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Variability in oxygen isotope compositions of herbivore teeth: reflections of seasonality or developmental physiology?

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Abstract

Oxygen isotope compositions of herbivore tooth enamel from two areas in Kenya were measured using a laser fluorination approach. Isotope heterogeneity was found within four sets of teeth in the jaws of different individuals (~ 2‰), as well as within individual teeth. The rear molar (M3) of a zebra shows a 1.4‰ variability, whereas, the middle and rear molars (M2 and M3) of a gazelle show variations of 1.7 to 2.9‰. The front molar (M1) of a gazelle is relatively homogeneous (~ 0.25‰). Compositional heterogeneities are spatially correlated, and comparison to theoretical models suggests that they largely reflect different times of tooth growth coupled with seasonal changes in forage composition, rather than developmental physiology. Spatially-specific enamel analysis combined with knowledge of genus-specific diet, water turnover, and physiology allows paleoclimate seasonality to be assessed.

Keywords: Oxygen isotope composition; Herbivore teeth; Kenya

1. Introduction

Mammal oxygen isotope compositions are potentially useful monitors of climate because they are sensitive to local water composition, which is climate-dependent, as well as to humidity (e.g., Longinelli, 1984; Luz et al., 1984, 1990; Luz and Kolodny, 1985; Ayliffe and Chivas, 1990; D'Angela and Longinelli, 1990; Huertas et al., 1995). Of the many different oxygen-bearing tissues, tooth enamel is one of the best records of animal $\delta^{18}O$. It is precipitated as fully crystalline apatite in which oxygen is strongly bound, and it is not replaced during the animal's lifetime. Therefore, enamel compositions are unaffected by later changes in animal behavior or location, and are also probably less susceptible to diagenetic alteration than less well crystallized tissues. Systematic temporal differences in the timing of enamel precipitation within a single tooth and among teeth in a single jaw (e.g., Hillson, 1986) imply that different teeth or parts of teeth may provide a continuous record of $\delta^{18}O$ changes during the enamel precipitation period. Because of seasonal changes in rainfall, humidity, and temperature that affect forage and drinking water compositions, analysis of compositional differences among or within teeth can potentially elucidate climatic seasonality. However, developmental changes in animal diet also occur during part of the enamel precipitation period, and the inter- and intratooth $\delta^{18}O$ signal may potentially reflect the isotope effects of physiologically dictated dietary changes.

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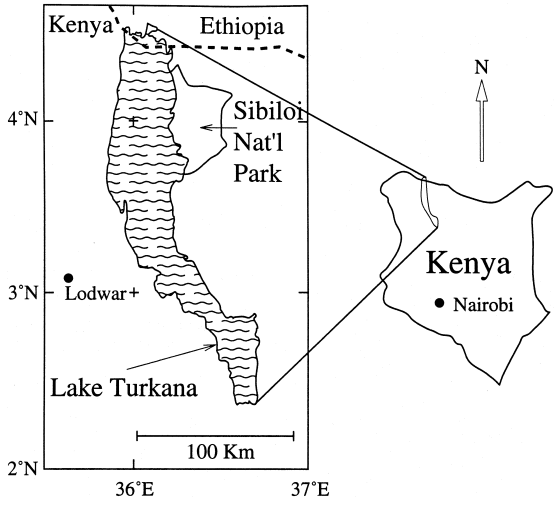

Fig. 1. Locations of the Sibiloi National Park, on the east side of Lake Turkana, northern Kenya, and of Nairobi, central Kenya. The same species are present in the two areas, but the climates and seasonality are quite different.

The purpose of this study was to measure the magnitude of $\delta^{18}O$ variations among teeth in single jaws and within single teeth, and to investigate whether any observed variations were the result of seasonality or physiology. Two different areas in Kenya were selected, near Lake Turkana and near Nairobi, because many of the same herbivore species live in both areas (e.g., gazelle and zebra), and because the climates are quite different (Fig. 1; summarized in Table 1). The Lake Turkana area is hot and dry with an average yearly temperature, humidity, and precipitation amount of $\sim 29°C$, $\sim 47\%$, and ~ 200 mm, whereas Nairobi is cooler and wetter ($\sim 19°C$, $\sim 65\%$, and ~ 800 mm; Meteorological Office, 1983). Both areas have a rainy season peaking in April. However, the climate of Lake Turkana does not strongly vary for the remainder of the year, whereas, Nairobi has a more marked seasonality, with an additional rainy period peaking in November and larger changes of temperature.

