tocrystalline anisotropy. Finally, (v) they adopt a preferred orientation when deposited onto a polymeric film.

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9. In a typical synthesis, a blue-violet solution containing both $Co(OH)_4^{2-}$ and hydrazine was prepared from $CoCl_2 \cdot 6H_2O$ (25 mg), water (3 ml), a 50% aqueous solution of NaOH (1 ml), and an 85% solution of $N_2H_4 \cdot H_2O$ (1 ml). The product was purified and stored under nitrogen.
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Isotopic Tracking of Change in Diet and Habitat Use in African Elephants

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The carbon, nitrogen, and strontium isotope compositions of elephants in Amboseli Park, Kenya, were measured to examine changes in diet and habitat use since the 1960s. Carbon isotope ratios, which reflect the photosynthetic pathway of food plants, record a shift in diet from trees and shrubs to grass. Strontium isotope ratios, which reflect the geologic age of bedrock, document the concentration of elephants within the park. The high isotopic variability produced by behavioral and ecological shifts, if it is representative of other East African elephant populations, may complicate the use of isotopes as indicators of the source region of ivory.

In many African parks and reserves, woodlands have been replaced by grasslands in recent decades (1). Potential causes of this transformation include changes in climate, fire frequency, and feeding by large ungulates such as elephants (*Loxodonta africana*) (1, 2). At the same time, poaching and human land use near parks have altered ungulate migration and habitat use patterns, often accelerating vegetation change within protected areas (1, 2). Knowledge of foraging and habitat use patterns in ungulates, and of recent changes in these patterns, are essential to understand controls on ecological transformation and to develop robust conservation strategies. Typically, such data have been gathered through long-term observation (3). Isotopic analysis offers an alternate source of information on diet, habitat, and migration that can be collected rapidly from living or dead animals (4). Isotope composition has also been proposed as a marker to indicate the source region of ivory, for use in wildlife forensics (5).

Most carbon, nitrogen, and strontium in herbivores are derived from food plants. Because a herbivore's isotopic composition is similar to that of its food, isotopic differences in diet are reflected in herbivore tissues (6, 7). For example, African trees and most shrubs, herbs, and cool-climate grasses are C_3 plants, with low $\delta^{13}C$ values (≈ -27 per mil), whereas warm-climate grasses are C_4 plants, with less negative values (≈ -13 per mil) (8). Consequently, the $\delta^{13}C$ value of collagen (the major protein in bones and ivory) reflects the proportion of browse (leaves, twigs, and shrubs) to grass in the diet (4, 5). The N isotope compositions of plants and herbivores covary with rainfall abundance, and isotope ratios are high in arid regions and low in wet regions (7, 9). Finally, ^{87}Sr is produced by radioactive decay of ^{87}Rb, whereas ^{86}Sr is a stable isotope. Soils have variable $^{87}Sr/^{86}Sr$ ratios, depending on the initial Rb/Sr ratio and the age of the underlying bedrock. Soils are the source of Sr in plants, which in turn supply the Sr that is deposited in bone and tooth mineral. Overall, animals in areas with old granitic crust have high Sr isotope ratios; in areas with young volcanic rocks or marine sediments, animals have low values (5).

Here we examine the isotopic ecology of elephants from Amboseli National Park, Kenya, to address the degree to which the bones and teeth of Amboseli elephants preserve an isotopic record of changes in diet

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and habitat use. Earlier studies on isotopic characterization of elephant populations for ivory forensics were promising, but sampling was limited (*5*). We also explore here whether isotopic discrimination between populations is maintained when rapidly changing ecosystems are included.

