History of Animals using Isotope Records (HAIR): A 6-year dietary history of one family of African elephants

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The dietary and movement history of individual animals can be studied using stable isotope records in animal tissues, providing insight into long-term ecological dynamics and a species niche. We provide a 6-year history of elephant diet by examining tail hair collected from 4 elephants in the same social family unit in northern Kenya. Sequential measurements of carbon, nitrogen, and hydrogen isotope ratios in hair provide a weekly record of diet and water resources. Carbon isotope ratios were well correlated with satellite-based measurements of the normalized difference vegetation index (NDVI) of the region occupied by the elephants as recorded by the global positioning system (GPS) movement record; the absolute amount of C4 grass consumption is well correlated with the maximum value of NDVI during individual wet seasons. Changes in hydrogen isotope ratios coincided very closely in time with seasonal fluctuations in rainfall and NDVI whereas diet shifts to relatively high proportions of grass lagged seasonal increases in NDVI by ~2 weeks. The peak probability of conception in the population occurred ~3 weeks after peak grazing. Spatial and temporal patterns of resource use show that the only period of pure browsing by the focal elephants was located in an over-grazed, communally managed region outside the protected area. The ability to extract time-specific longitudinal records on animal diets, and therefore the ecological history of an organism and its environment, provides an avenue for understanding the impact of climate dynamics and land-use change on animal foraging behavior and habitat relations.

Plants and animals differ in the isotopic signatures they record because different pathways of carbon and hydrogen are found in different types of plants and animals. 

Stable isotopes in animal tissues record dietary preferences and ecological conditions experienced by an individual, with substrates such as hair containing longitudinal records of isotope ratios. 13C/12C, 15N/14N, and 34S/32S ratios record dietary input and habitat characteristics (e.g., refs. 8–11), and D/H and 18O/16O ratios record information about water sources (12). One of the most strongly delineated isotopic signals occurs in the δ13C ratios of plants, using the C3 and C4 photosynthetic pathways: Most C3 plants have δ13C values between ~11 and ~14‰, whereas most C4 plants have δ13C values between ~25 and ~29‰. Tropical grasses almost exclusively use the C4 pathway; most trees, shrubs, and forbs use the C3 pathway. Therefore, isotope ratios in animal tissues such as hair, which record dietary input, provide a clear indicator of these dietary preferences. Studies of African savanna elephants (Loxodonta africana) show that they prefer grass during the wet season but rely on browse during the dry season (6, 13–16). It is anticipated that significant changes in vegetation will take place in sub-Saharan Africa in the next few decades because of resource competition between animals and humans and because of global climate change. Therefore, it is of interest to trace the relationship between elephant diet and vegetation change over a long time interval, particularly in respect to the key role role elephants play in savanna ecosystems (17, 18).

Here, we present a 6-year chronology of temporally fine-scale data on diet changes of a single elephant family in Samburu-Buffalo Springs National Reserves in northern Kenya. This study builds on our long-term observations of elephants in northern Kenya (19–24), on our interests in understanding isotope incorporation into animal tissues (12, 25–30), and on our interests in applying those principles to wildlife ecology (14, 15, 16). Diet records are interpreted from multiple hair samples collected annually or subannually over the study interval. We compare this diet record to rainfall and remotely sensed records of net primary productivity (NPP) in the form of normalized differential vegetation index (NDVI) data from the same region. Diet shifts are also related to reproductive activity and spatial behavior. With ecological and environmental changes occurring from regional to global scales (including land use change and global climate change) as the result of human activities, shifts in ecological communities are likely to occur. Monitoring diet changes as food resource availability shifts via continuous, long-term isotope records provides an important means to


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identify and study the effect of environmental change on an animal’s ecological interactions.

Results

Background Isotope Values of the Environment: Plants and Water. Over 250 individual plant samples were collected from October 2004 to July 2005, and in May 2006; this former interval corresponded to a drier than normal period whereas the latter was at the end of a near-normal “long rains” season. The average $\delta^{13}C$ of C3 plants was $-27.4 \pm 1.0\%e$ and that for C4 plants was $-13.4 \pm 1.0\%e$ (Table S1). Ranges in $\delta^{13}C$ of individual plants and plant species varied by $\geq 3\%e$, generally having more negative values during the wet season and more positive values during the dry season for C3 plants. No significant correlations between NDVI and $\delta^{13}C$, $\delta^{15}N$, or %N were found for the 10-month collection period.

