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PALAEO

Palaeogeography, Palaeoclimatology, Palaeoecology 206 (2004) 367–376

www.elsevier.com/locate/palaeo

Orphans' tales: seasonal dietary changes in elephants from Tsavo National Park, Kenya

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Received 16 July 2002; accepted 19 September 2003

Abstract

The similarity of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ patterns in hairs of different individuals from the Tsavo East orphaned elephant herd indicates that a single hair represents the dietary preferences and behavior of the entire group. Multiple tail hairs from the same individual collected at different times allows a chronology to be established because of the overlap in isotope patterns in hair, and there is a very high correlation between hair from different individuals in the same group. Forward modeling using a three-component isotope turnover model for hair allows a precise estimate of diet of these elephants over a 2-year interval. Elephants from Tsavo East National Park in Kenya feed predominantly on C_3 leaves, although they have a significant fraction of C_4 grass in their diet for a short time at the beginning of the rainy season. The overall integrated diet for the elephants studied is between 10% and 15% C_4 grass, although it reaches up to 60% for short intervals.

Stable carbon isotope analyses of elephant tooth enamel show that the average integrated dietary preference of elephants in Tsavo National Park remained less than 25% grass between 1940 and the present.

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Keywords: Carbon-13; Diet; Stable isotopes; African elephant

1. Introduction

Stable isotopes have been used to determine dietary preferences of fossil and modern mammals (DeNiro and Epstein, 1978, 1981; Cerling et al., 1997). Most isotope studies have used tooth enamel

as the record of diet because it is well preserved in the fossil record (e.g., Lee-Thorp and van der Merwe, 1987; Cerling et al., 1999).

A few studies have used hair to study diet (e.g., White, 1993; Macko et al., 1999; Schoeninger et al., 1999) and it has been shown that a detailed dietary history can be obtained from a single individual by analyzing beard shavings (Cerling and Cook, 1999).

In this study we examine the diet of African elephants (*Loxodonta africana*) recorded by elephant hair and tooth enamel. Seasonal changes in

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the diets of many mammals are difficult to quantify because of the difficulty of observing the same animal regularly on a long-term basis. In addition, there is still some controversy about the diet of modern African elephants. Many authors credit savanna elephants with a very high component of grass in their diet (e.g., Laws et al., 1974; Kingdon, 1979; Moss, 1988; Chadwick, 1992) while others regard savanna elephants to be predominantly browsers with little grass in their diet (Spinage, 1994; Dublin, 1995). Stable isotope studies from across the continent indicate that most African elephants are primarily browsers (<ca. 15% grass in their diets) (van der Merwe et al., 1988, 1990; Tieszen et al., 1989; Vogel et al., 1990; Cerling et al., 1999). However, we note that moderate amounts of grass are present in the diets of a few populations (e.g., Tsavo and Amboseli in Kenya) as indicated by observation (Moss, 1988) and by isotope analysis (Koch et al., 1995; Cerling et al., 1999). Archived samples from Tsavo are used to determine whether the fraction of C_4 biomass in the Tsavo elephants has changed significantly over the past 50 years.

In this study we report the results of stable isotope analyses of single elephant hairs represent-

ing several seasons. We show that matching isotope patterns permit a chronology to be established for the rate of hair growth, and that two different elephants of the same herd have virtually the same isotope record of diet recorded in their hairs. Using this chronology, and other factors such as the rainfall history and the vegetation growth and regeneration pattern of the region, we then show that in Kenya's Tsavo East National Park elephants consume significant quantities of grass only at the beginning of the rainy season. Archived samples of tooth enamel from Tsavo are used to determine whether the fraction of C_4 biomass in the Tsavo elephants has changed significantly over the past 50 years.

