

## DIETS OF EAST AFRICAN BOVIDAE BASED ON STABLE ISOTOPE ANALYSIS

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We provide stable carbon isotope data from 37 species of African bovids to document dietary preferences for C<sub>3</sub> browse (or fruits) or C<sub>4</sub> grass. These data provide a quantitative measure of the fraction of C<sub>4</sub> grass in bovid diets, can be applied on regional to local scales, can be derived from tooth enamel and hair or other tissues, and permit the diets of bovids to be considered in the context of a grazer–browser continuum. We recognize hypergrazers (>95% C<sub>4</sub> grass), grazers (70–95% C<sub>4</sub> grass), mixed feeders (>30% C<sub>4</sub> grass and >30% C<sub>3</sub> browse), browsers (70–95% C<sub>3</sub> browse), and hyperbrowsers or frugivores (>95% C<sub>3</sub> browse or fruit). Our results suggest that, of the extant East African Bovidae, impala (*Aepyceros melampus*), Thomson's gazelle (*Gazella thomsonii*), and oribi (*Ourebia ourebi*) can be construed as mixed feeders. Dietary estimates based on stable isotope analysis are in broad agreement with other measures of diet such as hypsodonty index, mass relationships, and wear scratches on enamel.

Key words: bovid, browser, carbon isotopes, carbon-13, diet, East Africa, grazer, stable isotopes

African bovids are a diverse group of mammals that live in habitats ranging from tropical rain forests to deserts. The radiation of bovids in Africa has been particularly pronounced during the last 7 million years (Vrba 1995), and they are now the dominant herbivores in most of Africa. Their diets range from those dominated by fruits and leaves of dicotyledonous plants (dicots) to those dominated by monocotyledonous plants (monocots). Most dietary estimates of African bovids are based on a combination of methods including observation of ingested plants (Sinclair 1977; Talbot 1962), examination of fecal matter or stomach contents (Field 1972), and occasionally stable isotope analysis (Tieszen and Imbamba 1980). Syntheses of information about bovid diets have been primarily based on field observations, and results give qual-

itative estimates of dietary classes along a continuum from frugivores to browsers and grazers (Bodner 1990; Gagnon and Chew 2000; Hofmann 1989; Hofmann and Stewart 1972; McNaughton and Georgiadis 1986).

The isotopic composition of animal tissues, such as hair or bioapatite, records the diet of animals (Cerling and Harris 1999; DeNiro and Epstein 1978; Lee-Thorp and van der Merwe 1987). The diets documented by this technique pertain to food ingested weeks to years before obtaining the samples. The technique is based on the carbon isotopic distinction between C<sub>3</sub> and C<sub>4</sub> photosynthesis. Most dicots use the C<sub>3</sub> photosynthetic pathway, whereas most tropical grasses (monocots) use the C<sub>4</sub> photosynthetic pathway (Tieszen et al. 1979). Because of the large difference in <sup>13</sup>C:<sup>12</sup>C ratios of C<sub>3</sub> dicots compared with C<sub>4</sub> mono-

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cots, a stable isotope classification of mammalian diets provides a useful addition to the debate on dietary preferences of mammals. A principal advantage that analysis of carbon isotopes has over observational methods is that it does not require, and is unbiased by, direct observation. It is therefore an independent measure of dietary preferences. Moreover, this technique permits dietary information to be assessed years after the death of the animal, allows regional quantitative assessments of diets, and can provide dietary reconstruction for fossils (Cerling et al. 1997, 1999; Harris and Cerling 2002; Koch 1998; Lee-Thorp and van der Merwe 1987; Quade et al. 1992). The interpretation presented here of bovid diets from stable isotope analysis augments, but does not replace, dietary classifications based on field observations.

East Africa is an ideal region for studying the dietary distinctions between grazing and browsing animals using stable isotopes because in tropical regions, virtually all the  $C_3$  plants are dicots and all the  $C_4$  plants are grasses (Cerling and Harris 1999; Tieszen et al. 1979). Important exceptions are high-elevation grasses, which use the  $C_3$  photosynthetic pathway because of cooler temperatures. In Kenya, almost 100% of grasses growing below 2,500 m use the  $C_4$  photosynthetic pathway (Tieszen et al. 1979).

In this article, we first document the isotopic endmembers of vegetation found in modern ecosystems of East Africa, including xeric and mesic savannas and both open- and closed-canopy forests. We then present results of a regional stable isotope survey of East African bovids based on field collections and museum archives. This survey is interpreted in the context of isotopic mixing lines with dicots and monocots representing isotope endmembers, where endmembers have average  $\delta^{13}C$  values for  $C_3$  or  $C_4$  vegetation in extant ecosystems in East Africa. The results of our isotopic analyses are contrasted with field observations and with other syntheses of information about diets of African Bovidae

such as correlations with body size or hypsodonty of teeth.

#### MATERIALS AND METHODS

*Study areas and collection of samples.*—Our data were collected during a series of field seasons, principally from 1997 through 2000, in some of the major East African national parks and reserves, supplemented by material archived in the National Museums of Kenya and at national park and reserve headquarters. We collected plants from a variety of ecosystems during different seasons of the year and collected teeth and sometimes keratin (hair, horn, or hoof) from extant mammals. Our field samples consisted mostly of mammals that had died less than a few months before the samples were collected; for others, the date of death was known to within a few years. In this study, most mammals are from elevations <2,500 m. Therefore, we distinguish those populations of mammals that lived above 2,500 m. Bovid taxa are discussed in the order they are treated by McKenna and Bell (1997).

Our principal collecting areas were in Kenya and Uganda, with most of the samples from savanna or bushland regions and some additional samples from forested regions. We distinguish between mesic and xeric types of savannas and bushlands based on the observation that different subpathways of  $C_4$  photosynthesis tend to be associated with different moisture regimes and because mesic and xeric grasses have slightly different  $^{13}C:^{12}C$  ratios (Hattersley 1982, 1992). The 3 main subpathways are nicotinamide adenine dinucleotide phosphate (NADP), nicotinamide adenine dinucleotide (NAD), and phosphoenolpyruvate carboxykinase (PCK). Details of differences in these subpathways are discussed by Sage et al. (1999). Mesic savannas are dominated by grasses using the NADP subpathway (except for the genus *Aristida*—Hattersley 1992). In this article, “mesic grasses” refer to those using the NADP subpathway (except *Aristida*). Mesic savannas are represented by collections from the Athi Plains region of Kenya (including Nairobi National Park) and from Queen Elizabeth Park in Uganda. We also report some data from Garamba National Park in the Democratic Republic of Congo (formerly Zaire), which is a mesic savanna.

Xeric savannas and bushlands are dominated by *Aristida*, NAD, and PCK grasses, which are

hereafter referred to as "xeric grasses." Although *Aristida* uses the NADP pathway, it is more primitive in anatomy than other NADP grasses and is found in xeric environments (Chapman 1996; Chapman and Peat 1992; Dengler and Nelson 1999; Sage et al. 1999). These different subpathways are known to have slightly different  $^{13}\text{C}:^{12}\text{C}$  ratios (Hattersley 1982, 1992). Xeric savannas and bushlands were sampled in Kenya from the Turkana region, Tsavo East and West National Parks, and the Samburu Reserve area. The Laikipia plateau of Kenya is transitional from xeric at the lower elevations to mesic at higher elevations. Nakuru National Park is in a mesic moisture regime, but the alkaline nature of the soils at Lake Nakuru leads to a dominance of xeric grasses.