Nitrogen isotopes showed that only Indogofera could be considered to be N-fixing during this period. Indogofera schimperi had $\delta^{15}N$ values near 0%e; most of these samples were from the more-xeric upland localities; I. schimperi from riparian zones had higher %N and higher $\delta^{15}N$ values (+3 to +9%e). All I. spinosa samples had high $\delta^{15}N$ values (+4 to +11%e) regardless of %N. $\delta^{15}N$ values of all Acacia (Acacia eliator, Acacia reficiens, Acacia tortilis) had elevated $\delta^{15}N$ values, ranging between +3.5 and +15.9%e and cannot be considered to be exclusively N-fixing plants in this environment. Grasses and sedges generally had high $\delta^{15}N$ values with average values as high as +12%e (Table S1).

An 18-month survey of $\delta^{18}O$ and $\delta D$ in river water from the Ewaso N’gioro showed seasonal fluctuations; $\delta D$ and $\delta^{18}O$ values were more negative in the wet season and more positive in the dry season. Deuterium excess [Dex = $\delta D - 8 \delta^{18}O$ (31)] is used to evaluate meteoric waters with respect to the global meteoric water line [GMWL: $\delta D_{\text{GMWL}} = 8 \delta^{18}O + 10$; (32)]. Two waters with high Dex values (>35%e) were not included in the trends discussed below. Stable isotope ratios of the Ewaso N’gioro during the wet season (NDVI monthly average $>0.25$) are well correlated ($r^2 = 0.94$) with a trend of $\delta D = 6.8 \delta^{18}O + 7.1$, a similar slope and intercept as the GMWL and to other unevaporated meteoric waters in Kenya (33, 34). Waters from the river in the dry seasons (monthly average NDVI < 0.25) show evaporative enrichment of D and $\delta^{18}O$: $\delta D = 4.1 \delta^{18}O + 3.3$ ($r^2 = 0.81$).

Growth Rates and Correlations Between Members of the Same Family. Hair was collected and analyzed from 4 different members of the same family unit; Royals: mother Queen Elizabeth (M1) and siblings Victoria (M2), Cleopatra (M4), Anastasia (M5), and growth rates were calculated using the method of Wittemyer (16). Growth rates of the tail hairs were between 0.73 and 1.04 mm/day. We found little evidence for variable growth rates within a single hair even during periods of high metabolic stress related to reproduction (16). Individual hair samples were up to 580 mm long (median: 460 mm) and had individual chronologies covering up to 20 months (median: 18 months). The correlation between isotope chronologies between different familial members was very high ($r^2 = 0.79$), slightly lower than correlations between hairs collected from a single individual ($r^2 = 0.89$ to 0.93) but higher than two individuals from different family units ($r^2 = 0.44$; ref. 16). Fig. S1 shows the $\delta^{13}C$ and $\delta^{15}N$ records for hair samples collected from M4 and M5 in July 2004.

Isotope ratios from dung samples collected on the same days from M4 and M5 were also highly correlated [reduced major axis (RMA): $\delta^{13}C$(M5) = 1.133 $\delta^{13}C$(M4) - 4.49; $r^2 = 0.68$; n = 13]. Unfortunately, few samples were collected during the wet season, when the greatest variance in isotope values occurred, because the focal elephants dispersed to regions inaccessible to our field team during these periods.
and “dry season” cases, respectively, with maximum intake values between 58% and 60% for all 3 cases occurring in May 2002.

Results of Nitrogen Isotope Analyses. $\delta^{15}N$ values for hair from the Royals family unit are shown in Fig. 1C. $\delta^{15}N$ tends to have high values when $\delta^{13}C$ values are also high (with correlation coefficients of $r^2 > 0.7$ for periods of 3 months or longer), demonstrating that C4 plants tend to have a higher $\delta^{15}N$ value in the ecosystem as corroborated from vegetation samples presented previously. This is true for the single-day survey of plants and for dung samples: $\delta^{15}N$ in dung is positively correlated with $\delta^{13}C$ [RMA: $\delta^{15}N_{\text{dung}} = 0.39 \times \delta^{13}C_{\text{dung}} + 16.2$ ($r^2 = 0.63$; $n = 26$)]. Sponheimer (25) observed 0.8‰ depletion in $\delta^{15}N$ in dung compared with diet for different domestic species (cattle (Bos taurus), goat (Capra hircus), alpaca (Lama pacos), llama (Lama glama), rabbit (Oryctolagus cuniculus)). $\delta^{15}N$, however, is enriched in $\delta^{13}C$ compared with the diet by 0.5 to 3‰ (26, 37, 38). Elephant dung consist of poorly digested material so that the isotope fractionation during digestion is likely to be less than in animals with a more efficient digestive physiology.