2. Methods

We analyzed the $\delta^{13}C$ and $\delta^{15}N$ values for tail hairs from two elephants from Tsavo East National Park, Kenya. Uaso, a young male (b. May 1996) and Malaika, a somewhat older female (b. January 1989), live in the elephant orphanage at Tsavo East. Uaso was brought to the park in November 1997 after being orphaned by poachers on the Laikipia

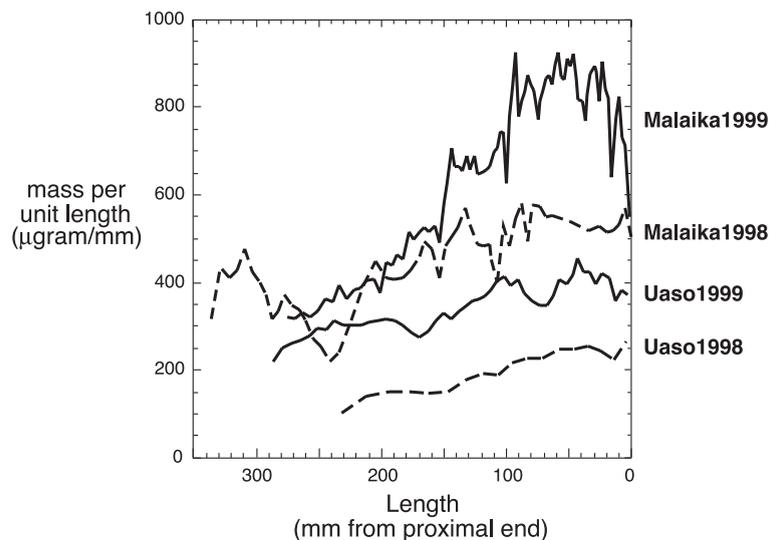


Fig. 1. Mass/length of elephant hair used in this study. The ages of the elephants at the time of hair collection was 2 years (Uaso, 1998), 3 years (Uaso, 1999), 9 years (Malaika, 1998), and 10 years (Malaika, 1999).

plateau. Malaika is a young adult who has been in the orphanage since she was 3 months old and was the oldest of the orphanage herd. Elephants in the orphanage forage together as a supervised group in the region surrounding the park headquarters during the day, and are escorted to a safe enclosure at night.

On 16 July 1998 we collected single tail hairs from Uaso and Malaika, and repeated the sampling on 19 July 1999. Samples were cleaned in the laboratory with acetone prior to sectioning. The hairs were serially sectioned and analyzed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using a continuous-flow isotope ratio mass spectrometer (CF-IRMS). Results are reported using the conventional δ -notation relative to the

isotope references PDB for carbon and atmospheric air for nitrogen.

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 1000$$

where R_{sample} and R_{standard} are the isotope ratios ($^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$) in the sample and standard, respectively. Isotope fractionation factors are:

$$\alpha_{\text{AB}} = [1000 + \delta_{\text{A}}/(1000 + \delta_{\text{B}})]$$

Isotope enrichment ε from diet to hair or enamel is:

$$\varepsilon = [1000 + \delta_{\text{A}}]/(1000 + \delta_{\text{diet}}) - 1 \times 1000$$

We also collected tooth enamel of elephants from Tsavo East Park. We sampled 19 elephant molars