Open-canopy forest is represented by collections from the Aberdare National Park in Kenya, which spans a wide elevation range from about 1,700 to >3,500 m.  $\text{C}_4$  grasses are dominant below 2,500 m in Kenya (Tieszen et al. 1979), so results from animals that could have fed above 2,500 m must be interpreted accordingly. Lowland open-canopy forest is represented by a few samples from the Arobuko-Sokoke Forest on the Kenyan coast. We briefly report some data from the Ituri Forest in the Democratic Republic of Congo. Small numbers of samples from some other areas in East Africa are also included in this report. Precipitation and temperature data for the major sampling regions are available from the authors.

*Stable isotope analysis.*—Stable isotope results are reported using the standard stable isotope terminology and per mil (‰; parts per thousand difference from a standard) notation (Craig 1953):

$$\delta^{13}\text{C} (\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1,000,$$

where  $R_{\text{sample}}$  and  $R_{\text{standard}}$  are the  $^{13}\text{C}:^{12}\text{C}$  ratios of the sample and standard, respectively. The standard used here is Vienna-Pee Dee Belemnite (Coplan 1996). Isotope enrichment factors  $\epsilon$  (Hoefs 1973) are

$$\epsilon_{\text{AB}} = (R_{\text{A}}/R_{\text{B}} - 1) \times 1,000,$$

where  $R_{\text{A}}$  and  $R_{\text{B}}$  are the  $^{13}\text{C}:^{12}\text{C}$  ratios of A and B, respectively. In this study, we used the isotopic enrichment factors of 14.1‰ and 3.1‰ for

bioapatite diet and keratin diet (Cerling and Harris 1999), respectively.

The isotopic separation  $\Delta$  (Hoefs 1973) between 2 endmembers is given as

$$\Delta_{\text{AB}} = \delta_{\text{A}} - \delta_{\text{B}} \quad \text{which approximates } \epsilon_{\text{AB}}.$$

Organic samples were combusted and analyzed using a flow-through inlet system on a continuous-flow isotope ratio mass spectrometer. Bioapatites consist only of tooth enamel and were pretreated using standard methods (Lee-Thorp and van der Merwe 1987) and reacted in anhydrous  $\text{H}_3\text{PO}_4$  before cryogenic cleaning and analysis on a dual-inlet mass spectrometer. Precision for  $\delta^{13}\text{C}$  measurements for plants, enamel, and hair is 0.1‰. Variation from average values is reported as the *SE* for suites of plants that are considered in the context of mixing models, whereas *SD* is reported for the variations in the isotopic composition of enamel, keratin, and diets of individual mammals grouped by species.

In several cases, we analyzed both apatite and keratin from the same individual. We report both numbers because they represent diets from different times in the individual's life. Likewise, on some samples (principally from the Ituri Forest), we include results from different teeth in a single mandible because they were formed at different intervals in the animal's life span.

## RESULTS

*C<sub>3</sub> and C<sub>4</sub> plants: isotopes and nutrients.*—We analyzed 22 dicots from the closed-canopy Kakamega Forest in western Kenya, 7 dicots from the open-canopy Aberdare Forest in central Kenya, and 122 dicots from savannas and bushlands. These had  $\delta^{13}\text{C}_{\text{leaf}}$  values of  $-31.4 \pm 0.5\text{‰}$ ,  $-27.8 \pm 0.3\text{‰}$ , and  $-27.0 \pm 0.2\text{‰}$ , along with total nitrogen concentrations of  $3.0 \pm 0.3\%$ ,  $2.8 \pm 0.3\%$ , and  $3.1 \pm 0.1\%$ , respectively (Table 1).

Because different subpathways of  $\text{C}_4$  plants reflect different rainfall preferences (Hattersley 1992), we separated the East African grasses into mesic and xeric types. Mesic grasses had an average  $\delta^{13}\text{C}_{\text{leaf}}$  value of  $-11.8 \pm 0.2\text{‰}$ , with a nitrogen concentration of  $1.3 \pm 0.2\%$  ( $n = 72$ ). The  $\delta^{13}\text{C}_{\text{leaf}}$  values of xeric grasses were  $-13.1 \pm 0.3\text{‰}$

TABLE 1.—Summary of  $\delta^{13}\text{C}$  values and nitrogen contents of plants from various ecosystems in East Africa.<sup>a</sup>

	<i>n</i>	$\delta^{13}\text{C}$		N content (%)	
		$\bar{X}$	<i>SE</i>	$\bar{X}$	<i>SE</i>
C <sub>3</sub> dicots					
Closed canopy forest	22	-31.4	0.5	3.0	0.2
Open canopy forest	7	-27.8	0.3	2.8	0.3
Savanna and bushland	122	-27.0	0.2	3.1	0.1
C <sub>4</sub> grasses, mesic <sup>b</sup>					
NADP <sup>c</sup>	72	-11.8	0.2	1.3	0.2
C <sub>4</sub> grasses, xeric <sup>b</sup>					
<i>Aristida</i>	10	-13.1	0.3	1.1	0.3
NAD	32	-13.1	0.2	1.0	0.2
PCK	35	-12.9	0.1	1.4	0.2

<sup>a</sup> NADP, nicotinamide adenine dinucleotide phosphate; NAD, nicotinamide adenine dinucleotide; PCK, phosphoenolpyruvate carboxykinase.

<sup>b</sup> NADP, NAD, and PCK refer to different subpathways of C<sub>4</sub> photosynthesis. NADP grasses (except *Aristida*) are generally found in more mesic ecosystems, whereas *Aristida*, NAD, and PCK grasses are generally found in more xeric ecosystems (Hattersley 1992).

<sup>c</sup> All NADP, except *Aristida*.

for *Aristida*,  $-13.1 \pm 0.2\text{‰}$  for the NAD subpathway, and  $-12.9 \pm 0.1\text{‰}$  for the PCK subpathway, with nitrogen concentrations of  $1.1 \pm 0.3\%$ ,  $1.0 \pm 0.2\%$ , and  $1.4 \pm 0.2\%$ , respectively (Table 1). Mesic grasses were isotopically distinct from xeric grasses (*t*-test,  $P < 0.0001$  versus NAD, PCK, and NADP—*Aristida*).

*Variations in  $\delta^{13}\text{C}$  with aridity.*—Subcanopy C<sub>3</sub> plants from closed-canopy forests have  $\delta^{13}\text{C}_{\text{leaf}}$  values averaging  $-31.4\text{‰}$ , whereas C<sub>3</sub> plants from an open-canopy forest or mesic savannas have  $\delta^{13}\text{C}$  values averaging between  $-27.7\text{‰}$  and  $-28\text{‰}$  (Table 2). C<sub>3</sub> plants in xeric savannas during nondrought periods are only slightly more positive, averaging  $-27.1\text{‰}$  to  $-27.6\text{‰}$ . C<sub>3</sub> plants from the Turkana region were enriched in <sup>13</sup>C in drought conditions compared with nondrought conditions ( $\delta^{13}\text{C}$  values of  $-26.5\text{‰}$  and  $-27.6\text{‰}$ , respectively). C<sub>3</sub> plants sampled over a 4-month period in the Mpala region had an average  $\delta^{13}\text{C}$  value of  $-24.6\text{‰}$  ( $n = 15$ ). Therefore, there is a considerable range in  $\delta^{13}\text{C}$  of C<sub>3</sub> plants in different ecosystems, both temporally as well as spatially.