Hydrogen and Oxygen Isotope Results from Hair. Fig. 2 shows the record of NDVI, $\delta^{13}C_{\text{diet}}$ and $\delta^{18}O_{\text{hair}}$ for the ~6-year period presented as the median value over 1-month periods; here we also provide the first derivatives of each of these records ($\Delta$NDVI, $\Delta$($\delta^{13}C_{\text{diet}}$, $\Delta$($\delta^{18}O_{\text{hair}}$, respectively). There are 9 periods where the $\Delta$NDVI exceeds the 2σ (standard deviation) value, and 1 where it approaches the 2σ value (Fig. 2D). These are the periods of most rapid change in the vegetation index and serve as a reference for changes in carbon and hydrogen isotope changes in hair.

Discussion

Long-Term Diet, NDVI, and Rainfall. The fraction of dietary C4 biomass in the Royals family unit was strongly seasonal, with rainy season $\delta^{13}C_{\text{diet}}$ values generally 3‰ to 6‰ higher than in the dry season. This corresponds to a baseline diet between 5% and 20% C4 biomass (Fig. 1E) in the dry season to peaks between 40% and 60% C4 biomass in the wet season for this family unit. To compare maximum NDVI and maximum percentage C4 contribution to the elephant diets over the 6-year interval we considered the periods from 1 March to 1 September and 1 September to 1 March to capture the 2 rainy seasons in this environment. The fraction of C4 biomass in the diet (i.e., C4-grasses) is highly correlated with NDVI (Fig. 3; RMA: %C4 = 99.8 NDVI-7; $r^2 = 0.61$). Therefore, the fraction of C4 biomass in the diets of savanna elephants is highly dependent on seasonal rain and net primary productivity (NPP). During periods of low NPP, the maximum percentage of C4 biomass was <30%, whereas during favorable periods it exceeded 40% for this family unit. The minimal increase in dietary grass during the droughts of 2000 and in late 2005, as exhibited by the NDVI and the stable isotope records, provides further evidence of the strong relationship between NPP/rainfall and diet among elephants.

The timing of diet in forage and water isotopic shifts are strongly related to changing ecological conditions, as exemplified by the synchronicity of the maximum rates of increase, peaks, and maximum rates of decrease among rainfall, NDVI, $\delta^{18}O_{\text{hair}}$, and $\delta^{13}C_{\text{diet}}$ during the 6-year study (Fig. 4). These temporal relationships are compared with the timing of reproduction in the greater Samburu population (22, 29). Seasonal diet changes were abrupt at the beginning of the wet season but tapered off gradually at the end of the wet season (Fig. 4D). Changes in $\delta^{13}C_{\text{diet}}$ track the chronology of NDVI values but lags changes in NDVI by several weeks. The temporal lag between $\delta^{13}C_{\text{diet}}$ and NDVI was the same when comparing either NDVI$_{\text{max}}$ with $\delta^{13}C_{\text{max}}$ or NDVI$_{\text{max}}$ with $\delta^{13}C_{\text{max}}$ (Figs. 2 and 4). Changes in $\delta^{18}O$ are more closely synchronized with NDVI, where the maximum rate of increase and peak occur simultaneously (Fig. 4). The strong synchronicity between NDVI and $\delta^{18}O_{\text{hair}}$, which lags the onset of seasonal rains, demonstrates the importance of changing water sources associated with the seasonal rains; this could be in the form of new or replenished drinking water supplies and forage-derived water. The delay between changes in NDVI and diet switching appears in part to relate to the handling time associated with short, early season grasses; the new-growth grass must grow to a certain height before it can readily be grasped by the trunk (G.W., personal observation). In
addition, protein quantity in savanna grasses varies over the wet season (40) such that grass quality peaks toward the latter part of the growing phase as grass species seed. This peak in protein content is probably influential to the timing of dietary switching and corresponding peak in reproductive activity. Previous endocrine work demonstrated that the elevation of pregnanolone levels (a hormone controlling ovulation) is strongly correlated with seasonal productivity (23). The peak in conceptions occurs ~5 weeks after the peak in NDVI, and ~3 weeks after the peak in C4 grass consumption (Fig. 4E). The gestation period for elephants is 22 months; thus the peak in births occurs at the beginning of the rainy season when water is readily available and grass productivity is about to increase (22). The timing of dietary protein pulses related to peak grass consumption is the likely driver of this ecological and physiological relationship.

