The Isotopic Ecology Of Plants And Animals In Amboseli National Park, Kenya

Paul L. Koch, Anna K. Behrensmeyer, and Marilyn L. Fogel*

Variations in the stable isotope ratios of carbon ($^{13}C/^{12}C$), nitrogen ($^{15}N/^{14}N$), and oxygen ($^{18}O/^{16}O$) provide information about the ecology, physiology, and habitats of living and extinct animals. For example, the $\delta^{13}C$ values of an animal's tissues are controlled by the isotopic composition of its diet, which, for herbivores, is related to the photosynthetic pathway of food plants (DeNiro and Epstein, 1978; Vogel, 1978). Although affected by dietary $\delta^{15}N$ values, N isotopes in animals vary with rainfall amounts among ecosystems and among trophic levels in an ecosystem (DeNiro and Epstein, 1981; Heaton *et al.*, 1986).

We are investigating the isotopic ecology of plants and animals in Amboseli National Park, Kenya, for several reasons. First, investigations of floral and faunal isotopic composition in terrestrial ecosystems are uncommon (e.g., Ambrose and DeNiro, 1986; Sealy *et al.*, 1987), and none evaluates C, N, and O isotopes simultaneously. Ecosystem studies test the generality of relationships determined either in the laboratory or in comparisons of individuals from different regions. Second, stable and radiogenic isotopes have been employed to identify sources of elephant ivory and rhinoceros horn, in order to control sales of poached versus legally hunted animals (van der Merwe *et al.*, 1990; Vogel *et al.,* 1990). Ivory from various African parks can be distinguished by its N, C, and either Sr or Pb isotopic composition. However, if the isotopic composition of elephants varies with time, because of habitat, diet, or climate change, isotopic identification of source region may be unreliable. Either the isotopic composition of a species must be constant through time within an ecosystem, or the secular trends must be minor when compared to differences between populations. Finally, isotopic patterns in modern ecosystems can serve as analogs for interpretation of the fossil record. African faunas, with their diversity of large mammals, are excellent analogs of typical faunas before the Pleistocene extinction.

*Department of Paleobiology, National Museum of Natural History, Smithonian Institution, Washington, DC

Study Area, Materials, and Methods

Amboseli Park is located in southern Kenya (20°40'S, 37°15'E; mean elevation, 1140 m). Annually, temperature averages 23°C and ranges from 15° to 31°C. Rain falls in two seasons and averages 300 cm/year. However, the park is continuously supplied with spring water fed by melting snow on Mt. Kilimanjoro. Habitats in the park include grasslands, bushlands, swamps, seasonal lakes, and woodlands. Woodlands have retreated since the early 1970s, perhaps due to overbrowsing by elephants or increased soil salinity. Tree loss has altered the abundances of herbivores; there are more grazers (animals that eat grass) and fewer browsers (animals eating herbaceous and woody plants) and mixed feeders (D. Western, pers. comm.).

Plant samples (mixtures of leaves and stems) were collected in September 1990 at eight localities in the woodland, swamp, swamp edge, plains, and bush habitats. Faunal samples (tooth dentin or bone) were collected from carcasses throughout the park. Samples were collected from 1975 through 1990, and were in different states of weathering. The minimum number of years since death can be estimated from weathering stage (Behrensmeyer, 1978). For carcasses in advanced weathering stages, however, determining actual time since death is difficult.

Plants were air dried in the field, freeze-dried in the laboratory, and then lightly crushed. Bones and teeth were demineralized with EDTA or 0.1N HCl to isolate collagen (Tuross *et al.*, 1988), and then treated with chloroform/methanol solution to remove lipids. Plant and collagen samples were placed in preheated quartz tubes with CuO and Cu metal. Tubes were evacuated, sealed, combusted at 910°C for 2 h, then cooled at a controlled rate. Standard deviations for analysis of standards were ±0.2‰ for $\delta^{13}C$ and $\delta^{15}N$.