The Amboseli ecosystem lies immediately north of Mount Kilimanjaro, on the Kenya-Tanzania border (Fig. 1). The Amboseli Basin occupies a dry Pleistocene lake basin that is bordered by Precambrian gneiss and carbonate rocks to the north and by Plio-Pleistocene volcanic rocks from Kilimanjaro to the south and east (*10*). The climate is semiarid and rainfall is seasonal (≈350 mm), but springs in the lake basin provide water year-round (*11*). The flanks of Kilimanjaro to the south of the ecosystem are covered by woodlands (C_3 plants). In the 1950s, the lake basin contained a mixture of habitats, including dense and open woodlands with abundant C_3 browse as well as swamps and grasslands dominated by C_4 grasses and sedges. From the 1960s to the early 1970s, woodlands in the lake basin decreased by 90%. Tree loss in Amboseli has been attributed to a rise in the water table that increased soil salinity and, more recently, to intensified browsing by elephants congregating within the park (*2*, *11*, *12*). Bushed grassland, with a mixture of C_3 browse and C_4 grasses, covers the remainder of the ecosystem outside the lake basin (*11*).

Amboseli elephants have been studied intensively since 1972, and all elephants that frequent the park have been identified (*12*). We obtained bone samples from carcasses of both known and unidentified elephants and recorded sex, year of death, and age at death (Table 1). We collected bone from the mandibular symphysis for analysis when available (*13*). As a result of rapid growth followed by slow turnover, bones hold a long-term record of diet that is weighted toward early developmental years and show little intraskeletal isotopic variation (*14*). In contrast, tooth dentin grows by accretion with little remodeling, retaining a subannual record of body chemistry in molars and tusks (*15*). We obtained time series from four animals by microsampling sequential growth laminations in molar roots, ending at the pulp cavity, which contains dentin deposited immediately before the animal's death (Fig. 2). We estimate that the 12- to 15-mm-long series collected from molars accreted over 4 to 5 years (*16*); on average, each microsample yielded an isotopic record of ≈3 months.

Bones from Amboseli elephants exhibited no consistent trends in $\delta^{15}N$ value, either with year of death or age (Table 1). No clear temporal trends were present in microsamples from molar roots (*17*). Mean $\delta^{15}N$ values estimated from bones (10.7 ± 0.8 per mil) and molars (11.1 ± 1.5 per mil) did not differ significantly (Mann-Whitney test, $P > 0.4$). Amboseli elephant $\delta^{15}N$ values were in the range expected for African herbivores in a semiarid habitat (*9*).

In contrast to the stability of N isotopes, elephant bone $\delta^{13}C$ values increased with year of death, from ≈−18 per mil for animals that died in the early 1970s to ≈−13 per mil for late 1980s deaths (*18*). From this isotopic shift, we estimate that the proportion of C_3 plants in animals' diets dropped from 75 to 40% (*19*). A shift in diet from browse to grass also explains the relation between $\delta^{13}C$ and age observed for the animals that died in the 1980s (*18*). Bones record a weighted average of long-term carbon intake; thus, older animals (for example, Teresia: age = 62, $\delta^{13}C$ = −17.3 per mil) had lower $\delta^{13}C$ values than did younger animals (for example, Tamar: age = 12,

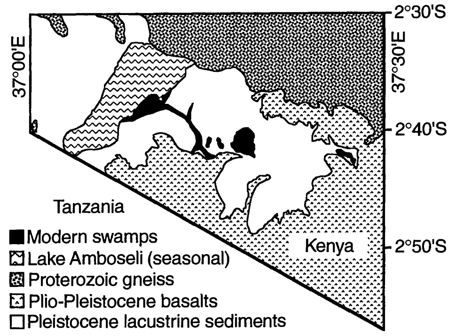

Fig. 1. Map of the Amboseli Basin on the Kenya-Tanzania border.