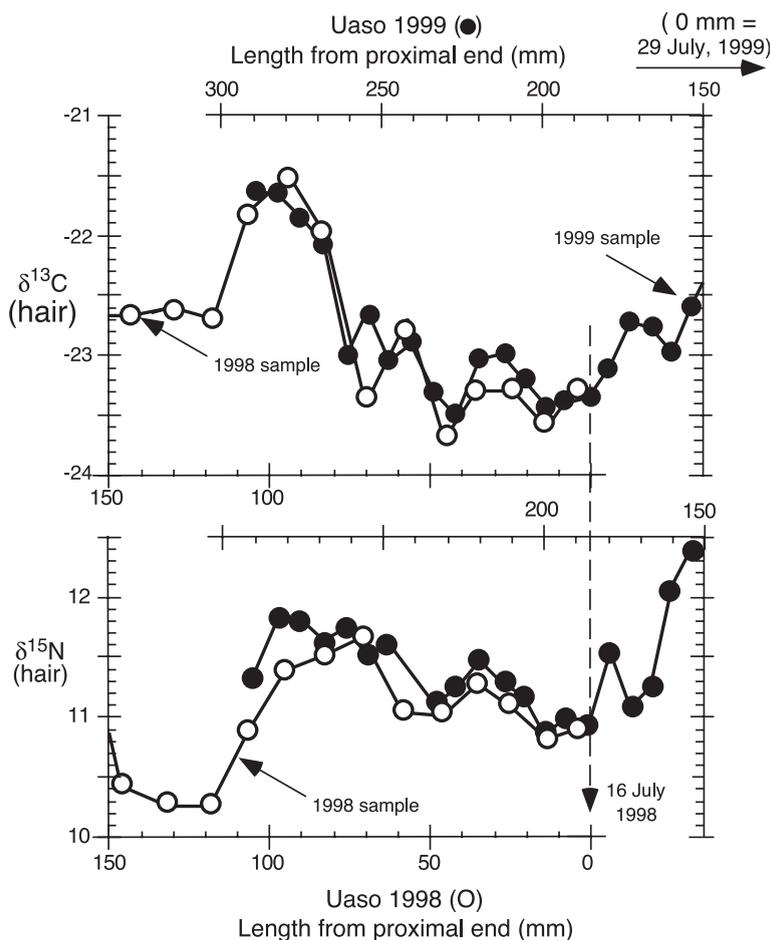


Fig. 2. Comparison of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in hair from two samples of tail hair collected from the same elephant (Uaso) on 16 July 1998 and 29 July 1999. Correlation is based on peak matching of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in segments 0–110 and 180–290 mm, respectively.