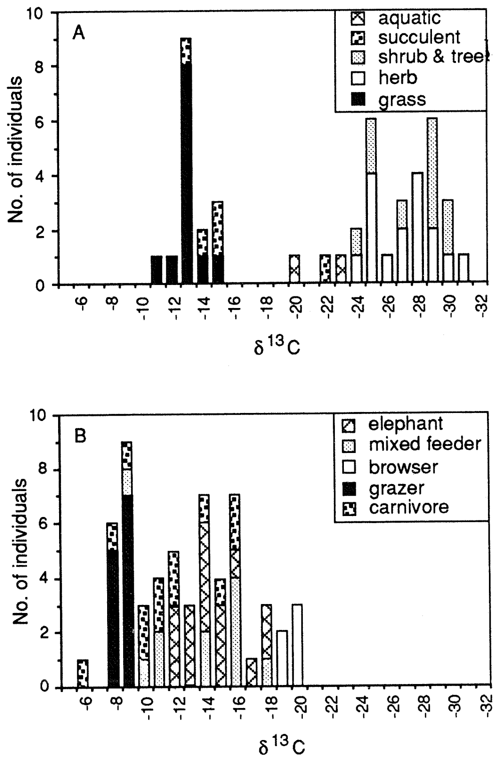

FIG. 92. (A) Histogram of carbon isotope compositions for Amboseli plants subdivided according to physiogamy. (B) Histogram of carbon isotope compositions for Amboseli mammals subdivided according to feeding type.

Isotopic Variation in Amboseli Plants

The plants of Amboseli segregate into two populations isotopically (Table 25, Fig. 92A). The $\delta^{13}C$ values of grasses, which use C_4 photosynthesis, have a mean value ± one standard deviation of -13.2 ± 0.9 ‰. The herbaceous plants and woody plants employ C_3 photosynthesis and have mean values of -27.1 ± 1.9 ‰ and -27.7 ± 2.4 ‰, respectively. This isotopic segregation between C_3 shrubs, trees and herbs and C_4 grasses is expected in a hot, dry region (Tieszen and Boutton, 1988). Succulent herbaceous and woody plants exhibit a

TABLE 25. Isotopic data for Amboseli plants collected in 1990

Species	Family	Habitat	$\delta^{15}N$	$\delta^{13}C$
	Grasses and Sedges			
Cynodon dactylon	Graminae (m)	swamp	10.6	-13.0
Sporobolus consimilis	Graminae (m)	swamp edge	8.9	-13.4
Sporobolus spicatus	Graminae (m)	swamp edge	8.6	-13.2
Sporobolus kentrophyllum	Graminae (m)	swamp edge	10.1	-13.4
Cynodon plectostachys	Graminae (m)	woodland	9.4	-14.2
Sporobolus helvolus	Graminae (m)	bush	8.8	-15.1
Sporobolus ioclades	Graminae (m)	bush	11.9	-13.0
Chloris roxburghiana	Graminae (m)	bush	8.7	-13.4
Chloris virgata	Graminae (m)	bush	10.6	-13.2
Enneapogon cenchroides	Graminae (m)	bush	9.4	-13.3
Cyperus immensus	Cyperaceae (m)	swamp	4.4	-11.2
Cyperus laevigatus	Cyperaceae (m)	swamp	7.8	-12.2
	Submerged Aquatic Plants			
Ceratophyllum sp. 1	Ceratophyllaceae	swamp	6.4	-23.0
Ceratophyllum sp. 2	Ceratophyllaceae	swamp	9.3	-19.7
	Herbs			
Pistia stratiotes	Araceae (m)	swamp	11.5	-29.0
Solanum incanum	Solanaceae	swamp edge	10.4	-25.0
Justicia odora	Acanthaceae	woodland	13.3	-27.6
Diplictera albicauda	n.d.	woodland	8.0	-27.8
Abutilon mauritanium	Malvaceae	plains	11.0	-29.7
Pluchea ovalis	Asteraceae	plains	8.1	-30.5
Cissampelos mucronata	Menispermaceae	plains	7.5	-27.7
Commicarpus sp.	Nyctaginaceae	plains	8.6	-28.9
Achyranthes aspera	Amaranthaceae	plains	11.4	-28.4
Withania somnifera	Solanaceae	plains	9.4	-25.2
Indigofera sp.	Leguminosae	bush	10.4	-25.0
Duosperma eremophiloum	Acanthaceae	bush	8.2	-27.1
Barleria spinisepala	Acanthaceae	bush	11.2	-24.3
	Shrubs, Trees, and Succulent Plants			
Trianthema ceratosepala	Aizoaceae	bush	12.8	-21.8
Sansevieria sp.	Agavaceae (m)	bush	12.6	-14.5
Euphorbia sp. 1	Euphorbiaceae	bush	13.3	-14.9
Euphorbia sp. 2	Euphorbiaceae	bush	13.9	-14.0
Sueda monoica	Chenopodiaceae	swamp edge	13.6	-13.3