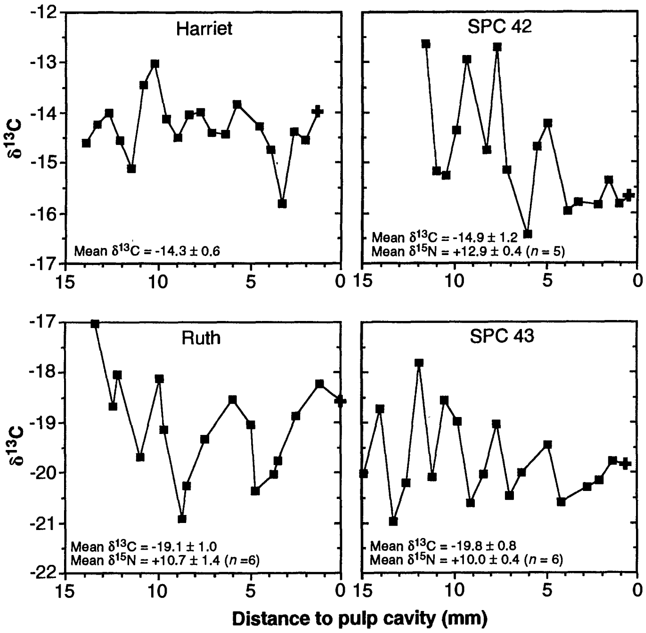

Fig. 2. Plot of change in $\delta^{13}C$ (squares) across molar roots from four elephants. Sampling started at a distance of ≈15 mm from the pulp cavity, then proceeded toward the pulp cavity. The samples collected from adjacent to the pulp cavity (cross) were deposited in the months immediately before death. Mean $\delta^{13}C$ and $\delta^{15}N$ values for samples from each individual are indicated on plots.

Table 1. Isotope values for Amboseli elephant bones listed by year of death (YD). Age at death was determined through observation, tooth eruption, or stature (or a combination thereof) (*14*). C75 and SPC numbers indicate samples from carcasses that could not be firmly identified as part of the Amboseli elephant study group.

Name	Age	YD	$\delta^{13}C$	$\delta^{15}N$	$^{87}Sr/^{86}Sr$
		Females			
Annabelle	44	74	−18.3	12.0	0.70597
C75-17	Ad	75	−18.2	11.3	
Vera	22	76	−17.1	10.7	0.70556
Gabriella	17	78	−13.2	10.3	0.70460
Daphne	18	79	−12.3	10.2	0.70449
Tamar	12	83	−13.9	10.3	0.70490
Ruth	23	83	−19.4	11.4	0.70695
Zoe	30	84	−13.3	10.8	
Tia	34	84	−15.3	10.1	0.70462
Priscilla	41	84	−13.4	10.1	
Teresia	62	84	−17.3	9.7	0.70532
Sara	39	85	−15.5	11.6	0.70486
Calandra	22	86	−12.6	9.1	0.70456
Big T	53	86	−14.3	10.1	
Ophelia	20	87	−15.5	10.4	
Harriet	49	87	−15.5	10.2	0.70521
Gardenia	8	88	−12.0	8.6	0.70452
Emily	41	89	−14.2	9.8	
		Males			
SPC 33	35	70	−18.8	10.2	0.70533
SPC 39	50	70	−16.8	11.3	0.70539
C75-27	Ad	72	−17.9	11.3	
C75-6	Ad	72	−18.2	9.5	
M33	39	76	−17.7	12.4	0.70573
Rex	5	84	−13.3	10.4	
Noah	5	85	−14.1	11.2	
M252	15	85	−13.7	11.9	
M185	16	85	−13.2	10.7	
M153	28	85	−15.1	10.7	0.70474
M144	29	85	−15.3	10.3	0.70464
Daniel	9	86	−11.9	10.4	
Zeppo	9	86	−13.9	11.4	0.70475
SPC 23	21	86	−14.7	10.7	
Zach	24	87	−18.4	10.8	0.70737
Ali 83	5	88	−11.9	10.7	0.70458
M178	28	90	−15.0	11.9	0.70469
SPC 31	28	90	−15.6	12.0	

$\delta^{13}C$ = −13.9 per mil), because more of their bone growth occurred before the drop in browse intake.