The variation in C<sub>4</sub> plants was also sig-

nificant, although not as great as within the C<sub>3</sub> plants. The most positive  $\delta^{13}\text{C}_{\text{leaf}}$  values for mesic grasses are for those in forested regions (Aberdares and Mount Kenya) or during the El Niño rains of 1997–1998, with  $\delta^{13}\text{C}_{\text{leaf}}$  values of about  $-11.5\text{‰}$ , whereas the most negative  $\delta^{13}\text{C}_{\text{leaf}}$  values were found at Mpala (September through December 1998), averaging  $-12.9\text{‰}$ .  $\delta^{13}\text{C}$  values for xeric grasses were the most positive in mesic savannas and the most negative in xeric drought-stressed ecosystems, with average  $\delta^{13}\text{C}_{\text{leaf}}$  values of  $-12.1\text{‰}$  to  $-12.2\text{‰}$  and  $-13.9\text{‰}$  to  $-14.4\text{‰}$ , respectively (Table 2).

These differences in the  $\delta^{13}\text{C}$  values of C<sub>3</sub> and C<sub>4</sub> plants are critical when considering mixing lines between the C<sub>3</sub> and C<sub>4</sub> isotopic endmembers (Fig. 1). The ambiguity that results from having multiple endmembers means that approximate fractions of C<sub>3</sub> or C<sub>4</sub> biomass, rather than absolute percentages, should be discussed for the various species of bovinds.

*Carbon isotopes in East African bovinds.*—We report below the stable isotope results for bioapatites ( $n = 408$ ) and for keratin ( $n = 151$ ) from East African bovinds,

TABLE 2.— $\delta^{13}\text{C}$  values for  $\text{C}_3$  dicots and  $\text{C}_4$  grasses from different ecosystems in East Africa. Xeric grasses are those using the NAD and PCK photosynthetic subpathways, along with *Aristida* (NADP) grasses. Mesic grasses are those using the NADP subpathway (excluding *Aristida*). The average  $\delta^{13}\text{C}$  for grasses is the numerical average of all  $\text{C}_4$  grasses analyzed, without taking into account the relative abundances of the different species in the local ecosystem.<sup>a</sup>

Locality	Date	$\text{C}_3$ dicots			$\text{C}_4$ xeric			$\text{C}_4$ mesic			$\Delta (\text{C}_3 - \text{C}_4)$
		$\bar{X}$	SE	n	$\bar{X}$	SE	n	$\bar{X}$	SE	n	
Closed-canopy forest											
Kakamega	July 1999	-31.4	0.5	22							
Open-canopy forest											
Aberdares	July 1999	-27.8	0.3	7	-12.1	0.5	4	-11.5	0.4	6	16.1
Mesic savanna: NADP dominated											
Ngong	September 1997 to August 1998	-28.5	0.2	18				-11.5	0.2	18	17.0
NP	July 1997 and July 1998	-28.6	0.4	7	-12.2	0.3	3	-11.7	0.1	11	16.9
Mesic savanna: NAD+PCK dominated or NAD+PCK/NADP mixed											
Mpala	July 1997	-27.1	1.0	3	-12.8	0.4	39	-12.2	0.2	16	14.4
Mpala	September 1998 to December 1998	-24.6	0.3	15	-14.0	0.4	9	-12.9	0.1	6	11.0
Nakuru	August 2000	-27.6	0.5	3	-14.1	0.2	13				13.5
QEP	July 1998	-27.7	0.2	7	-13.3	0.3	4	-12.3	0.2	7	15.4
Xeric bushland: NAD+PCK dominated											
Turkana	July 1997	-27.6	0.2	20	-13.2	0.2	11				14.4
Samburu	July 1997	-27.4	0.9	6	-13.4	0.5	4	-12.0	0.3	4	14.7
Xeric bushland: drought											
Turkana	January 1997	-26.7	0.4	17	-13.9	0.1	2				12.8
Turkana	July 1999	-26.3	0.4	22	-14.4	0.4	4				11.9
Turkana	July 2000	-25.8	0.4	12	-13.2	0.2	6				12.6
Tsavo	July 2000	-27.1	0.8	6	-13.8	0.4	6				13.3

<sup>a</sup> NADP, nicotinamide adenine dinucleotide phosphate; NAD, nicotinamide adenine dinucleotide; PCK, phosphoenolpyruvate carboxykinase; NP, Nairobi National Park; QEP, Queen Elizabeth Park.

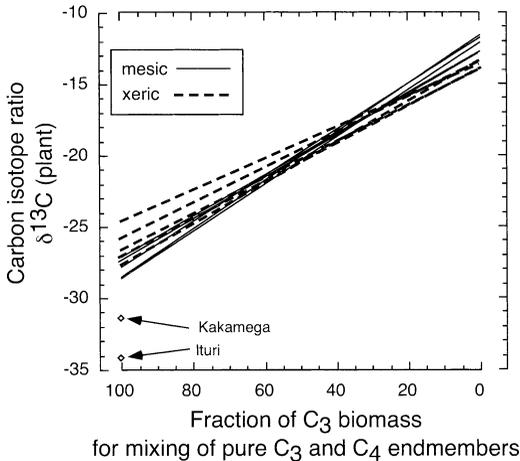


FIG. 1.—Mixing lines between  $C_3$  and  $C_4$  biomass in different East African savanna or forest ecosystems between 1997 and 2000. Solid lines indicate samples from mesic ecosystems dominated by NADP grasses. Dashed lines are for samples from xeric ecosystems dominated by NAD and PCK grasses. The  $\delta^{13}C$  for the understory  $C_3$  plants from the closed-canopy Kakamega and Ituri forests are shown for comparison (diamonds).

along with estimates of the fraction of  $C_4$  biomass in the diet. This fraction is a direct measure of the amount of grazing. The isotope results are grouped by tribe. The distribution of different taxa according to locality is provided in Appendix I. Average  $\delta^{13}C_{\text{bioapatite}}$  and  $\delta^{13}C_{\text{keratin}}$  for bovids are presented in Table 3 and Fig. 2. The estimated  $\delta^{13}C_{\text{diet}}$  was calculated using the  $\epsilon_{\text{bioapatite diet}}$  and  $\epsilon_{\text{keratin diet}}$  factors of 14.1‰ and 3.1‰, and the fraction of  $C_4$  biomass in the diets of the mammals was estimated assuming isotope endmember mixing models of each of the localities studied (Table 2).