Thus, the isotope and precipitation archives, satellite-based measurements of productivity, and ground observations record the sequence of rains, changes in NPP, changes in diet, and periods of highest fertility of elephant females. Approximately 80% of the seasonal rainfall occurs before peak NDVI (Fig. 4A), and NDVI peaks a few weeks after peak rainfall (Fig. 4B). The change in the isotopic composition of body water, as recorded by δD in hair, closely echoes NDVI measurements (Fig. 4C), with the most negative δD values occurring within a few days of peak NDVI. A major increase in C4 grass consumption occurs near the period of peak NDVI, with the maximum consumption of grass being reached ~2 weeks after peak NDVI (Fig. 4D). Grass consumption reaches baseline values ~75 days after peak NDVI.

The peak in conceptions occurs ~5 weeks after peak NDVI, and well after the peak in C4 grass consumption (Fig. 4E).

Changes in δD in Hair and Water. Fig. 5 shows that the δD of local river water and the δD of elephant hair are well correlated. For this study, we also observed a strong relationship among these parameters (δDhair = 0.30 δDwater - 77.9; r² = 0.46; n = 18); the slope of the relationship is similar to that of humans (12). Thus, the δD of elephant tail hair recorded local changes in δD of local waters. However, the δD response in times when the rains were absent, as indicated by low NDVI values, was muted (Fig. 2). In contrast, δ15O of hair and 18O of river water were not significantly correlated (δ15Ohair = 0.0623 δ18Owater + 21.037; r² = 0.016; n = 18), which was surprising given other studies that have demonstrated a significant relationship between hair and water oxygen isotope values (12, 30, 41).

Over the last decade, the primary water source in the study system, the Ewaso N’guro river, has maintained only subterranean flow during droughts and extended dry seasons. During these times, surface water is only available from isolated springs, although elephants often dig for water in the dry river bed.

**Comparison of δ13C**

δ13C and δ15N were compared in both dung samples and in the hair-derived diet-estimate (see Methods). Dung samples from the Royals family unit were collected primarily in the dry seasons when the family unit was more easily seen. Many periods of high correlation between δ13C in hair occurred (Fig. 1). Both the dung and estimated diet correlations give δ15N values between 5 and 7‰ for the C3 end-member plants, and between 11 and 16‰ for the C4 end-member plants. This is in agreement with observations showing that plant δ13N values for plants using different photosynthetic pathways are generally higher in C4 plants than in C3 plants in these regions (Table S1). The only N-fixing plant
observed in the vegetation survey was *I. schimperi*, a favorite C₃ food item of elephants in every season.

**Spatial Distribution, NDVI, and Diet Change.** The movements of at least 1 member of the Royals family unit were recorded by a global positioning system (GPS) collar the entire length of this study. Fig. 6 shows the 95% kernel (42) incorporating the location of the Royals family unit. During periods of low (< 20%) C₄ intake the family unit was usually within ~2 km of the riparian corridor of the Ewaso N’giro (Fig. 6). During periods when C₄ biomass was a high portion of the diet (> 20% C₄), the family unit was found much further from the riparian corridor, and was more commonly found outside the Samburu and Buffalo Springs National Reserve boundaries (Fig. 6). These linkages and co-variances between water and food distributions have significant management implications, particularly when interannual shifts in seasonal precipitation alter availability of C₄ food resources.