Bushland soils on the Proterozoic gneiss north of the lake basin had $^{87}Sr/^{86}Sr$ ratios of ≈0.7067, whereas lake basin soils and soils on Plio-Pleistocene volcanic rocks ranged from 0.7047 to 0.7049 (*20*). The mean strontium isotope ratio for elephant bones (0.70518 ± 0.00079) was closer to that of Plio-Pleistocene volcanic rocks (Table 1). However, as with carbon, there was a trend in strontium with time; bones of animals that died in the early 1970s had higher $^{87}Sr/^{86}Sr$ ratios than did bones of animals that died in the late 1970s and 1980s, with several exceptions such as Ruth and Zach (Table 1).

The negative correlation between carbon and strontium isotope values in bones (Fig. 3) can be interpreted as mixing between two isotopically distinct regions—the C_3-rich bushlands on Precambrian soils (low $\delta^{13}C$, high $^{87}Sr/^{86}Sr$) and the C_4-rich grassland on volcanic and lakebed soils (medium to high $\delta^{13}C$, low $^{87}Sr/^{86}Sr$). No elephants in our sample had isotopic values that were unambiguously characteristic of a third foraging area, the Kilimanjaro forest (low $\delta^{13}C$, low $^{87}Sr/^{86}Sr$). Mixing can be produced both by bone turnover and by migration between habitats. Microsamples from molars provide subannual estimates of body chemistry that allow discrimination between potential causes of mixing.

Microsamples from SPC 43, an animal that died in the early to mid-1970s, and Ruth, who died in 1983, yielded low $\delta^{13}C$ values, confirming that they ate diets rich in browse in the 1970s and earliest 1980s (Fig. 2). In addition, both individuals exhibited regular cyclic $\delta^{13}C$ variations on a scale of ≈3 to 4 mm, most likely as a result of seasonal shifts in the proportion of browse to grass in the diet. Microsamples from Harriet, who died in 1987, had more positive $\delta^{13}C$ values, indicating a greater reliance on grass in the mid-1980s. Harriet exhibited low-amplitude cyclic variation on a scale of ≈3 mm (Fig. 2). SPC 42 showed no clear cyclic isotope variations, though it did switch to lower $\delta^{13}C$ values (more browse) immediately before its death in 1993 (Fig. 2).

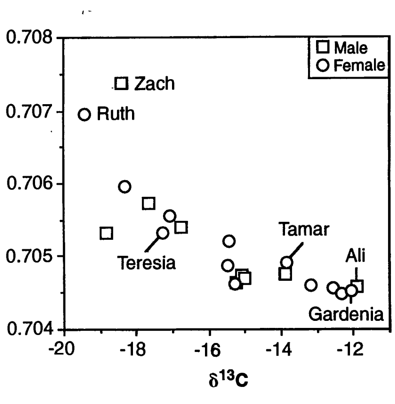

Fig. 3. Plot showing relation between $\delta^{13}C$ and $^{87}Sr/^{86}Sr$ in elephant bones. Individuals named in the text are indicated.

We conclude that animals that died in the early 1970s, which had bone with intermediate Sr and C isotope values and molars with strong cyclic C isotope variations, were regular migrants between the lake basin and bushland. Most elephants that died in the late 1970s and 1980s had high $\delta^{13}C$ values indicating a grass-rich diet, Sr isotope ratios similar to those of volcanic soils, and irregular or attenuated fluctuations in the molar $\delta^{13}C$ values, which we interpret as a result of disrupted seasonal migration and concentrated grazing within the park. Two individuals, Ruth and Zach, defied this trend, apparently continuing to browse in the bushland into the 1980s. Finally, the drop in $\delta^{13}C$ values in the last microsamples from SPC 42 may indicate a switch to more C_3-rich browse consumption outside the park.