Grant's gazelle (*Gazella granti*) is represented by samples from Athi Plains, Laikipia, and from the more xeric Tsavo and Turkana regions (Appendix I). All Grant's gazelle samples give an average  $\delta^{13}C_{\text{diet}}$  value of  $-24.0 \pm 3.0\text{‰}$  ( $n = 79$ ), with an average calculated diet of 22%  $C_4$  biomass. These results suggest that the diet of many individual Grant's gazelles includes a sig-

nificant  $C_4$  component—from 0% to 80%  $C_4$  grass. However, on the whole, the species is primarily a browser. Thomson's gazelle (*Gazella thomsonii*) has an average diet  $\delta^{13}C_{\text{diet}}$  value of  $-16.9 \pm 2.6\text{‰}$  ( $n = 31$ ), which is 68%  $C_4$  biomass using the  $\delta^{13}C_{\text{plant}}$  endmember values measured in this ecosystem. Gerenuk (*Litocranius walleri*) was sampled from a variety of localities. The  $\delta^{13}C$  values of tooth enamel and keratin correspond to a diet of about 99%  $C_3$  dicots for gerenuks ( $n = 11$ ).

We present data for several different members of the Neotragini. The dwarf antelope (*Neotragus batesi*) is represented only by 1 individual from the Ituri Forest in Zaire. Three different teeth from this individual have  $\delta^{13}C_{\text{bioapatite}}$  values that range from  $-24.5\text{‰}$  to  $-26.0\text{‰}$ , which are the most  $^{13}C$ -depleted bioapatite samples from the more than 1,000 extant mammals we have analyzed in our lab. The suni antelope (*Neotragus moschatus*) also may be a pure browser, although only 1 specimen was analyzed.

Two species of dikdik were sampled: Guenther's dikdik (*Madoqua guentheri*) and Kirk's dikdik (*Madoqua kirkii*). The average diet of all dikdiks ( $n = 26$ ) exceeds 95%  $C_3$ . The oribi (*Ourebia ourebi*) is represented by 4 samples, which suggest a diet of about 84%  $C_4$  grass.

Three different Cape buffalo (*Syncerus caffer*) groups were sampled: savanna dwellers from Kenya and Uganda, forest dwellers from high elevations in the Aberdares or Mt. Kenya, and forest dwellers from lowland regions (Ituri Forest in the Democratic Republic of Congo and the Arobuko-Sokoce Forest on the Kenyan coast). Savanna buffalo has  $\delta^{13}C_{\text{enamel}}$  and  $\delta^{13}C_{\text{keratin}}$  values that are consistent with a virtually pure (about >95%) grazing diet ( $n = 94$ ), and thus the savanna buffalo is considered to be a pure grazer. Buffalo from lowland forests has a different diet: it has a significant  $C_3$  component to its diet, which could be due to either  $C_3$  grasses in the understory of forest or to browse. Buffalo

TABLE 3.—Summary of  $\delta^{13}\text{C}$  values for tooth enamel, keratin, and calculated average diet for East African bovids using the isotopic enrichment factors of 14.1‰ and 3.1‰ for bioapatite diet and keratin diet, respectively. Also given are the percentages of  $\text{C}_4$  biomass in the diet, assuming  $\text{C}_3$  and  $\text{C}_4$  end-members from the respective ecosystems of Table 2. Hypsodonty indices (HI) are from Janis (1988) and average mass (female) for each species is from various sources, principally Kingdon (1982a, 1982b) and Estes (1991).

Tribe Species	Enamel			Keratin			Diet			% $\text{C}_4$	HI	Mass (kg)
	$\bar{X}$	<i>SD</i>	<i>n</i>	$\bar{X}$	<i>SD</i>	<i>n</i>	$\bar{X}$	<i>SD</i>	<i>n</i>			
Antilopini												
<i>Gazella granti</i>	-11.0	3.3	40	-20.3	2.4	39	-24.0	3.0	79	22	3.45	45
<i>G. thomsonii</i>	-3.7	2.8	9	-13.6	2.5	22	-16.9	2.6	31	68	3.77	18
<i>Litocranius walleri</i>	-11.8	1.5	8	-21.5	0.8	3	-25.3	1.4	11	2	1.32	31
Neotragini												
<i>Madoqua guentheri</i>	-12.3	1.8	16	-21.6	0.7	3	-25.8	1.7	19	1	2.63	4
<i>M. kirkii</i>	-12.9	1.1	6	-20.4		1	-26.1	1.6	7	0	2.63	5
<i>Neotragus batesi</i>	-25.2	0.7	3				-38.8	0.7	3	0	2.94	3
<i>N. moschatus</i>				-24.5		1	-27.5		1	0		7
<i>Ourebia ourebi</i>	-5.3		1	-9.7	3.6	3	-14.4	4.3	4	84	3.80	11
<i>Oreotragus oreotragus</i>				-22.4		1	-25.4		1	4	3.82	13
<i>Raphicerus campestris</i>				-21.3		1	-24.3		1	18	3.44	11
Bovini												
<i>Syncerus caffer</i>												
Forest	-6.5	5.4	13	-14.0	6.6	4	-19.5	5.5	17	52		
Savanna	1.1	1.0	74	-10.6	1.4	20	-13.0	1.1	94	100	3.00	576
Tragelaphini												
<i>Taurotragus oryx</i>	-10.6	1.3	16	-21.6		1	-24.7	1.2	17	18	2.91	392
<i>Tragelaphus eurycerus</i>	-14.9	0.4	2	-25.1		1	-28.4	0.4	3	0	1.92	240
<i>T. imberbis</i>	-12.5	0.8	4				-26.2	0.8	4	0	1.97	62
<i>T. scriptus</i>	-13.9	0.2	2	-26.2	2.3	5	-28.7	2.1	7	0	2.54	42
<i>T. spekii</i>	-16.7	1.1	3				-30.4	1.1	3	0	2.90	53
<i>T. strepsiceros</i>	-11.8	1.0	4				-25.5	1.0	4	4	2.29	170
Reduncini												
<i>Kobus ellipsiprymnus</i>	0.6	1.1	31	-10.5	1.5	2	-13.4	1.1	33	92	3.47	186
<i>K. kob</i>	1.1	0.4	9	-9.8	0.3	2	-12.8	1.2	11	95	3.72	63
<i>Redunca redunca</i>	2.1	1.8	9				-11.9	1.8	9	100		40
<i>R. fulvorufula</i>	1.0		1				-12.9		1	94	3.79	29
Hippotragini												
<i>Oryx gazella</i>	-0.5	1.5	16	-10.3	2.5	3	-14.2	1.7	19	88	3.37	162
<i>Hippotragus equinus</i>	3.6	1.3	2				-10.4	1.3	2	100	4.28	260
<i>H. niger</i>	1.0	2.5	4				-12.9	2.4	4	94	3.77	220
Alcelaphini												
<i>Alcelaphus buselaphus</i>	2.2	1.3	31	-8.8	0.6	4	-11.8	1.2	35	100	5.23	126
<i>Connochaetes taurinus</i>	1.9	1.3	38	-7.9	0.7	5	-11.9	1.3	43	100	4.94	163
<i>Damaliscus hunteri</i>	0.3	0.3	3	-10.4	0.2	2	-13.5	0.2	5	92	4.14	80
<i>D. lunatus</i>	1.9	1.0	11				-12.1	1.0	11	100	5.10	108
Aepycerotini												
<i>Aepyceros melampus</i>	-6.0	3.0	38	-14.9	1.4	12	-19.3	2.7	50	52	4.89	45
Cephalophini												
<i>Cephalophus dorsalis</i>	-15.3	0.7	4				-29.0	0.7	4	0	1.15	22
<i>C. leucogaster</i>	-15.2	0.7	4				-28.9	0.7	4	0		12
<i>C. monticola</i>	-14.5		1	-22.3		1	-26.8	2.0	2	0	1.90	5
<i>C. natalensis</i>				-24.1	0.3	3	-27.7	0.3	3	0		14
<i>C. nigrifrons</i>	-15.5		1	-23.9	0.3	3	-27.7	1.3	4	0		18
<i>C. silvicultor</i>	-15.2	1.3	2				-28.9	1.3	2	0	2.23	68
<i>C. weynsi</i>	-15.9	0.1	2				-29.6	0.1	2	0		
<i>Sylvicapra grimmia</i>				-23.0	1.4	9	-26.0	1.4	9	0	2.97	15