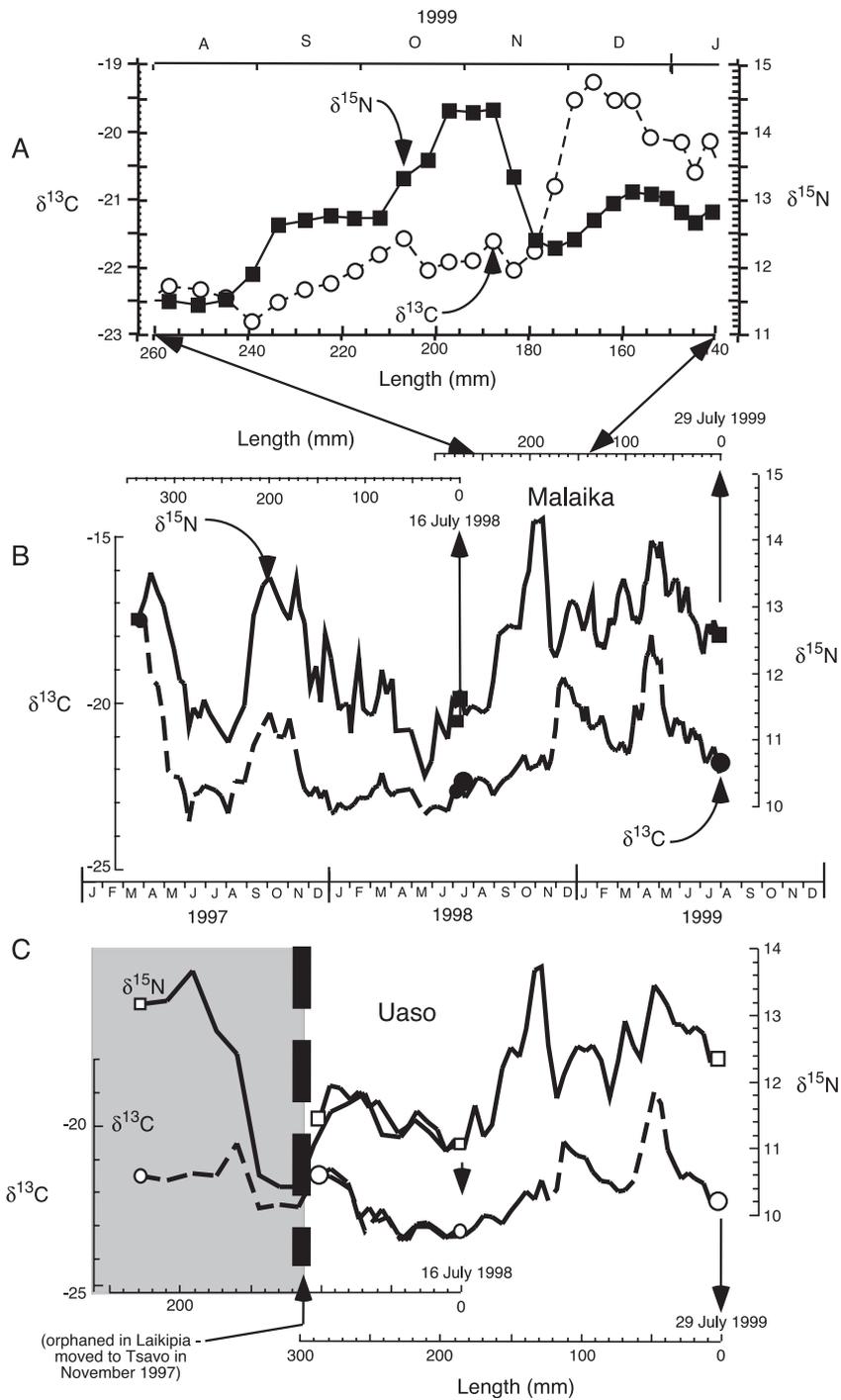


Fig. 3. (A) Detailed isotope record for Malaika. (B) Changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ with in hair from Malaika. Chronology was established using the overlapping isotope patterns Uaso (Fig. 2) and matching the isotope patterns of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ between Uaso and Malaika using time series analysis (see text). Hair growth is assumed to be constant for each elephant throughout the length of the hair. (C) As in panel B, for Uaso.

archived in the early 1970s at the Research Station of Tsavo East National Park, and 18 elephants that died in the 1990s. Age at death and age of tooth formation were estimated using criteria established by Laws et al. (1974). Tooth enamel was reacted with 100% H_3PO_4 after conventional treatment (Lee-Thorp and van der Merwe, 1987) and analyzed on a dual inlet mass spectrometer.

In the discussion below, we use the isotope enrichment factors of 3.0‰, 3.1‰, and 14.1‰ for $\delta^{15}N$ (hair), $\delta^{13}C$ (hair), and $\delta^{13}C$ (enamel) (DeNiro and Epstein, 1981; Cerling and Harris, 1999) compared to diet.

3. Results

The first notable observation is that each hair thins away from its proximal end. Fig. 1 shows the mass per unit length of the four hairs analyzed in this study. The mass/length at the proximal end varied from about 220 to about 500 $\mu g/mm$, although some parts of the hair were even more massive, up to 900 $\mu g/mm$. At their distal ends (200–300 mm long) the hairs had eroded significantly and had masses of only 100–400 $\mu g/mm$.

Fig. 2 shows that the proximal end of the 1998 sample from Uaso could be correlated with the distal end of his 1999 sample based on the peaks and valleys in the 1998 and 1999 hairs for both $\delta^{13}C$ and $\delta^{15}N$. Comparing the records of both individuals (Fig. 3),

we note very good correlation in the isotope patterns between the two elephants for the 1999 sample. Correlation coefficients (r^2) for hair from two different elephants sampled on the same day were 0.96 and 0.93 for $\delta^{13}C$ and $\delta^{15}N$, respectively, when corrected (using the time series program of Paillard et al., 1996) for different growth rates. The correlation of different hairs from one individual, and of $\delta^{13}C$ and $\delta^{15}N$ patterns of two different individuals (Fig. 3), establishes a chronology for the hairs and permits the rate of growth to be estimated and seasonal changes to be evaluated.

Uaso's tail hairs grew at a rate of about 180 mm/year, whereas Malaika's tail hairs grew at a rate of about 260 mm/year. The proximal end of the hair, the mass of Malaika's hair was about 500–800 $\mu g/mm$, compared to Uaso's values of 360 $\mu g/mm$ and 260 $\mu g/mm$ for 1999 and 1998 hair samples, respectively. Averaged over the last month of growth, the growth rate of Malaika's hair was 650 $\mu g/day$ in 1999 while that for Uaso was 130 $\mu g/day$ (for the 1998 sample) and 200 $\mu g/day$ (1999 sample). Sample requirements are on the order of 300 μg per sample, so that it is possible to sample on a scale close to daily resolution, although in this study our samples are averaged over about 1–3 weeks.