Ultimately, Sr isotope analysis of molar microsamples will be used to address uncertainties about the historical pattern of seasonal migration in individual Amboseli elephants. However, our current isotopically based interpretation of elephant behavior is supported by radio tracking, aerial survey, and direct observation. Before 1977, most elephants foraged outside the park during wet seasons and spent dry seasons feeding near water on grasslands, swamps, and scattered woodlands of the lake basin (*11*, *12*). Seasonal migrations outside the park were curtailed after 1977, and large numbers of elephants congregated and fed in lake basin habitats year-round (*11*). Concentrated browsing on already reduced lake basin woodlands accelerated tree loss, causing elephants to rely heavily on grass for food (*11*, *12*), although elephants apparently made short nocturnal forays to the woodlands south of the park to browse during this interval. In 1991, elephants once more began to spend substantial amounts of time browsing outside the park.

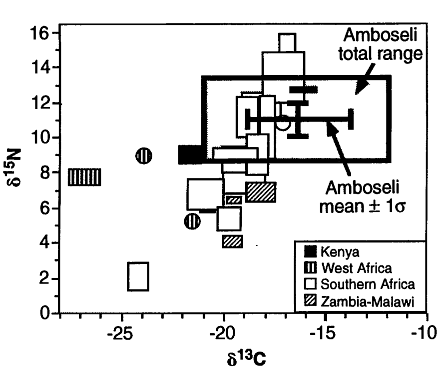

Fig. 4. Carbon and nitrogen isotope map of African elephant populations. Boxes map mean ± 1 SD for each population; circles refer to single specimens. There is significant overlap between the Amboseli population and several other populations, especially when total range is plotted for Amboseli. Data for all populations except that of Amboseli were compiled from the literature (5).

Our results have general implications for understanding elephant ecology and conservation. Although elephants are mixed feeders, they do forage with a degree of selectivity that can be assessed by observation, fecal analysis, or examination of stomach contents (*3*). Isotopic analysis offers an alternate, cumulative record of assimilated carbon. For example, although the bushland habitat is a mosaic with scattered C_3 shrubs and trees and an abundant ground cover of C_4 grasses, we estimate (*19*) that bushland animals (such as Ruth and Zach) ate ≈80% browse. Likewise, despite the loss of trees in the lake basin, we estimate that animals that lived their entire lives in this habitat in the 1980s (for example, Rex, Ali 83, and Gardenia) consumed from 35 to 50% browse, perhaps through nocturnal feeding on woodlands at the southern edge of the park. Amboseli elephants preferentially exploited the diminishing supply of browse.

Isotopic tracking confirmed that Amboseli elephants engaged in relatively local migration between different habitats. Analysis of isotopic time series from tusks, which span much of an individual's life, could provide a record of elephant migration in response to poaching, habitat encroachment, or drought in other regions. Concentration of elephants as a result of these factors has occurred in many protected areas in Africa besides Amboseli (*21*). A method for determining the source of immigrants to protected areas would be valuable in designing conservation programs.

If African elephant populations are isotopically discrete, isotopes could be used to determine where a piece of ivory originated in order to prevent trade in poached ivory (*5*). Our study highlights two potential complications for isotope forensics. First, because of tree loss and range restriction, Amboseli elephants were much more variable than were the chiefly southern African populations examined in earlier studies (Fig. 4). Amboseli elephants overlapped many other populations in C and N isotope composition and overlapped one population (Tuli Block, Botswana) for three isotopes (C, N, and Sr). Cycles in vegetation and range compression have occurred in many East African nations (*1*, *2*, *21*); thus, elephant herds in these nations may have undergone ecological and behavioral shifts similar to those that generated high variability in Amboseli. In contrast, southern African nations have kept elephant densities low through culling, and many have not suffered intense poaching. Consequently, southern African herds (*5*) may have had low isotopic variability because of greater ecosystem stability induced by park management strategies.