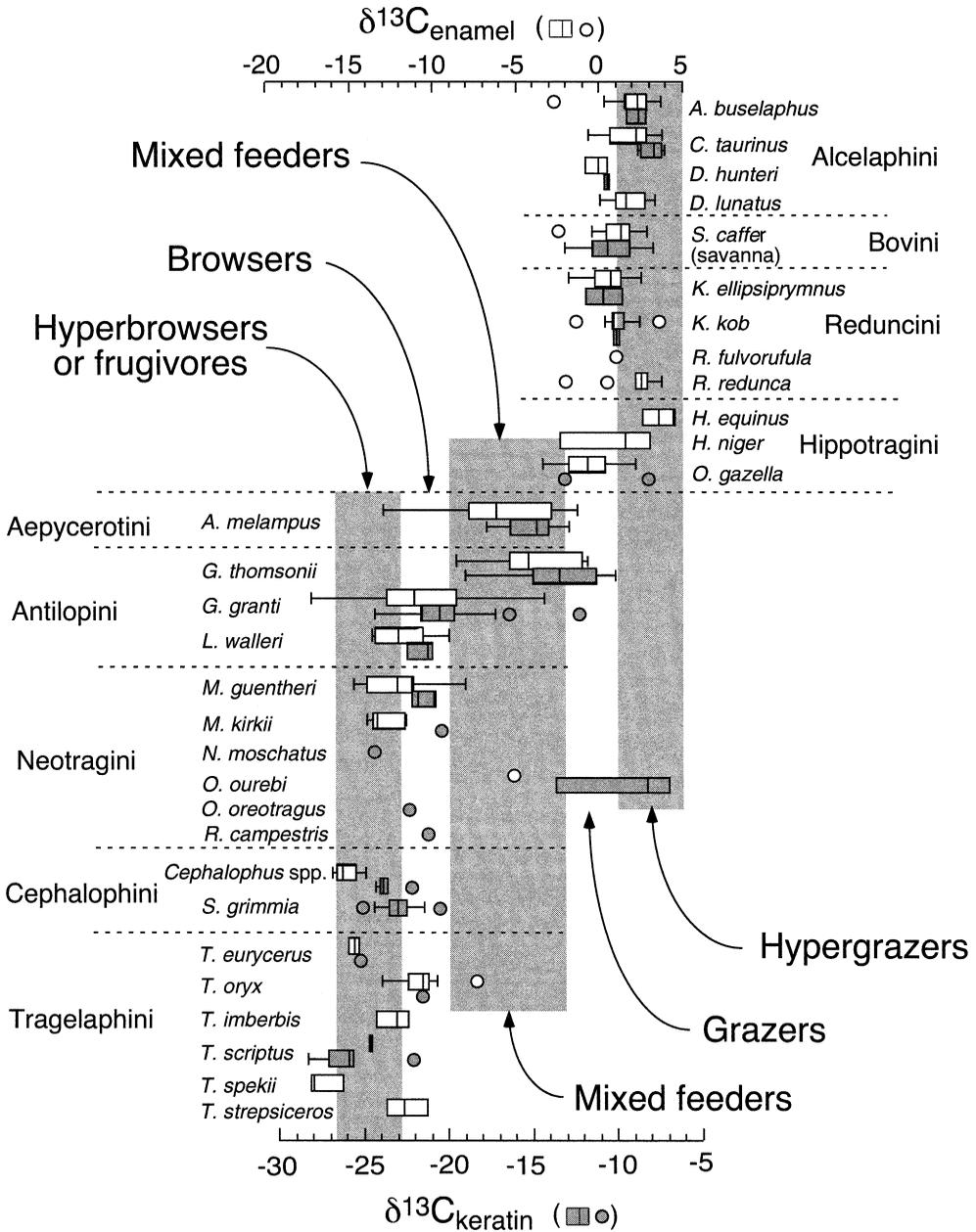


FIG. 2.—Ranges of  $\delta^{13}\text{C}_{\text{enamel}}$  and  $\delta^{13}\text{C}_{\text{keratin}}$  for bovid tribes and species. The  $\delta^{13}\text{C}_{\text{enamel}}$  and  $\delta^{13}\text{C}_{\text{keratin}}$  scales are offset by 11.1‰ because enamel is enriched by 11.1‰ relative to keratin (Cerling and Harris 1999). Open circles show outliers.

from the Kenyan Highlands in Aberdare National Park and from Mt. Kenya National Park have a wide range of  $\delta^{13}\text{C}_{\text{bioapatite}}$  values, from +0.5‰ to -13.6‰. However, some of these individuals were from

>3,000 m, where  $\text{C}_3$  grasses are more abundant than  $\text{C}_4$  grasses. It is impossible to deduce where the animals were living when their tooth germs were forming, which typically was several years before the death of

the animal. It seems likely that the isotopic variation in the mountain populations of buffalo may reflect feeding from different elevations within and outside the parks.

The tragelaphins sampled indicate diets dominated by browse. The bongo (*Tragelaphus eurycerus*) has sufficiently negative  $\delta^{13}\text{C}$  values to indicate a diet of closed-canopy browse. Lesser kudu (*Tragelaphus imberbis*) has  $\delta^{13}\text{C}_{\text{diet}}$  values compatible with a pure  $\text{C}_3$  diet ( $n = 4$ ). Eland (*Taurotragus oryx*) was sampled from both the mesic Athi Plains region and the somewhat more xeric Laikipia plateau region. The estimated  $\delta^{13}\text{C}_{\text{diet}}$  of  $-24.7\text{‰}$  ( $n = 17$ ) indicates that the average eland consumes a small but detectable fraction (18%) of  $\text{C}_4$  grasses. Bushbuck (*Tragelaphus scriptus*) samples have average calculated  $\delta^{13}\text{C}_{\text{diet}}$  values of  $-28.7\text{‰}$ , indicating a pure  $\text{C}_3$  browsing diet ( $n = 7$ ). The sitatunga (*Tragelaphus spekkii*) samples are from the Ituri Forest and from Garamba in the Democratic Republic of Congo and have a calculated  $\delta^{13}\text{C}_{\text{diet}}$  of  $-30.4\text{‰}$ , which indicates a closed-canopy habitat and virtually no  $\text{C}_4$  grass intake at either locality. The greater kudu (*Tragelaphus strepsiceros*) have a calculated  $\delta^{13}\text{C}_{\text{diet}}$  of  $-25.5\text{‰}$  ( $n = 4$ ), indicating a diet of only about 4%  $\text{C}_4$  grass, and thus can be considered to be almost a pure browser.