Continued on next page

TABLE 25. Continued

Species	Family	Habitat	$\delta^{15}N$	$\delta^{13}C$
	Shrubs and Trees			
Salvadora persica	Salvadoraceae	swamp edge	5.3	-25.4
Maerua triphyllum	Capparidaceae	bush	8.8	-29.3
Commiphora sp.	Burseraceae	bush	15.4	-29.3
Boscia angustifolia	Capparidaceae	bush	11.2	-24.6
Acacia sp.	Leguminosae	bush	10.2	-23.7
Azima tetracantha	Salvadoraceae	woodland	7.6	-26.8
Balanites glabra	Balanitaceae	woodland	7.7	-29.9
Phoenix reclinata	Palmae (m)	woodland	7.1	-29.4
Acacia tortilis	Leguminosae	woodland	8.9	-29.7

(m) indicates monocotyledons, all other plants are dicotyledons

range of $\delta^{13}C$ values and may use either C_4 or Crassulacean acid metabolism. Finally, submerged aquatic plants have $\delta^{13}C$ values that can range between -12 and -33 ‰, depending on the pathway of carbon uptake. Unlike terrestrial plants, which directly incorporate atmospheric CO_2, submerged plants may accumulate either dissolved CO_2 or HCO_3^- (Raven, 1987). Amboseli aquatic plants have $\delta^{13}C$ values intermediate between C_3 and C_4 plants.

The $\delta^{15}N$ values of Amboseli plants form a unimodal distribution with a mean of 9.8 ± 2.4 ‰ (Table 25, Fig. 93A). This mean value is slightly higher than that reported by Sealy et al. (1987) for plants from a region receiving 300 mm of rain. Plant $\delta^{15}N$ values are not dependent on either location or habitat type, although plants from the bush habitat may be slightly ^{15}N-enriched. Plant $\delta^{15}N$ values are not influenced by physiogamy or photosynthetic pathway, with one exception. All Amboseli succulents are ^{15}N-enriched (13.2 ± 0.5 ‰). These species are only distantly related to each other, and the cause of ^{15}N enrichment is unclear.

Isotopic Variation in Amboseli Mammals

The C isotope difference between C_3 and C_4 plants provides a tool for tracing the diets of Amboseli mammals. Previous field studies demonstrate a consistent difference in $\delta^{13}C$ values between diet and collagen of ~+5 ‰ (Vogel 1978; van der Merwe, 1989). Amboseli mammals with pure grazing diets should have $\delta^{13}C$ values of -8 to -9 ‰. All Amboseli grazers (buffalo, spring hare, warthog, wildebeest, zebra) have collagen $\delta^{13}C$ values in this range (Table 26, Fig. 92B).

In contrast, Amboseli animals with pure browsing diets should have collagen $\delta^{13}C$ values of -22 to -23 ‰. None of the browsers (rhinoceros, giraffe) have values this low, indicating a small but persistent fraction of grasses or succulents in their

Table 26. Isotopic data for Amboseli mammals, excluding elephants.