The $\delta^{13}C$ values for tooth enamel range between $-7‰$ and $-13‰$ for enamel formed between 1940 and 1967, and between $-6‰$ and $-13‰$ between 1985 and 1993 (Fig. 4). These populations have average $\delta^{13}C$ values of $-9.8 \pm 1.3‰$ ($n=19$) and

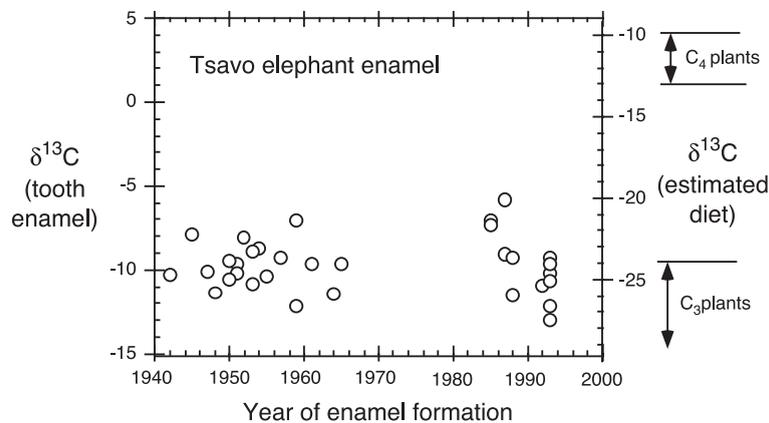


Fig. 4. $\delta^{13}C$ of enamel from Tsavo elephants and estimated diets based on the isotope enrichment between diet and enamel using a three-pool isotope turnover model.

$-9.7 \pm 2.0\text{‰}$ ($n=18$), respectively, which are not significantly different at the 95% confidence interval.

4. Discussion

4.1. Implications for wildlife study: establishing a chronology from hair growth rate

The tail hairs of Uaso and Malaika are correlated by two major $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ peaks and a number of minor

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ peaks (Fig. 3). The major $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ peaks are not coincident in time, that for $\delta^{15}\text{N}$ preceding the $\delta^{13}\text{C}$ peak by about 1 month. Based on the chronology developed from multiple Uaso hairs, the first 1998 $\delta^{15}\text{N}$ peak represents October–November while the following $\delta^{13}\text{C}$ peak represents December. The major peaks in 1999 are in April–May for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The peaks in $\delta^{13}\text{C}$ correspond to the onset of the rainy seasons (Fig. 5).

This study establishes two important aspects in the study of the diets of wildlife. First, hair samples from