Second, because ecological and behavioral shifts are preserved as time series in elephant tusks, ivory may be more isotopically variable than bone (*22*). Carbon and nitrogen isotope variation in molar microsamples ($1\sigma = 2.6$ and 1.5 per mil, respectively) was greater than that in bone ($1\sigma = 2.2$ and 0.8 per mil, respectively). We detected carbon isotope shifts in molars of ≈4 per mil over 1 cm, and microsamples from different individuals differed by as much as 8.5 per mil. In the face of such high within-tusk variability, it may be difficult to characterize a tusk or ivory artifact on the basis of a single, small (for example, 20 mg) isotopic sample. Isotopic discrimination between populations could probably be obtained if multiple samples of different geologically controlled isotopes (Sr, Nd, and Pb) were examined for each artifact. However, this approach is untested and it may be too expensive for routine forensic work. The full scope of isotopic variability intrinsic to ivory must be assessed before isotopic composition can be reliably applied as an indicator of the source area of ivory.

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6. Isotope ratios for C and N are presented as δ values. $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, where $R = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$; the standards are Pee Dee belemnite for C and AIR for N. Units are per mil (parts per thousand). Sr isotopes are reported as ratios of ${}^{87}Sr$ to ${}^{86}Sr$.
7. There is a consistent small offset between the isotopic composition of diet and of vertebrate tissues for light stable isotopes, C and N, because of fractionation during metabolism. In field studies, the diet-collagen fractionation for C isotopes is ≈+5 per mil [J. A. Lee Thorp, J. C. Sealy, N. J. van der Merwe, *J. Archaeol. Sci.* **16**, 585 (1989)]. The diet-collagen fractionation for N isotopes ranges from +3 to 5 per mil; the higher values occur in arid regions [M. J. Schoeninger and M. J. DeNiro, *Geochim. Cosmochim. Acta* **48**, 625 (1984); S. H. Ambrose and M. J. DeNiro, *Oecologia* **69**, 395 (1986)]. Strontium isotopes are not measurably fractionated by metabolic processes; therefore, ${}^{87}Sr/{}^{86}Sr$ ratios in animals and in their diets are identical [J. C. Sealy, N. J. van der Merwe, A. Sillen, F. J. Kruger, H. W. Krueger, *J. Archaeol. Sci.* **18**, 399 (1991)].
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13. Carbon and nitrogen isotope composition was determined for collagen, which was extracted with the use of 1 M HCl, defatted with chloroform-methanol solution, converted to CO_2 and N_2 by combustion, and analyzed [S. A. Macko, M. L. Fogel (Estep), P. E. Hare, T. C. Hoering, *Chem. Geol.* **65**, 79 (1987)]. Standard deviations for replicate analyses of standards are 0.1 per mil for C and 0.2 per mil for N. Sr occurs as a trace-level substitute for calcium in hydroxylapatite, the mineral in bones and teeth [A. Sillen, in *The Chemistry of Prehistoric Human Bone*, T. D. Price, Ed. (Cambridge Univ. Press, Cambridge, 1989), pp. 211–229]. Bone samples were rinsed in water, leached with dilute acetic acid to remove soil minerals, ashed at 700°C to remove organic matter, dissolved in HCl, subjected to standard ion exchange techniques to isolate $SrCl_2$, and analyzed on a VG 354 thermal ionization mass spectrometer [R. J. Walker *et al.*, *Geochim. Cosmochim. Acta* **53**, 1583 (1989)]. Soil samples were crushed with a mortar and pestle, ashed, and then leached with 1 M HCl to generate soluble and insoluble soil fractions. The insoluble fraction was dissolved with HF and HNO_3, then both soluble and insoluble fractions were analyzed as above. Strontium isotope compositions are referenced to a value of ${}^{87}Sr/{}^{86}Sr = 0.71025$ for the National Bureau of Standards 987 Sr standard. Repeat measurements of this standard have an external reproducibility of 0.000022 (2σ).