Secies	Common Name	Year of death	$\delta^{15}N$	$\delta^{13}C$
	Carnivores, Insectivores, and Omnivores			
Crocuta crocuta	Spotted hyena	*1984	16.7	-9.2
Panthera leo	Lion	n.d.	17.1	-10.1
Panthera leo	Lion	n.d.	15.6	-6.4
Acinonyx jubatus	Cheetah	*1984	17.2	-15.7
Canis adustus	Jackal	*1989	15.4	-11.2
Canis adustus	Jackal	*1988	13.8	-9.9
Canis adustus	Jackal	*1988	14.9	-14.8
Otocyon megalotis	Bat-eared fox	*1971	12.2	-10.6
Otocyon megalotis	Bat-eared fox	n.d.	14.6	-12.0
Otocyon megalotis	Bat-eared fox	*1974	14.2	-15.7
Ichneumia albicauda	White-tailed mongoose	n.d.	17.4	-8.3
Orycteropus afer	Aardvark	n.d.	9.7	-12.1
Papio cynocephalus	Yellow baboon	1989	10.8	-14.3
	Grazers			
Pedetes capensis	Spring hare	*1975	9.8	-9.0
Equus burchelli	Burchell's zebra	1974	9.8	-8.6
Equus burchelli	Burchell's zebra	*1984	9.1	-8.6
Equus burchelli	Burchell's zebra	1990	10.0	-8.5
Connochaetes taurinus	White-bearded wildebeest	1975	12.4	-8.0
Connochaetes taurinus	White-bearded wildebeest	1974	11.0	-8.7
Connochaetes taurinus	White-bearded wildebeest	*1988	13.8	-7.8
Connochaetes taurinus	White-bearded wildebeest	*1989	11.8	-9.0
Syncerus caffer	Buffalo	1968	10.1	-7.9
Syncerus caffer	Buffalo	*1984	10.8	-8.0
Phacochoerus aethiopicus	Warthog	1990	10.8	-8.8
Phacochoerus aethiopicus	Warthog	*1989	11.0	-9.2
	Browsers			
Diceros bicornis	Black rhinoceros	1961	6.4	-19.8
Diceros bicornis	Black rhinoceros	1974	8.2	-18.7
Diceros bicornis	Black rhinoceros	*1984	7.9	-19.0
Giraffa camelopardalis	Giraffe	*1989	11.5	-20.3
Giraffa camelopardalis	Giraffe	*1986	11.6	-19.7
	Mixed Feeders			
Hystrix cristata	Porcupine	*1973	9.9	-15.6
Hippopotamus amphibius	Hippopotamus	*1973	8.9	-10.0
Hippopotamus amphibius	Hippopotamus	1990	13.1	-8.6
Hippopotamus amphibius	Hippopotamus	*1989	8.9	-10.9
Aepyceros melampus	Impala	1985	12.4	-14.0
Aepyceros melampus	Impala	*1986	11.7	-13.6
Aepyceros melampus	Impala	*1988	13.1	-15.8
Gazella granti	Grant's gazelle	*1988	10.5	-16.0
Gazella granti	Grant's gazelle	*1989	10.2	-15.6
Gazella thomsoni	Thomson's gazelle	1990	14.2	-10.7
Gazella thomsoni	Thomson's gazelle	*1986	10.8	-17.6

* determined by weathering stage

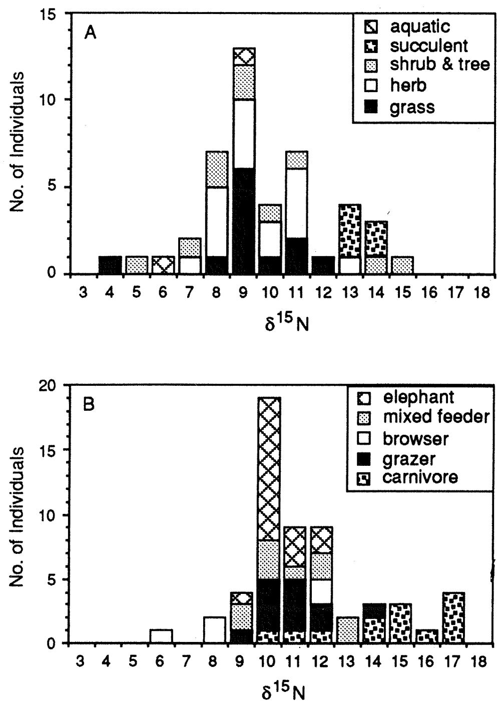

FIG. 93. (A). Histogram of nitrogen isotope compositions for Amboseli plants subdivided according to physiogamy. (B) Histogram of nitrogen isotope compositions for Amboseli mammals subdivided according to feeding type. Note that the difference between the mean $\delta^{15}N$ values of plants and animal collagen is only ~+1 ‰.

TABLE 27. Isotopic data for Amboseli elephants.