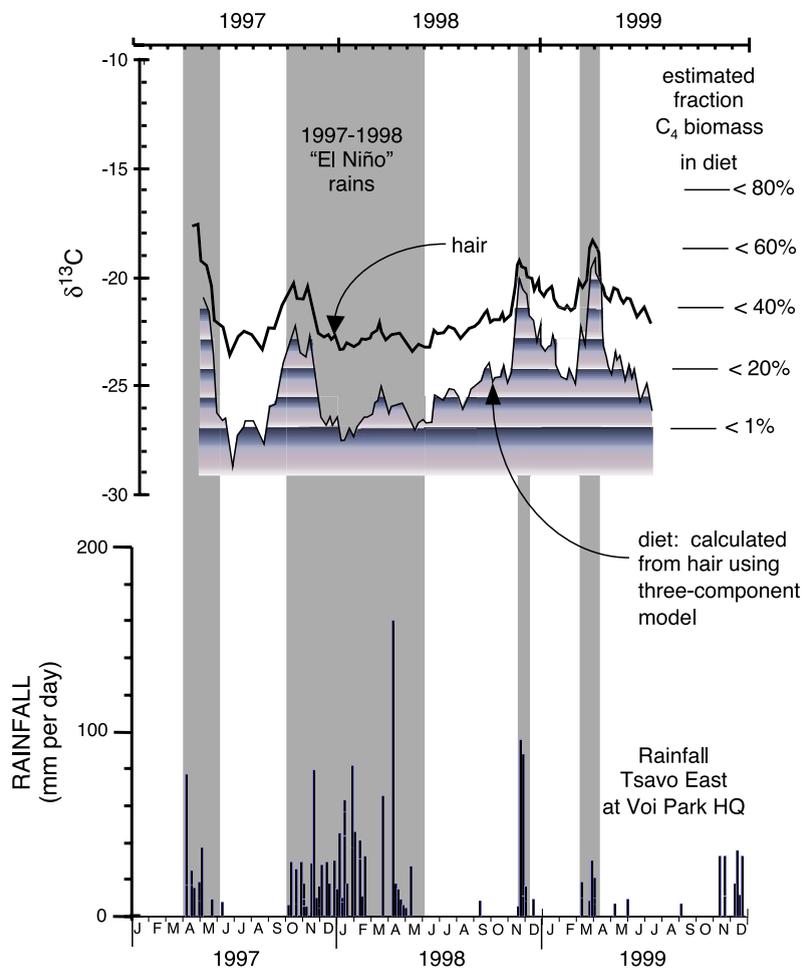


Fig. 5. $\delta^{13}\text{C}$ data for Malaika with calculated $\delta^{13}\text{C}$ values of diet based on the three-pool isotope turnover model. The percentage of estimated C_4 biomass is based on a linear mixing model between C_3 and C_4 biomass with values of -27‰ and -13‰ , respectively. Daily rainfall data from Tsavo East National Park shows the normal “short rains” in November–December 1998, the normal “long rains” of April–May 1997 and March–April 1999, and the record “El Niño” rains from October 1997 to May 1998. These data show that elephants consume C_4 grass for only a few weeks after the beginning of the rainy season, and the C_3 leaves makes up the bulk of the diet for most of the year. No diet estimates are presented for the oldest two hair segments (see text).

two different animals from the same herd have very similar isotope patterns and thus are recording diet changes of the entire group. While this study was done on semi-wild individuals, we have recorded the same patterns in wild forest hogs from the same sounder (Cerling and Viehl, in press). Second, the overlap of isotope patterns for hair collected at different times allows a growth rate to be determined, and thus the changes in diet can be compared to climate records.

The composite record of the two hairs from Uaso establishes a chronology for the growth of elephant hair, and also records the traumatic orphaning of this elephant. Uaso was orphaned at 18 months of age in November 1997 in the Laikipia plateau of central Kenya, shortly after which he was removed to Tsavo. Once Uaso was moved to Tsavo, the trends in the isotope patterns of the two different elephants, one a recent orphan and the other an established member of the herd, become similar in early 1998 (Fig. 3B and C). In 1999 the patterns are virtually identical indicating that the diets of the two animals are very similar, although the isotope changes show significant variations that are most likely due to changes through the season as dietary preferences change.

4.2. Direct estimate of diet from sequential samples of hair

Recent studies of isotope turnover in body tissues by Ayliffe et al. (in press) allow a precise estimate of the fraction of C_4 biomass in the diet of animals. Here we calculate the precise $\delta^{13}C$ of the diet of elephants assuming the same model parameters determined by Ayliffe et al. for equids; we expect minor modifications to these results when (and if) these parameters can be determined for elephants. We model the carbon isotope composition of hair and diet using a three-pool turnover model. These pools have half-lives of 0.5, 4, and 140 days and whose fractions make up 0.41, 0.15, and 0.44 of the total isotope signal, respectively (Ayliffe et al., in press). In the ensuing discussion, the subscripts 1, 2, 3 refer to the pools with the shortest, intermediate, and longest half-lives, respectively. The isotope composition of each pool changes with time as:

$$\delta_{i(t)} = \delta_{i(t-1)}e^{-\lambda_i(\Delta t)} + \delta_{D(t)}(1 - e^{-\lambda_i(\Delta t)}) \quad (1)$$

The half-lives are related to first order rate constants by:

$$\lambda_i = 0.693/t_{1/2(i)} \quad (2)$$

The isotope composition of body tissues contributing to hair formation with isotope fractionation from diet to body tissues removed is:

$$\delta_{B(t)} = \sum f_{i(t)}\delta_{i(t)} \quad (3)$$

where f_i are the fractions of the different isotope pools. The isotope fractionation factors for diet to body tissues to hair are (written as enrichment):

$$\alpha_{HB} = (1000 + \delta_H)/(1000 + \delta_B) \quad (4)$$

$$\alpha_{BD} = (1000 + \delta_B)/(1000 + \delta_D) \quad (5)$$

and thus:

$$\alpha_{HD} = (1000 + \delta_H)/(1000 + \delta_D) \quad (6)$$

where $\delta_{H(t)}$ is the $\delta^{13}C$ value of hair at time t , $\delta_{B(t)}$ is the $\delta^{13}C$ value of body at time t , $\delta_{D(t)}$ is the $\delta^{13}C$ value of diet at time t , and α_{HD} is the equilibrium fractionation factor between diet and hair (= 1.0031).