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15. H. F. Osborn, *Proboscidea* (American Museum of Natural History, New York, 1936); R. M. Laws, *East Afr. Wildl. J.* **4**, 1 (1966); D. C. Fisher, *Paleobiology* **10**, 338 (1984); P. L. Koch, D. C. Fisher, D. L. Dettman, *Geology* **17**, 515 (1989).
16. Annual laminations are not well marked in animals from regions such as Amboseli that lack strong seasonal swings in temperature; therefore, determination of the number of years transected by each time series was not possible. Putatively annual growth laminations in tooth dentin have been identified for many large mammals, and apposition rates vary from 0.1 mm/year for bottlenose dolphins to 6 mm/year for mammoth tusks [G. A. Klevezal and S. E. Kleinenberg, *Age Determination of Mammals from Annual Layers in Teeth and Bones* (Israel Program Scientific Translation, Jerusalem, 1969); A. A. Hohn, *Sci. Rep. Whales Res. Inst.* **32**, 39 (1980); P. L. Koch, thesis, University of Michigan (1989)]. Dentin apposition rates in molar roots from four late Pleistocene mastodons (extinct relatives of elephants) with pronounced annual laminations averaged 1.6 ± 0.1 mm/year.
17. P. L. Koch *et al.*, data not shown.
18. The correlation between bone C isotope values and year of death is described by the following regression: $\delta^{13}C = (0.22 \pm 0.05)(\text{year of death}) - 443 \pm 106$. For animals that died in the 1980s, a regression of bone C versus age at death has the following equation: $\delta^{13}C = (-0.05 \pm 0.002)(\text{age}) - 13.27 \pm 0.63$.
19. Percent composition of browse versus grass in the diet is calculated with the assumption of a mass balance between two end members: collagen from a pure C_3-browse diet ($\delta^{13}C = -21.5$ per mil) and collagen from a pure C_4-grass diet ($\delta^{13}C = -7.5$ per mil). $\delta^{13}C_{\text{collagen}} = (-21.5)(x) + (-7.5)(1 - x)$, where x is the percent of browse. This simple mass balance requires an assumption that grass and browse are equally digestable. However, grasses eaten by elephants in dry seasons may be less digestable than browse [R. Sukumar, *The Asian Elephant: Ecology and Management* (Cambridge Univ. Press, New York, 1989)], so the mass balance may overestimate the proportion of browse consumed by elephants. However, it does accurately record the relative importance of carbon from browse versus grass in meeting the nutritional requirements of elephants.
20. Soil ${}^{87}Sr/{}^{86}Sr$ ratios were analyzed in four habitats. Acid-soluble and acid-insoluble residue fractions were analyzed to assess the difference in ${}^{87}Sr/{}^{86}Sr$ ratio between bulk soil and the Sr available to plants. Lakebed grassland: soluble = 0.70470, insoluble = 0.70489. Swamp edge: soluble = 0.70466, insoluble = 0.70458. Lakebed woodland: soluble = 0.70467, insoluble = 0.70466. Bushland on Proterozoic gneiss: soluble = 0.70668, insoluble = 0.70572.
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22. In earlier tests of isotope forensics, bone was the dominant sample material (*5*). Because ivory is likely to be more variable than bone, the method must be tested on tusks. With permission from the Kenya Wildlife Service, we collected broken tusk fragments found in Amboseli, but the U.S. Fish and Wildlife Service would not permit importation of this material, even for forensic purposes related to control of ivory trade, as ivory importation for scientific purposes is banned under Section 2202 of the African Elephant Conservation Act. Ironically, this act allows importation of ivory from a number of trophy hunted animals each year, but as we did not kill the animals in our study, we could not apply for importation under this provision. Consequently, we tested the method on molar roots, which grow in a fashion similar to ivory, albeit at a lower rate. Because tusk dentin accretes more rapidly than molar dentin and can be sampled at a finer scale, isotopic variability in tusks should be greater than the variability in molar roots.

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