Cattle are generally excluded from the Samburu and Buffalo Springs Reserves, resulting in little competition between elephants and livestock for resources within these protected areas. Yet the stable isotope data suggest periods when these animals may compete for resources. Late April to early May 2003 was a time of anomalous diet for the Royals family unit (Figs. 1 and 2, and Fig. S1). During this apparently normal rainy season, the Royals family unit did not switch to grazing as was normal, but had a diet that was virtually 100% C₃; in fact, it was the most negative δ¹³C value for the entire 6-year observation period (Figs. 1 and 2). During this period GPS data showed that the elephants were mostly beyond the northern edge of Samburu Reserve, in an area heavily used by the local pastoralists (Fig. 6). The region is an *Acacia mellifera* and *A. reficiens* woodland subject to heavy overgrazing by livestock. Although the reasons for use of this area by the Royals family unit are not known, the impact of overgrazing by cattle on the typical wet season diet of elephants is clear; competition with cattle results in poor access to high quality grass forage because cattle keep the grass very short and out-compete elephants for this resource. This example shows that human activities have a large impact on elephant diets and ecological function.

**Conservation Implications.** The findings presented here have important implications for management of elephant populations in relation to global climate change on one scale, and local land use change at another scale. NDVI can change over the long term for many reasons, but increasing temperature in regions with minimal rainfall is likely to decrease NPP and NDVI. Similarly, changes in land use due to increased stocking rates as human population increases can result in changes in NDVI.

Elephants are a keystone species in savanna ecosystems, shaping the relative densities of grass and woody vegetation (17, 40). In many ecosystems, elephant range restriction concentrates and amplifies impacts of elephants on vegetative communities, leading to effects on species composition across trophic levels (43, 44). With climate models predicting greater variation in annual rainfall in Eastern Africa (45), the dynamics between elephant populations and their environments are likely to be strongly regulated by the relationship between climatic fluctuation and diet. During droughts, the combination of constrictions of feeding ranges to areas with permanent water (Fig. 6) and increased reliance on woody vegetation by elephants is likely to extenuate the impacts on vegetative species age distributions and composition (46). In addition, elephant ranging behavior, sociality and reproduction are strongly mediated by climate variation (22–24). Climatic-induced diet changes may alter re-
cruitment regimes—driving more pronounced seasonality in conceptions related to the proportion of $C_4$ vegetation in female diets.

**Conclusions**

Long-term diet histories of mammals are recorded in animal tissues such as hair, and these histories can be interpreted in the context of stable isotope ecology. A 6-year history of a single elephant family unit in northern Kenya shows that seasonal diet changes are well correlated with changes in NDVI. During the dry season, $\delta^{13}C$ values have a baseline value that indicates a diet composed of 5% to 20% $C_4$ biomass depending on the values used for end-member $C_3$ and $C_4$ vegetation. The absolute amount of grass consumption in any wet season is well correlated with the maximum value of NDVI associated with that wet season, and the peak in grass consumption occurs ~2 weeks after the peak in NDVI. These results show the adaptability of elephants in the face of climate change. However, long-term changes in NDVI, whether due to land use change, competition with livestock, or to long-term climate trends, are likely to be accompanied by changes in the amount of grass available to be consumed by elephants during the wet season—shaping the ecological role played by elephants across their range.

Changes in the $\delta D$ of hair are well correlated with the isotope composition of local drinking water, and the minimum value for $\delta D$ occurs at essentially the same time as the peak NDVI. The high temporal resolution of hair $\delta D$ can be used as a unique ecological tracer in future research. Not only can $\delta D$ accurately identify the timing of seasonal resource changes, but coupling this data with fine-scaled spatial information on water sources can offer new directions of research regarding animal behavior.

Tail hair of wild animals represents an archive of dietary behavior that provides an opportunity to quantify diet and the environmental conditions experienced by those animals. This archive can be accurately dated and is closely linked to local climate parameters. Such information can be used to reconstruct historic climatic events at fine temporal scales and spatial scales if coupled with GPS observations. It also provides insights to resource use and environmental interaction not previously accessible for animal ecological and evolutionary studies.

**Methods**

**Study Area and Population.** The elephants (*Loxodonta africana*) sampled in this study inhabit the region in and around the 220 km² Samburu and Buffalo Springs National Reserve in northern Kenya (37.5° E 0.5° N). These semi-arid parks are dominated by Acacia-Commiphora savanna and scrub bush and located along the Ewaso N’guro River (Fig. 7), the major permanent water source in the region (47). Rainfall averages ~350 mm per year and occurs during biannual wet seasons that generally take place in April/May and November/December; Archer’s Post (Fig. 6) is the nearest meteorological station. The elephants using these reserves (Fig. 7) are individually identified, following well-established methods (19), allowing hair sampling from the same individual across time. For a more detailed description of the study population and ecology of the study area, see ref. 16.