Reduncins have diets dominated by  $\text{C}_4$  grass. The waterbuck (*Kobus ellipsiprymnus*) is widespread in East Africa and is well represented in this study. Thirty-three waterbuck from Nakuru National Park, Tsavo National Park, the Laikipia region, and Garamba National Park have  $^{13}\text{C}$  values that indicate a diet of approximately 97%  $\text{C}_4$  grass. Uganda kob has an average  $\delta^{13}\text{C}_{\text{diet}}$  value of  $-12.8\text{‰}$  ( $n = 11$ ), which indicates the essentially pure  $\text{C}_4$  diet. Nine Bohor reedbucks have a pure  $\text{C}_4$  diet with an average  $\delta^{13}\text{C}_{\text{diet}}$  value of  $-11.9\text{‰}$ . A single Chanler's mountain reedbuck (*Redunca fulvorufula*) has a  $\delta^{13}\text{C}_{\text{bioapatite}}$  compatible with a pure  $\text{C}_4$  diet.

Hippotragins are  $\text{C}_4$  dominantly grazers to pure grazers. The sample sizes of the

roan (*Hippotragus equinus*) and sable (*Hippotragus niger*) antelopes are small ( $n = 2$  and 4, respectively), but the results suggest that they have essentially pure  $\text{C}_4$  diets. Oryx (*Oryx gazella*) is well represented by individuals from the Tsavo and Turkana regions. The  $\text{C}_4$  component in the oryx diet is about 88% ( $n = 19$ ), indicating a small, but significant, fraction of browse.

The alcelaphins are predominately pure grazers. The isotopic results indicate that kongoni (*Alcelaphus buselaphus cokei*), Jackson's hartebeest (*Alcelaphus buselaphus jacksoni*), blue wildebeest (*Connochaetes taurinus*), and topi or tiang (*Damaliscus lunatus*) are obligate grazers with diets of about 100%  $\text{C}_4$  biomass. The hirola (*Damaliscus hunteri*), however, has a significant fraction of  $\text{C}_3$  biomass in its diet, on the order of 5–10% (Table 3). Notably, the hirola has a lower  $\delta^{13}\text{C}_{\text{bioapatite}}$  value than does topi from the same region (Tana River), confirming a small but significant  $\text{C}_3$  component in the diet of hirola.

We treat Aepycerotini as distinct from the Alcelaphini (following Kingdon 1982b). The sole extant aepycerotin is the impala, *Aepyceros melampus*. Samples of the impala were collected from widely separated parts of Kenya (Appendix I). The impala has the greatest range of  $\delta^{13}\text{C}$  values in this study. Taken together, the average value for 50 stable isotope analyses indicates a mixed  $\text{C}_3$ – $\text{C}_4$  diet, with an estimated fraction of 52%  $\text{C}_4$  biomass. These results indicate that impalas are mostly mixed feeders but also opportunistic and that individual specimens may vary greatly in the proportions of  $\text{C}_3$  or  $\text{C}_4$  biomass in their diets.

The tribe Cephalophini includes the duikers and consists of 2 genera, *Cephalophus* (12 species) and *Sylvicapra* (1 species). Cephalophins are mostly forest dwellers and frugivores, although some, such as the common duiker (*Sylvicapra grimmia*), are found in bushland. Most of our cephalophin samples are from the closed-canopy Ituri Forest where duikers subsist on fruits fallen

from the canopy. Fruits from the Ituri Forest have an average  $\delta^{13}\text{C}_{\text{fruit}}$  value of  $-30.2 \pm 1.7\text{‰}$  ( $n = 18$ ). The average  $\delta^{13}\text{C}_{\text{bioapatite}}$  for samples of bay duiker (*Cephalophus dorsalis*), white bellied duiker (*C. leucogaster*), blue duiker (*C. monticola*), black-fronted duiker (*C. nigrifrons*), yellow-backed duiker (*C. silvicultor*), and Weyn's duiker (*C. weynsi*) from the Ituri Forest is  $-15.3 \pm 0.7\text{‰}$  ( $n = 14$ ). This is compatible with a pure  $\text{C}_3$  diet. Six duikers from the Aberdares and 3 duikers from the Arobuko-Sokoke Forest (*C. monticola*, *C. natalensis*, *C. nigrifrons*) have an average  $\delta^{13}\text{C}$  value that indicates a pure  $\text{C}_3$  diet of about  $-28\text{‰}$  for today's (AD 2000) ecosystems. Nine samples of *S. grimmia* have an average  $\delta^{13}\text{C}$  value indicating a virtually pure  $\text{C}_3$  diet. Thus, all cephalophin species sampled for this study have a virtually pure  $\text{C}_3$  diet, with no indication of any measurable  $\text{C}_4$  component (Table 3; Fig. 2).

*Hypsodonty, body size, and diets of bovids.*—Browsing mammals have a hypsodonty index (height/width of unworn 1st molar—Janis 1988) between 1 and 4, whereas grazers have an index between 3 and 6. This study confirms the previous observations that hypsodonty is related to diet, but it also provides a quantification of diet estimates in the context of hypsodonty (Fig. 3A).

Our results (Fig. 3B) show that grazing mammals can weigh as little as 11 kg and that there is no upper limit to the size of browsers. Most large ( $>100$  kg) bovids are grazers, with the tragelaphins being the only large ( $>100$  kg) browsers. The size relationship may be related to higher metabolism of smaller mammals (Demment and van Soest 1985) and to low nitrogen concentrations of  $\text{C}_4$  grasses compared with  $\text{C}_3$  dicots in East Africa (Table 1).

#### DISCUSSION

*Ecosystem differences and isotope mixing lines.*—Stable isotope ratios have been used in many studies to estimate the fraction of  $\text{C}_3$  or  $\text{C}_4$  biomass in various ecosys-

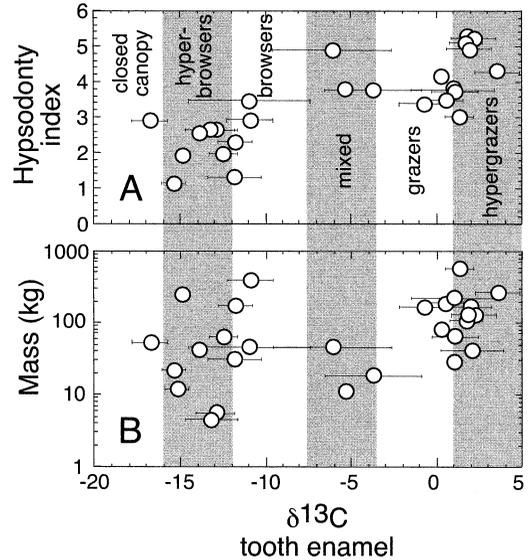


FIG. 3.—Comparison of  $^{13}\text{C}_{\text{enamel}}$  with hypsodonty and with body mass. A)  $^{13}\text{C}_{\text{enamel}}$  versus hypsodonty index (Janis 1988) for mammals in this study. (Forest buffalo not included in this figure.) B)  $^{13}\text{C}_{\text{enamel}}$  versus average mass (female) for mammals in this study.

tems or in the diets of mammals. In most studies, single-endmember values have been used to describe mixing lines between the  $\text{C}_3$  and  $\text{C}_4$  endmembers. Our results on plants from different environments illustrate that different mixing lines should be applied in different localities.