For our study, each hair segment represents more than five half-lives of the shortest half-life and therefore the shortest pool approaches isotope equilibrium with the diet (>95% equilibrated). This means that the isotopic composition of diet can be directly determined in a time series of hair segments. The two shortest isotope pools are insensitive to the initial conditions after five half-lives (i.e., 2.5 and 20 days), which corresponds to the first two hair segments of this study. Therefore, the only initial condition that needs to be determined is the pool with the longest half-life, which we take to be the diet in equilibrium with the entire period sampled. Eqs. (1)–(6) reduce to:

$$\delta_{D(t)} = \frac{\left(\frac{\delta_H + 1000}{\alpha_{HD}} - 1000\right) - \left(\sum_{i=1}^3 f_i \delta_{i,t-1} e^{-\lambda_i \Delta t}\right)}{\left(\sum_{i=1}^3 f_i (1 - e^{-\lambda_i \Delta t})\right)} \quad (7)$$

The estimates of the isotopic composition of diet using this model are presented in Fig. 5, along with

the rainfall record from Tsavo National Park. The amplitude of the diet is strongly attenuated during hair formation so that the isotope amplitude recorded in hair is about half that of the original diet signal for short-term diet changes. Fig. 5 includes an estimate of the fraction of C_4 biomass in the diet of one elephant. Exact values for the fraction of C_4 biomass in diet cannot be calculated because of the uncertainties in the isotopic composition of the C_3 and C_4 endmember values. Cerling et al. (2003) found that average $\delta^{13}C$ values in East African savanna ecosystems range between -24‰ and -28‰ for C_3 plants, and between -11‰ and -14‰ for C_4 plants; some of this variation was seasonal with greater isotope separation in the wet season compared to the dry season (see discussion in Cerling et al., 2003).

4.3. Diets of African elephants: carbon isotopes

Fig. 5 shows that the diet of elephants is strongly seasonal: in the dry season the diet is comprised predominantly of C_3 plants, whereas C_4 plants make up 30–60% of the diet within a few days of the beginning of the rains. The high fraction of C_4 plants in the diet only last a few weeks before a return to C_3 plants being the dominant dietary source. This interpretation agrees with the observations that most savanna elephants have only a minor fraction of grass in their overall diet (van der Merwe et al., 1988; Cerling et al., 1999), but that in some regions they will take significant grass in their diet in the rainy season (Kingdon, 1979). Analyses of tooth enamel from many African elephant populations indicate that Tsavo elephants appear to have more grass in their diet than savanna elephants from most parts of Africa (Cerling and Harris, 1999). It will be of interest to compare the detailed diet of elephants using hair from elephants from other populations where grass is of lesser importance in the diet than it is in the Tsavo population.

The long-term record of diet at Tsavo is also recorded in elephant enamel. The stable isotope ratios of tooth enamel document the diet when the tooth germ was forming. Using the tooth age chronology derived from the wear patterns of elephant molars (Laws et al., 1974) we could use the collection at Tsavo Research Station from the early 1970s plus material collected in the 1990s (Cerling et al., 1999) to

calculate the diet of Tsavo Park elephants for the past several decades. Fig. 4 shows that the $\delta^{13}C$ values for elephant tooth enamel have not significantly changed between about 1940 and 1995, with C_4 grass making up between 0% and 25% of the diet of most individuals. This conclusion concurs with the results of Tieszen et al. (1989) for the period from about 1955 to 1970 based on bone collagen.

In the early 1960s Tsavo National Park underwent what has been referred to as “the elephant problem” (Spinage, 1994). During this time Tsavo had a very high population of elephants which reduced the woodlands that were gradually replaced by extensive grass cover. The increase in the grass cover greatly reduced the amount of browse. It is interesting that the longer term record of diet in Tsavo elephants is characterized by a long-term utilization of some grass in the diet, even before the destruction of the woodlands in the 1960s and after its re-establishment in the 1970s and 1980s.