GPS radio collars were fitted to elephants in the Samburu National Reserve, northern Kenya, between 2001 and 2006 (20). Collars were programmed to record positions at hourly intervals, offering detailed records of movement. Tail hairs (Fig. 7) from each elephant were collected during immobilization operations while the collars were being fitted, and later when batteries were being charged or when the collars were being removed. We sampled 4 different breeding females from the same family unit (Royals), known to maintain direct proximity with each other ~80% of the time (21). Two of the sampled females, M4 (Anastasia) and M5 (Cleopatra), were fitted simultaneously with GPS radio collars for a 6 month period, during which they spent >95% of the time within 1 km of each other (80% within 250 m), used identical ranges, and moved similar daily distances. Three of the family unit members, including the 2 radio-tracked females, were siblings, daughters of the 4th (M1: Queen Elizabeth), who died in 2000.

Dung samples were collected during observational transects during the years 2004–2005. Plant samples were collected from 1 riparian zone 3 times per month, for 10 months from October 2004 through July 2005. A single collection of plants was made on a single day during the wet season (21 May 2006); we visited 14 sites ranging from riparian zones to upland bush zones. Water samples were collected for 18 months, 1 sample monthly, from the Ewaso N’guro River from October 2001 to March 2003.

**Laboratory Methods.** Hair samples were wiped with acetone to remove dirt, grit, and oils. Hair samples were serially sampled, with 1 sample collected from each 5-mm interval for $\delta^{13}C$ and $\delta^{15}N$ analysis (~500 µg); the same segments were used for $\delta D$ and $\delta^{18}O$ organic analysis (~150 µg). Five mm corresponds to ~6 days for these samples. Dung and plant samples were oven-dried at 80 °C for 24 h, homogenized, and ground before analysis. $^{13}C/^{12}C$ and $^{15}N/^{14}N$ ratios of elephant hair, dung, and plant material were measured on an isotope ratio mass spectrometer (IRMS: Finnigan 252) after combustion in a flow-through modified Carlo-Erba system. Values are reported using the conventional permil (‰) notation where:

$$\delta^{13}C = ((^{13}C/^{12}C)_{\text{sample}}/(^{13}C/^{12}C)_{\text{standard}}) - 1) \times 1,000,$$

an analogous terminology describes D/H, $^{18}O/^{16}O$, and $^{15}N/^{14}N$ ratios. Standards are V-PDB and AIR for $\delta^{13}C$ and $\delta^{15}N$, respectively, and V-SMOW for $\delta D$ and $\delta^{18}O$. Isotope enrichment between hair and diet is ~3‰ for both $\delta^{13}C$ and $\delta^{15}N$. For $\delta D$ and $\delta^{18}O$ analysis of hair, ~150 µg of hair from samples or internal standards were equilibrated with water vapor in the laboratory atmosphere, desiccated under vacuum for 7 days, and analyzed. Internal standards were used to correct for exchangeable H (48). $\delta D$ and $\delta^{18}O$ were analyzed by pyrolysis of the hair to H₂ and CO in an elemental analyzer furnace (TC-EA) and analyzed for $^2H$ and $^{18}O$ content, using an IRMS operating in continuous
mode (49). Hair samples were analyzed using a zero-blank carousel to prevent isotopic exchange during the analysis period. Results are presented in the δ notation, using V-SMOW as the standard. Water analyses were performed using 2N-reduction to produce H2 gas and by CO2 equilibration for δ13C and δ18O before analysis using IRMS.

Data Analysis. We used 10-day composite NDVI data available through Satellite ProbaToire d’Observation de la Terre (SPOT) to determine NPP changes in season across the study area. NDVI is a remote sensing index value calculated as the ratio between red and near infrared reflection that is highly correlated with green (photosynthetically active) biomass (50, 51). Remotely sensed data provides a direct measure of photosynthetic activity over large spatial regions, offering advantages over the classically-used point sampled rainfall data in areas, like the study region, where weather stations are sparse (39). Isotope profiles for each elephant were compared with longitudinal 10-day NDVI records to determine the impact of seasonality on diet.