Two closed-forest ecosystems have average  $\delta^{13}\text{C}_{\text{leaf}}$  values that are very depleted in  $^{13}\text{C}$ . The Ituri Forest in Democratic Republic of Congo has  $\delta^{13}\text{C}_{\text{leaf}}$  values as negative as  $-37\text{‰}$  at the canopy floor, although open areas and fruits from high in the canopy have values of about  $-31\text{‰}$ . The Kakamega Forest has  $\delta^{13}\text{C}_{\text{leaf}}$  values averaging  $-31\text{‰}$  (Table 1). Closed-canopy forests have much more negative  $\delta^{13}\text{C}$  values than the average  $\delta^{13}\text{C}_{\text{leaf}}$  value from more open habitats, which is used in isotope mixing models (about  $-27\text{‰}$ ). The range in  $\delta^{13}\text{C}_{\text{leaf}}$  for  $\text{C}_3$  plants in bushland, open savannas, or relatively open forests is significant. Average  $\delta^{13}\text{C}$  values for  $\text{C}_3$  plants in bushlands

or savannas range from  $-28.6\text{‰}$  to  $-24.6\text{‰}$ .

Average  $\delta^{13}\text{C}_{\text{leaf}}$  value of the mesic NADP  $\text{C}_4$  plants ranges between  $-11.5\text{‰}$  and  $-12.9\text{‰}$ , whereas the average  $\delta^{13}\text{C}_{\text{leaf}}$  values of xeric NAD, PCK, and *Aristida*  $\text{C}_4$  plants range between  $-12.1\text{‰}$  and  $-14.4\text{‰}$ .  $\text{C}_4$  plants are more depleted in  $^{13}\text{C}$  at the ecosystem level during xeric conditions than during mesic conditions (Table 2), which corroborates the work of Buchmann et al. (1996).

The isotopic separation between  $\text{C}_3$  and  $\text{C}_4$  plants is quite different for mesic conditions compared with xeric conditions, and especially with xeric-stressed conditions. Mesic ecosystems have a  $\Delta_{\text{C}_3\text{-C}_4}$  separation of  $16\text{--}17\text{‰}$  (Table 2). Xeric ecosystems during nondrought conditions have a  $\Delta_{\text{C}_3\text{-C}_4}$  separation of  $14\text{--}15\text{‰}$ , whereas xeric ecosystems under drought conditions have a  $\Delta_{\text{C}_3\text{-C}_4}$  separation of  $11\text{--}13\text{‰}$  (Table 2). Therefore, interpretations of the fraction of  $\text{C}_3$  versus  $\text{C}_4$  biomass in diets must take into account the isotopic variability of the endmembers used in mixing models (Fig. 2).

*Comparison with previous dietary classifications.*—This is the 1st (along with the study by Sponheimer et al. 2003) quantitative estimate of the diet of a large and diverse group of mammals based on stable isotope analyses. In a broad sense, these results agree with general field observations (see review by Gagnon and Chew 2000). However, some important differences are evident between our quantitative measurements (Table 3) and previous qualitative observations.

Estimates of diet based on stable isotopes allow a somewhat different diet classification than has been previously proposed (Hofmann 1989; Hofmann and Stewart 1972) in that it is based solely on the  $\delta^{13}\text{C}$  differences between  $\text{C}_3$  and  $\text{C}_4$  plants. In our isotopic classification, we make no assumptions about quality of food. The advantage of this scheme is that the results are readily quantifiable, and they can be used even for animals that have been dead for millions of

years. The disadvantage is that they only distinguish between  $\text{C}_3$  and  $\text{C}_4$  fractions of the diet so that finer distinctions (e.g.,  $\text{C}_3$  browsers versus  $\text{C}_3$  frugivores) cannot be made.

It is possible to formulate an isotopic classification of diets based on the ranges of  $\delta^{13}\text{C}$  values of tooth enamel, keratin, or diets. We propose an isotope continuum from grazer to browsers that consists of hypergrazers, grazers, mixed feeders, browsers, and hyperbrowsers (Fig. 2). For the extant species, the boundaries are proposed to be at  $\delta^{13}\text{C}_{\text{plant}}$  values of  $-13\text{‰}$ ,  $-17.5\text{‰}$ ,  $-21.5\text{‰}$ , and  $-26\text{‰}$  and correspond to 100%, 70%, 30%, and 0%  $\text{C}_4$  component in the diets. In this classification, very few African bovids are seen to be truly mixed feeders; only Thomson's gazelle, oribi, and impala have median values that fall in the range of  $>30\%$   $\text{C}_3$  browse and  $>30\%$   $\text{C}_4$  grass. A few Grant's gazelle individuals fall into the mixed category, but the average  $\delta^{13}\text{C}$  diet of  $-24\text{‰}$  (Table 3) shows that most Grant's gazelles are browsers and some are hyperbrowsers. These results show that there are 2 distinct functional groups, the hypergrazer-grazer group and the hyperbrowser-browser group. It is likely that the mixed groups are those species that switch from one group to the other depending on the availability of fresh grass (Du Toit 1995; Du Toit and Cummings 1999). Future stable isotope profiles of hair, horn, or hooves could enhance understanding of seasonal diet changes.

This study shows remarkable agreement with the previous compilation of diet estimates of Gagnon and Chew (2000). It also agrees very well with the work of Sponheimer et al. (2003) on diets of South African bovids using stable isotope analyses of bioapatite and hair. Differences between diet estimates from East and South Africa are less than 10% for 17 of 18 species common to both studies based on stable isotopes; the only species with a significant difference in the diet estimates was the sitatunga (*T. spekii*), which had sample sizes

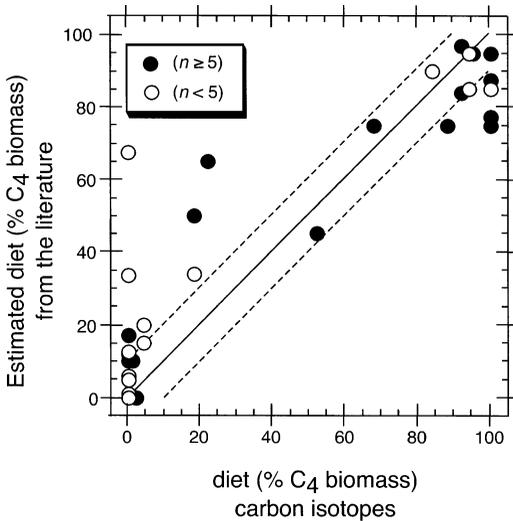


FIG. 4.—Comparison of diet estimates by stable isotopes with values from literature (Gagnon and Chew 2000). Solid line presents a 1:1 correlation, and dashed lines show differences of 10% between the 2 methods. Sample size: solid circles,  $n \geq 5$ ; open circles,  $n < 5$ .

of 3 and 4 for East and South Africa, respectively.

