkana Basin	<i>M. kirki</i>	M3
SU 4 M2	-10.3 ^b		1995	Turkana Basin	<i>M. kirki</i>	M2
SU96:10	-13.2		1996	Turkana Basin	<i>M. kirki</i>	M3
SU96:11	-14.0		1996	Turkana Basin	<i>M. kirki</i>	M3

Appendix 2. (Contd.)

Sample	$\delta^{13}\text{C}_e$	$\delta^{13}\text{C}^*$	Date	Region	Species	Tooth
SU96:17	-13.5		1996	Turkana Basin	<i>M. kirki</i>	M3
SU96:18	-14.8		1996	Turkana Basin	<i>M. kirki</i>	M3
SU96:21	-11.9		1996	Turkana Basin	<i>M. kirki</i>	M3
	Mean: -13.5 ± 1.1					
Kenya grazer, topi						
K97-120-M1	1.2		1996/1997	Turkana Basin	<i>Damaliscus lunatus</i>	M1
K97-120-M2	1.7		1996/1997	Turkana Basin	<i>D. lunatus</i>	M2
K97-121-M2	1.1		1996/1997	Turkana Basin	<i>D. lunatus</i>	M2
	Mean: 1.3 ± 0.3					
Kenya grazers, buffalo						
K97-235	1.9		1996	Mpala	<i>Syncerus caffer</i>	M3
K97-389	1.7		1996	Lewa	<i>S. caffer</i>	M2
K97-389	1.9		1996	Lewa	<i>S. caffer</i>	M3
	Mean: 1.8 ± 0.1					
Kenya grazers, Coke's hartebeest, 1969						
OM 117	3.1		1969	Kitengela	<i>Alcelaphus buselaphus cokei</i>	M2
OM 119	1.9		1969	Kitengela	<i>A. b. cokei</i>	M2
OM 4133	3.0		1969	Nairobi N.P.	<i>A. b. cokei</i>	M2
OM 4135	3.2		1969	Nairobi N.P.	<i>A. b. cokei</i>	M2
OM 4136	3.8		1969	Nairobi N.P.	<i>A. b. cokei</i>	M2
	Mean: 3.0 ± 0.7 (3.3 ± 0.4 excluding OM 119)					
Kenya grazers, Coke's hartebeest, Nairobi 1997						
K97-264A	2.9		1997	Nairobi N.P.	<i>A. b. cokei</i>	M3
K97-264B	3.0		1997	Nairobi N.P.	<i>A. b. cokei</i>	M2
K97-309	2.6		1997	Nairobi N.P.	<i>A. b. cokei</i>	M3
	Mean: 2.8 ± 0.2					
Kenya grazers, white-bearded wildebeest, Kitengela, 1968						
OM 42	2.9		1969	Kitengela	<i>Connochaetes taurinus albojubatus</i>	M2
OM 44	3.9		1969	Kitengela	<i>C. t. albojubatus</i>	M2
OM 47	3.2		1969	Kitengela	<i>C. t. albojubatus</i>	M2
OM 57	3.9		1969	Kitengela	<i>C. t. albojubatus</i>	M2
OM 58	3.7		1969	Kitengela	<i>C. t. albojubatus</i>	M2
	Mean: 3.5 ± 0.5					
Kenya grazers, white-bearded wildebeest, Nairobi game park, 1997						
K97-263A	2.4		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	M3
K97-263B	2.8		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	M2
K97-283-rM3	1.9		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	rM3
K97-283-lM3	1.9		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	lM3
K97-305-lm2	1.9		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	lm2
K97 305 m3t	2.4		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	lm3 (top)
K97 305 m3b	2.2		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	lm3 (bot)
K97-310-m2	3.0		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	m2
K97-310-m3	3.0		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	m3
K97-311-Nbi	3.1		1997	Nairobi N.P.	<i>C. t. albojubatus</i>	M2
	Mean: 2.5 ± 0.5					
Kenya browsers, black rhinoceros						
K97-207	-14.0	-14.0	1997	Abardares	<i>Diceros bicornis</i>	m1
OM 2180	-12.2	-13.2	1956	Makindu	<i>D. bicornis</i>	m2
OM 2195	-12.7	-13.4	1969	Ngureman	<i>D. bicornis</i>	M1
OM 2742	-10.2 ^b	-10.8 ^b	1971	Ngureman	<i>D. bicornis</i>	m2
OM 5482	-12.6	-13.1	1976	East Tsavo	<i>D. bicornis</i>	M2
K97-323	-13.0	-13.0	1997	Abardares	<i>D. bicornis</i>	M3
K89.1	-10.2 ^b	-10.6 ^b	1981	Koobi Fora	<i>D. bicornis</i>	M3
	Mean: -12.1	Mean: -13.4 ± 1.1				
Kenya browsers, giraffes						
OM 2214	-14.9	-15.6	1970	Kitengela	<i>Giraffa camelopardalis</i>	M2
OM 2278	-14.3	-15.0	1968	Athi River	<i>G. camelopardalis</i>	M2
ODW 6	-12.1	-12.2	1995	Chyulu Hills	<i>G. camelopardalis</i>	M

Appendix 2. (Contd.)

Sample	$\delta^{13}\text{C}_e$	$\delta^{13}\text{C}^*$	Date	Region	Species	Tooth
94Olor253	-12.9	-13.0	1994	Olorgesailie	<i>G. camelopardalis</i>	P3
K89.3	-12.2	-12.7	1974	Koobi Fora	<i>G. camelopardalis</i>	M3
K97-201	-12.0	-12.1	1996	Laikipia	<i>G. camelopardalis</i>	M3
K97-390	-12.9	-12.9	1997	Lewa	<i>G. camelopardalis</i>	M3
	Mean: -13.0	Mean: -13.3 \pm 1.7				

^a Corrected to 1997 using the change in the isotopic composition of the atmosphere

^b Excluded from average. See discussion in text

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