Growth rates of hairs were determined by comparing overlapping stable isotope patterns of δ13C and δ18O (14, 16) and are independent of NDVI measurements, rainfall, and observational data (e.g., births, pregnancies). We estimated the dietary components of C3 and C4 biomass, using the model of Cerling et al. (29); we assume the same parameters for isotope turnover pools and measurements, rainfall, and observational data (e.g., births, pregnancies). We determined the threshold value of 0.23 for NDVI, 20% C4 diet component for δ13Cdiet, and <4‰ Δ13Cdiet, considered to be the threshold value of 0.23 for NDVI, 20% C4 diet component for δ13Cdiet, and a return to the peak initialization value for δD. Regressions between stable isotopes are calculated using the reduced major axis (RMA) because relative errors in the dependent and independent variables are of similar magnitude (52, 53).

No distinction was made between peaks associated with the “long” versus “short” rains (during the period 2000–2005 the “long rains” and “short rains” had average rainfall values of 143 mm (n = 6; max: 259 mm; min: 63 mm) and 193 (n = 6; maximum 356 mm; minimum: 55 mm), respectively.}

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Fig. S1. $\delta^{15}N_{\text{hair}}$ and $\delta^{13}C_{\text{hair}}$ for hair collected from M4 (Cleopatra: blue) and from M5 (Anastasia: red) in July 2004; these show a high degree of correlation between $\delta^{13}C$ and $\delta^{15}N$ patterns ($r^2 = 0.79$ using method of Wittemyer (2009) Chem Geol, 10.1016/j.chemgeo.2008.08.010). Chronologies were independently determined using overlapping patterns in the distal portions of each hair to hair samples collected in November 2003 (M4) and April 2003 (M5).
Table S1. Nitrogen and carbon isotope data from plants collected in Samburu and Buffalo Springs Reserve, Kenya

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>δ¹⁵N</th>
<th>SD</th>
<th>δ¹³C</th>
<th>SD</th>
<th>%N</th>
<th>SD</th>
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<tr>
<td><strong>Riparian site STE1</strong></td>
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<td>Acacia elatior</td>
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<td>−28.0</td>
<td>0.8</td>
<td>2.2</td>
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<td>Acacia reficiens</td>
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<td>8.9</td>
<td>0.6</td>
<td>−27.4</td>
<td>0.5</td>
<td>1.6</td>
<td>0.3</td>
</tr>
<tr>
<td>Commiphora sp.</td>
<td>28</td>
<td>7.7</td>
<td>2.0</td>
<td>−27.2</td>
<td>0.9</td>
<td>1.2</td>
<td>0.4</td>
</tr>
<tr>
<td>Cordia sinensis</td>
<td>28</td>
<td>6.4</td>
<td>1.0</td>
<td>−27.6</td>
<td>0.7</td>
<td>2.5</td>
<td>0.4</td>
</tr>
<tr>
<td>Indigofera sp. A</td>
<td>10</td>
<td>1.0</td>
<td>2.7</td>
<td>−27.4</td>
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<td>1.9</td>
<td>0.4</td>
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<td>Indigofera sp. B</td>
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<td>−27.1</td>
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<td>0.5</td>
</tr>
<tr>
<td>Andropogon</td>
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<td>−12.7</td>
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<td>1.4</td>
<td>0.7</td>
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<tr>
<td>Cynodon dactylon</td>
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<td>0.9</td>
<td>−13.8</td>
<td>1.1</td>
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</tr>
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<td><strong>May 20 2006 (wet season); n is the number of different sites</strong></td>
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<td>2.9</td>
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<tr>
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<tr>
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<td>Cordia sp.</td>
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<td>2.5</td>
<td>0.3</td>
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<tr>
<td>Indigofera schimperi I*</td>
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<td>−28.0</td>
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<td>0.6</td>
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<td>3.8</td>
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<td>3.1</td>
<td>1.1</td>
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<td>−11.8</td>
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<td>Salvia sp.</td>
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</tbody>
</table>

1 Oct 2004 to 21 Jul 2005 (n is the number of samples)

Each plant (except Sporobolus) in the 1 October 2004 to 21 July 2005 set was collected from one riparian site, 3 times per month; Sporobolus was collected from a different riparian area. The 20 May 2006 collection was made at 14 different sites which included both riparian and open bushland sites. *, Indigofera schimperi I and II were from non-riparian and riparian zones, respectively.