Secimen	Year of death	$\delta^{15}N$	$\delta^{13}C$
African Elephant: *Loxodonta africana*			
C75-3	1974	12.0	-18.3
C75-6	*1973	9.4	-17.9
E-1	late 70s	10.4	-13.3
E-3	late 70s	10.3	-13.9
E-8	late 70s	9.7	-17.3
E-11	late 70s	10.7	-13.2
E-13	late 70s	11.4	-13.9
E-15	late 70s	11.9	-13.7
E-17	late 70s	10.3	-15.3
E-19	late 70s	10.1	-13.4
E-21	late 70s	10.4	-14.9
E-23	late 70s	10.4	-11.9
E-25	late 70s	10.2	-15.5
E-27	late 70s	10.4	-15.5
E-29	late 70s	10.3	-13.7
E-30	late 70s	10.7	-11.9
E-34	late 70s	9.8	-14.2

All specimens with Year of death of late 70s were collected by Cynthia Moss and have known dates of death that we have not yet received. For Fig. 94A, these animals are plotted as deaths in 1978.

diets. Animals known to eat a mixture of plants (elephant, Grant's and Thomson's gazelle, hippopotamus, impala, and porcupine) have $\delta^{13}C$ values intermediate between browsers and grazers (Tables 26 and 27).

The link between the $\delta^{13}C$ of diet and collagen is more difficult to unravel in carnivores and omnivores, because these animals obtain carbon both from different tissues within a body (fat, muscle, skin) and from plants. All these sources may have different $\delta^{13}C$ values. Generally, herbivore meat and carnivore collagen differ by ~ +5‰, but the difference between herbivore collagen and carnivore collagen is +2‰ (van der Merwe, 1989). Observations of hunting carnivores suggest that hyena and lion consume chiefly C_4-feeding herbivores (wildebeest and zebra), whereas cheetah eat mixed feeders (Thomson's and Grant's gazelle and impala). These observations are supported by $\delta^{13}C$ values (Table 26, Fig. 92B). The smaller carnivores (fox, jackal, mongoose) eat smaller animals from across the dietary spectrum and exhibit a spread of $\delta^{13}C$ values.

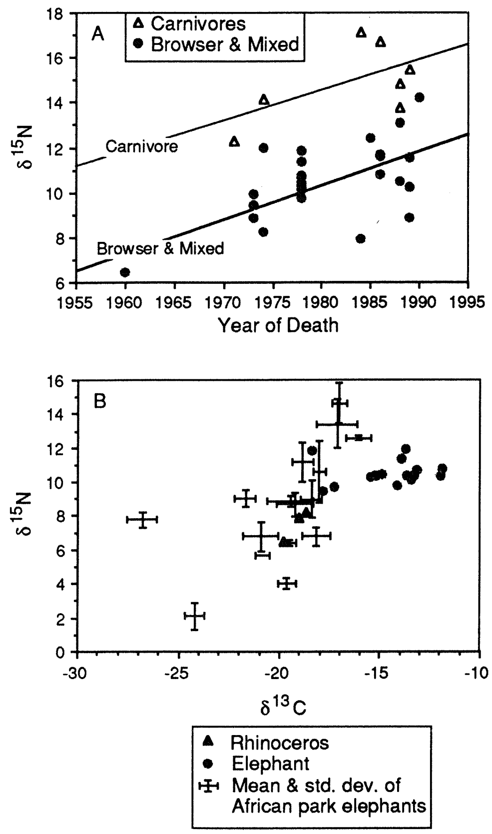

FIG. 94. (A) Secular variation in the nitrogen isotope composition of mammals. Grazers: Y= -68.25 +.0.04X r=0.24, slope is not significantly different from 0. Data and regression line are not plotted. Browsers: Y= -279.33 + 0.15X r=0.62, slope is significantly different than 0. Carnivores: Y= -253.66 + 0.14X r=0.58, slope is significantly different than 0. The elephants listed as late 70s deaths are included on the figure, and given 1978 as the year of death, but they were not used in the regression calculation. (B) Carbon and nitrogen isotopic composition of Amboseli elephants and rhinoceros. Also plotted are the means and standard deviations for elephant ivory from 16 other African parks and preserves. Firm determination of temporal isotopic trends within species must await analysis of specimens with a greater range of known ages of death. However, the spread in the isotopic data from both species may result from coupled increases in $\delta^{13}C$ and $\delta^{15}N$ values with time. Although values from Amboseli elephants do not overlap with values from many other parks, they vary by amounts as great as those used to discriminate between other park populations.