Comparison with the compilation of Gagnon and Chew (2000) shows general agreement between methods where we use their fraction of monocots to represent the  $C_4$  component. The estimated  $C_4$  component is within 10% for most species (Fig. 4). Eight species stand out as having significant ( $>10\%$ ) differences in their diets (species with  $n < 5$  are not considered to have large enough sample sizes for adequate comparison). The stable isotope results indicate that the hyperbrowsers and browsers dikdik, eland, and Grant's gazelle have less  $C_4$  grass in their respective diets than is estimated by Gagnon and Chew (2000). Conversely, the hypergrazers and grazers kongoni, wildebeest, oryx, roan antelope, and buffalo all have a higher  $C_4$  grass component than is suggested by the literature review by Gagnon and Chew (2000). The discrepancy is particularly great for eland and Grant's gazelle, which we find to be browsers ( $<25\%$   $C_4$  diet),

whereas the Gagnon and Chew (2000) review suggests that both have diets that are  $\geq 50\%$   $C_4$  grass. Field observations tend to overestimate the grass component in browsers and to overestimate the browse component in grazers (Fig. 4).

Dietary interpretation from wear scratches is in broad agreement with that from isotopic analysis. Both methods recognize wildebeest, waterbuck, and sable antelope as grazers and bongo, kudu, duikers, and renek as browsers. However, Solounias et al. (2000) interpret eland, bushbuck, Grant's gazelle, and Thomson's gazelle as seasonal mixed feeders, whereas most of our samples indicate that eland is a browser and bushbuck is essentially a pure browser. Moreover, we have determined that, despite being characterized as mixed feeders, Grant's gazelles tend to have a higher proportion of browse in their diet than do Thomson's gazelles. Solounias et al. (2000) recognize Cape buffalo as facultative grazers despite the low frequency of scratches on their enamel. Our results indicate that savanna-dwelling buffalo is a grazer but that forest buffalo may exploit a wider variety of browse.

CONCLUSIONS

Stable isotopes provide a quantitative means of documenting the fraction of  $C_3$  and  $C_4$  plants in bovid diets. For East Africa, the dietary endmembers are  $C_3$  browse and  $C_4$  grass. A survey of the diets of modern East African bovids shows that they can be classified into 5 distinct groups: hypergrazers ( $>95\%$  grass), grazers ( $>70\%$  grass), mixed feeders ( $>30\%$  grass and  $>30\%$  browse), browsers ( $>70\%$  browse), and hyperbrowsers ( $>95\%$  browse). Unfortunately, this method will not distinguish  $C_3$  frugivores from  $C_3$  browsers. Our survey of East African bovids reveals that few species are truly mixed feeders and that most have a marked preference for either grass or browse. Thomson's gazelle and impala have average diets that indicate a mixed  $C_3$ - $C_4$  intake of browse and grass.

This study also revealed that there is considerable variation in the  $\delta^{13}\text{C}$  of  $\text{C}_3$  plants among different ecosystems or in the same ecosystem at different times.  $\text{C}_3$  plants in savannas had  $\delta^{13}\text{C}$  values ranging from an average of about  $-28\text{‰}$  near the end of the rainy season to  $-25\text{‰}$  during drought conditions. Closed-canopy forests have  $\delta^{13}\text{C}$  values of  $-30\text{‰}$  (or even more negative) for plants growing in the subcanopy. The  $\delta^{13}\text{C}$  values for  $\text{C}_4$  plants become more negative under drought-stressed conditions. The  $\delta^{13}\text{C}$  values of mesic-adapted  $\text{C}_4$  plants (those using the NADP subpathway) are more positive than those of xeric-adapted  $\text{C}_4$  plants (those using the NAD and PCK subpathways, along with *Aristida*). In addition,  $\delta^{13}\text{C}$  values of individual plants from each of these subpathways become more negative under drought-stressed conditions. The result is that the isotope separation between  $\text{C}_3$  and  $\text{C}_4$  plants under mesic conditions is 16–17‰, whereas it can be as low as 11–12‰ under drought conditions. These considerations are important for defining the mixing-line endmembers for extant and fossil assemblages.

Correlation of isotopic dietary estimates with direct field observations is very good, although some minor differences have been observed. These estimates also help quantify the relationship between diet and hypsodonty. The stable isotope method of estimating diets is also an important and reliable technique for comparing diets of modern and fossil mammalian assemblages.

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#### APPENDIX I

Bovid materials sampled for analysis of carbon isotopes are listed below by tribe and species, with abbreviations for locations followed by numbers of specimens sampled in parentheses. Abbreviations are given by ecosystem type. Closed-canopy forest: I—Ituri, Democratic Republic of Congo; Kk—Kakamega, Kenya. Open-canopy forest: Mt—Aberdares and Mount Kenya, Kenya; AS—Arobuko-Sokoke Forest, Kenya. Mesic savanna: NP—Nairobi National Park, Kenya; TC—Tana River/Coast, Kenya; G—Garumba, Democratic Republic of Congo; Lai—Laikipia, Kenya; Nak—Nakuru, Kenya; QEP—Queen Elizabeth Park, Uganda; Ath—Athi Game Ranch, Kenya. Xeric bushland: Ol—Olorgesailie, Kenya; S—Samburu Reserve, Kenya; Ts—Tsavo National Parks, Kenya; Tu—Turkana, Kenya. Oth—other.

Antilopini.—*Gazella granti*: Nbi (6), Lai (12), Ath (55), Ts (2), Tur (4); *G. thomsonii*: Ath (31); *Litocranius walleri*: Lai (5), Ol (1), Tur (2), Oth (3).

Neotragini.—*Madoqua guentheri*: Tur (19); *M. kirkii*: Ol (3), Ts (2), Oth (1); *Neotragus batesi*: I (3); *N. moschatus*: Oth (1); *Oreotragus ourebi*: Oth (4); *O. oreotragus*: Oth (1); *Raphicerys campestris*: TC (1).

Bovini.—*Syncerus caffer* (forest): I (1), Mt (13), AS (3); *S. caffer* (savanna): Lai (24), Nak (34), QEP (5), Sam (1), Ts (29), G (1).

Tragelaphini.—*Taurotragus oryx*: Nbi (6), Lai (8), Ts (3); *Tragelaphus euryceros*: Mt (3); *T. imberbis*: Ts (4); *T. spekii*: I (2), G (1); *T. streptyceros*: Sam (1), Tur (3); *T. scriptus*: Kk (2), Mt (3), NP (2).

Hippotragini.—*Hippotragus equinus*: Oth (2); *H. niger*: Oth (4); *Oryx gazella*: Lai (3), Ts (5), Tur (11).

Reduncini.—*Kobus ellipsiprymnus*: Lai (5), Nak (15), Ts (12), G (1); *K. kob*: QEP (8), G (3); *Redunca fulvorufula*: Mt (1); *R. redunca*: Mt (6), Nbi (2), Oth (1).

Alcelaphini.—*Alcelaphus buselaphus*: Nbi (8), Ath (18), Lai (5), Sam (2), Ts (2); *C. taurinus*: Nbi (22), Ath (21); *Damaliscus hunteri*: TC (5); *D. lunatus*: TC (4), Tur (7).

Aepycerotini.—*Aepyceros melampus*: TC (1), Lai (22), Nak (3), Ath (17), Ol (2), Sam (1), Ts (4).

Cephalophini.—*Cephalophus dorsalis*: I (4); *C. leucogaster*: I (4); *C. monticola*: I (1), AS (1); *C. natalensis*: Mt (3); *C. nigrifrons*: I (2), Mt (2); *C. silvicultor*: I (2); *C. weynsi*: I (2); *Sylvicapra grimmia*: Mt (2), Lai (5).