4.4. Diets of African elephants: nitrogen isotopes

The changes in $\delta^{15}N$ during the 1998–1999 period are probably related to changes in soil properties as well as changes in diet. We have not documented $\delta^{15}N$ values for plants in the Tsavo region, but in other semi-arid to arid parts of Kenya, the $\delta^{15}N$ of vegetation ranges from about 0‰ to +14‰, averaging about +6‰ for C_4 grasses and about +3‰ for acacias collected in the dry season. $\delta^{15}N$ of hair is enriched by about 3‰ relative to diet, so the $\delta^{15}N$ values derived from the Tsavo elephants indicate dietary ranges from about +8‰ to +11‰. During some periods, the nitrogen and carbon isotopes are well correlated, while at other times they are poorly correlated. Without detailed studies of seasonal $\delta^{15}N$ changes in local vegetation and more information about dietary selection, it is only possible to speculate about causes for ^{15}N serial changes. It is particularly interesting that the $\delta^{15}N$ and $\delta^{13}C$ values remained relatively low during the anomalous rains of 1997–1998. During this time the elephants had a virtually pure C_3 diet. After the dry interval from June 1998 to October 1999, both elephants exhibit a large increase in $\delta^{15}N$ but little change in $\delta^{13}C$. This indicates a preference for some C_3 plants with a higher $\delta^{15}N$ value, or a period of high metabolic stress. This $\delta^{15}N$

spike lasted 2–3 weeks (Fig. 3) and was followed by an increase in the $\delta^{13}\text{C}_{\text{hair}}$ of both individuals (Fig. 3). The higher $\delta^{13}\text{C}$ value indicates that the animals were ingesting a small amount of grass ($\delta^{13}\text{C} = \text{ca.} -12\text{‰}$), perhaps 10–15% C_4 grasses in their otherwise C_3 -dominated dicot diet. In the “long rains” of April–May 1999, the animals once again increased their intake of grass, reaching a peak intake that was on the order of 40% grass for a short period of time (ca. 1 month) (Fig. 5). During the onset of the rains, grasses grow faster and become abundant as forage. Other plants bear green leaves later and become more palatable later in the rainy season.

4.5. Stable isotope composition of hair and the application to wildlife studies

This study illustrates the usefulness of detailed stable isotope profiles for quantitative determination of short-term and seasonal diet changes in wild mammals. Detailed diet history can be obtained from single and multiple hairs of wildlife in the absence of extensive field observations. In elephants, sample resolution to less than a single day is possible for carbon, oxygen, hydrogen, nitrogen, and sulfur isotopes. Dietary or nutritional differences between different members of the same herd, dietary comparisons between nearby herds, significance of the grass component of diet in regions where burning is contemplated or being carried out, and diet changes during migration are examples of possible applications of this method to understanding wildlife behavior patterns and their application to conservation management issues. These studies have been undertaken on “samples of opportunity”. We anticipate a much richer record of diet and metabolic change when isotope studies can be coupled with detailed observational and tracking data.

5. Conclusions

The stable isotopic composition of elephant hair records a detailed history of dietary fluctuations. Elephant hair from Tsavo East National Park record a diet that includes up to almost 60% grass; peak grass consumption occurs for several weeks at the beginning of the rainy seasons. Over the long-term, we find

that some elephants from Tsavo Park have had a small but significant fraction of C_4 grass in their diets from 1940 to 1995 with no obvious change in dietary preference over time. Tsavo elephants eat more grass than elephants from most other parts in Africa.

It is of particular significance that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from two different individuals track each other so closely, and record small details in seasonal changes in diet and nutrition. The close correspondence of the two records suggests that the dietary history of an elephant herd may be recorded in a single hair from one individual. Samples collected at different times from two individuals with similar diets allows a chronology of hair to be established, which can then be related to local climate records.

Acknowledgements

We thank R.E. Leakey for encouragement to do this study, and Kenya Wildlife Service for assistance. Meave G. Leakey and Louise Leakey helped obtain elephant molar samples. Isaac Maina was helpful in information about the habits of the elephants in Tsavo. We also thank the government of Kenya for permission to work in Tsavo, and thank the staff of Tsavo East National Park for hospitality. This work was performed under CITES permits US785963, US831854 and 02US053837/9, and was funded by the National Science Foundation and by the Packard Foundation. This manuscript benefited by the reviews of P. Higgins and M.T. Clementz.

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