A fractionation of ~ +3‰ between the $\delta^{15}N$ value of plant food and herbivore collagen has been reported in previous studies (DeNiro and Epstein, 1981; Hare *et al.*, 1991). Given this fractionation, the average Amboseli herbivore should have a collagen $\delta^{15}N$ value of 12-13 ‰. Although some animals have values in this range, most are more negative (Tables 26 and 27, Fig. 93B) Indeed, using the mean $\delta^{15}N$ of animals and a fractionation of +3 ‰, we would expect dietary plants with values of 7‰ or less. Few plants within the park have isotopic values this low.

There are several plausible explanations for this discrepancy. First, we analyzed only plants collected in a dry season. In the wet season, plants may have lower $\delta^{15}N$ values. Second, if the $\delta^{15}N$ value of plants from Amboseli has increased recently, current vegetation may not be representative of the foods eaten by the sampled animals. Finally, the fractionation between diet and herbivore collagen may not be +3‰. Variability in this fractionation has been detected previously (Ambrose and DeNiro, 1986; Heaton *et al.*, 1986; Sealy *et al.*, 1987), and attributed to differences in N metabolism between different herbivores. A fractionation of ~+1‰ is observed between current Amboseli plants and the sampled herbivores.

Differences in collagen $\delta^{15}N$ between herbivores and carnivores are well studied and range from +3 to +6 ‰ (Schoeninger and DeNiro, 1984; Ambrose and DeNiro, 1986; Sealy *et al.*, 1987). Amboseli grazers, mixed feeders and browsers averaged 10.9 ± 1.3 ‰, 9.1 ± 2.3 ‰, and 10.9 ± 1.3 ‰, respectively, whereas true Amboseli carnivores averaged 15.4 ± 1.6‰. Consequently, there is a trophic level fractionation of ~+5 ‰. The omnivorous yellow baboon has a lower $\delta^{15}N$ value, suggesting a preponderance of plant foods in the diet. Finally, the aardvark, which consumes ants and termites, has a $\delta^{15}N$ value within the herbivore range. However, insect chitin is known to be ^{15}N-depleted relative to dietary plants (Schimmelmann, pers. comm.), which would lead to lower values in the collagen of insectivores relative to carnivores.

Secular Trends in the Isotopic Composition of Amboseli Mammals

The Amboseli ecosystem has changed dramatically since 1960 because of a loss of trees and the expansion of grassland. To document isotopic trends in park mammals, multiple samples of individual species from different time periods must be examined. Our data are currently insufficient for such a treatment, but trends within broad feeding categories may be examined. Collagen $\delta^{15}N$ and $\delta^{13}C$ values, and thus the diet of grazers, have remained constant from 1968 to 1990 (Table 26). The $\delta^{15}N$ of browsers and mixed feeders has increased by a statistically significant amount (Fig. 94A). This trend, however, is strongly influenced by a low value for a single old specimen. Although most elephant deaths are only roughly dated to the late 1970s, the population seems to be trending towards higher $\delta^{15}N$ and $\delta^{13}C$ values (Fig. 94B). The magnitude of this variation is significant when compared to the differences between populations from different parks. There is a suggestion of similar coupled increases for rhinoceros, but the sample is quite small. Finally, carnivores also increase in $\delta^{15}N$ with time by amount similar to browsers (Fig. 94A).

We hypothesize that as the park was stripped of trees, browsers and mixed feeders have been forced to consume more grass. Increased grass consumption is particularly evident for elephants. However, grass is relatively nutrient-poor compared to browse. Eventually, the browsers and mixed feeders suffered nutritional stress. Nutritional stress may cause an animal to remetabolize previously deposited proteins, and can potentially produce an increase in collagen $\delta^{15}N$ in bones equivalent to that generated by feeding at a higher trophic level (Tuross, pers. com.). The grazers thrived as the grasslands expanded and exhibit no isotopic changes. Carnivores eat both types of herbivores, and consequently exhibit intermediate isotopic trends.

Conclusions

The carbon and nitrogen isotopes in most plants from Amboseli National Park varied as expected, with a strong differentiation in $\delta^{13}C$ between C_3, C_4, and aquatic plants, and a high mean $\delta^{15}N$ value. The ^{15}N enrichment of succulent plants was unexpected, and is currently unexplained. Differences in the $\delta^{13}C$ of plants is reflected in the collagen of the animals that consume these plants, and ultimately can be detected at higher trophic levels when these herbivores are preyed upon by carnivores. The fractionations of C and N isotopes between diet and collagen that we discovered match previous reports, with one exception. The fractionation of N between plant and herbivore collagen was much lower than expected. Finally, although our observations must be supported by more extensive sampling, there are statistically significant secular trends in the $\delta^{15}N$ of Amboseli browsers and mixed feeders and carnivores, whereas grazers are invariant. The substantial isotopic trends shown by Amboseli elephants may indicate that stable isotopes will be of limited utility in tracing the source of elephant ivory in changing habitats.

References

Ambrose, S. H., and M. J. DeNiro, The isotopic ecology of East African mammals, *Oecologia,* 69, 395-406, 1986.

Behrensmeyer, A. K., Taphonomic and ecologic information from bone weathering, *Paleobio.*, 4, 150-162, 1978.

DeNiro, M. J., and S. Epstein, Influence of diet on the distribution of carbon isotopes in animals, *Geochim. Cosmochim. Acta,* 42, 495-506, 1978.

DeNiro, M. J., and S. Epstein, Influence of diet on the distribution of nitrogen isotopes in animals, *Geochim. Cosmochim. Acta,* 45, 341-351, 1981.

Hare, P. E., M. L. Fogel, T. W. Stafford, Jr., A. D. Mitchell, and T. C. Hoering, The isotopic composition of carbon and nitrogen in individual amino acids isolated from modern and fossil proteins, *J. Archaeol. Sci*, in press, 1991.

Heaton, T. E., J. C. Vogel, G. von la Chevallerie, and G. Collett, Climatic influence on the isotopic composition of bone nitrogen, *Nature,* 322, 822-823, 1986.

Raven, J. ., The application of mass spectrometry to biochemical and physiological studies, in *The Biochemistry of Plants, Vol. 13*, Academic Press, Inc., New York, pp. 127-180, 1987.

Schoeninger, M. J., and M. J. DeNiro, Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals, *Geochim. Cosmochim. Acta, 48*, 625-639 1984.

Sealy, J.C., N. J. van der Merwe, J. A. Lee Thorp, and J. L. Lanham, Nitrogen isotopic ecology in southern Africa: implications for environmental and dietary tracing, *Geochim. Cosmochim. Acta, 51*, 2707-2717, 1987.

Tieszen, L. L., and T. W. Boutton, Stable carbon isotopes in terrestrial ecosystem research, in *Stable Isotopes in Ecological Research*, Rundel, P.W., J.R. Ehleringer, and K.A. Nagy, eds., Springer-Verlag, New York, pp. 167-195, 1988

Tuross, N., M. L. Fogel, and P. E. Hare, Variability in the preservation of the isotopic composition of collagen from fossil bone, *Geochim. Cosmochim. Acta, 52*, 929-935, 1988.

van der Merwe, N. J., Natural variations in ^{13}C concentration and its effect on environmental reconstruction using $^{13}C/^{12}C$ ratios in animal bones, in *The Chemistry of Prehistoric Human Bone*, Price, T.D., ed., Cambridge Univ. Press, New York, pp. 105-125, 1989.

van der Merwe, N. J., J. A. Lee-Thorp, J. F. Thackeray, A. Hall-Martin, F. J. Kruger, H.Coetzee, R. H. V. Bell, and M. Lindeque, Source-area determination of elephant ivory by isotopic analysis, *Nature, 346*, 744-746, 1990.

Vogel, J. C., Isotopic assessment of the dietary habits of ungulates, *S. Afr. J. Sci., 74*, 298-301, 1978.

Vogel, J. C., B. Eglington, and J. M. Auret, Isotope fingerprints in elephant bone and ivory, *Nature, 346*, 747-749, 1990.