2. Analytical and sampling methods

Teeth were analyzed using a laser fluorination approach described by Kohn et al. (1996). Briefly, this method involves grinding a 0.5–2 mg sample of enamel and initially pretreating overnight with a small amount of BrF_5 to eliminate adsorbed water and residual organic materials. Samples are then heated the next day with a focused CO_2 laser in the presence of BrF_5 to liberate oxygen, and the oxygen is purified and converted to CO_2, which is analyzed in a dual-inlet, gas-source mass spectrometer. Extensive chemical, spectroscopic, and isotope investigation of BrF_5-pretreated enamel indicates that the overnight pretreatment step does not affect $\delta^{18}O$. For samples that are initially bleached in either NaOCl or H_2O_2, analytical reproducibility is $\sim \pm 0.08‰$ (1σ). Some of the samples analyzed in this study were not prebleached, and it was subsequently determined that their analytical reproducibility was poorer ($\sim \pm 0.20‰$, 1σ), although the average $\delta^{18}O$ values for bleached vs. unbleached samples are the same to within 0.05‰. For this study, interpretations depend principally on compositional differences and so require analytical precision, but compositional accuracy and yields have also been determined. A 1.7‰ upward correction to raw data is required for accuracy, and analytical yields are typically $\sim 80\%$. The low yield and compositional correction may possibly result from forming a small quantity of high $\delta^{18}O$ P–O–F compounds in the sample chamber during lasing (see Kohn et al., 1996).

All teeth from the Turkana area were obtained from natural, surface-exposed skeletons, and weathering ranged from stages 0 to 3 (0–7 years of exposure; Behrensmeyer, 1978). This degree of weathering should not have affected oxygen isotope compositions (Koch et al., 1990). Teeth from near Nairobi were obtained from a game ranch. Teeth from the mandibles of four different animals were used to investigate intertooth compositional variability (Table 2; Fig. 2, filled symbols), and included one dikdik (*Rhynchotragus guentheri*) and one Grant's gazelle (*Gazella granti*) from the Turkana area, and two Grant's gazelles from near Nairobi. Wherever possible, enamel was sampled from either the mid-section or crown of each tooth, and encompassed 10–30% of the length of the tooth. In a few cases, only the base of the tooth could be sampled. A maxillary M3 zebra (*Equus burchelli*) molar from the Turkana area and mandibular M1, M2, and M3 gazelle molars from a single jaw from near Nairobi were also sampled in detail to elucidate intratooth

Table 1
Summary of climate data for Nairobi and Lake Turkana, East Africa

	Average daily T (°C)		Average	Average h (%)		Average	Average monthly
	Max.	Min.	T (°C)	0830	1430	h (%)	precipitation (mm)
Nairobi							
January	26.7	12.9	19.8	76	42	59	49
February	27.9	13.1	20.5	75	38	56	36
March	27.5	14.1	20.8	82	43	62	85
April	26.0	14.9	20.4	86	53	70	153
May	24.5	14.3	19.4	86	58	72	126
June	23.7	12.3	18.0	85	54	70	32
July	22.6	11.4	17.0	85	55	70	13
August	23.0	11.5	17.2	84	53	68	18
September	25.6	12.0	18.8	80	44	62	21
October	26.6	13.3	20.0	78	42	60	48
November	24.9	14.0	19.4	85	53	69	132
December	25.3	13.5	19.4	82	50	66	75
Year average:	25.4	13.1	19.2	82	49	66	788 (total)
Lake Turkana							
January	35.3	21.9	28.6	52	31	42	15
February	36.2	23.0	29.6	52	31	42	9
March	36.0	24.1	30.0	56	35	46	25
April	34.7	24.1	29.4	64	42	53	59
May	34.8	24.5	29.6	63	41	52	22
June	34.1	23.8	29.0	61	39	50	4
July	33.1	23.5	28.3	62	40	51	15
August	33.4	23.6	28.5	61	39	50	13
September	34.8	23.9	29.4	56	34	45	1
October	35.3	24.4	29.8	53	34	44	9
November	34.5	23.5	29.0	55	36	46	19
December	34.5	22.4	28.4	53	34	44	17
Year average:	34.7	23.6	29.3	58	36	47	208 total

Data are from the Meteorological Office (1983), and span 22 years of observations.
The observations for Lake Turkana are based on measurements at Lodwar, just west of the lake, and are consistent with data reported by Cerling et al. (1988).
Average h (%) is the average relative humidity, in percent, based on observations at 8:30 AM, and 2:30 PM.

isotope variations (Fig. 3; Table 2). Analyses of teeth for goat (*Capra hircus*), dikdik, Grant's gazelle, topi (*Damaliscus corrigum*), Burchell's zebra, gerenuk (*Litocranius walleri*), and oryx (*Oryx beisa*) have been described by Kohn et al. (1996) for the Turkana area. Data for that study are included in Fig. 2 (open symbols) and compared below with the new data (filled symbols).

3. Timing of tooth mineralization and eruption

The timing of tooth formation and eruption is an important concern for interpreting oxygen isotope trends, especially for the extensive data for gazelle discussed below. Of the herbivores studied, premolars, molars, and the first incisor are fully formed and erupted by an age of $\sim$2 years for dikdik (Kellas, 1955), $\sim$2 1/2 years for gazelle (Spinage, 1976) and $\sim$4 years for zebra (Levine, 1982). Timing of tooth eruption in dikdik was inferred by Kellas (1955) to have been: M1 prior to 6 months, M2 at $\sim$6 months, M3 at $\sim$6–12 months, and the premolars at $\sim$1 year or more. Robinette and Archer (1971), Spinage (1976), and Davis (1980) studied tooth eruption in gazelles and their observations indicate the following eruption times: M1 erupted

Table 2
Oxygen isotope analyses of tooth enamel from East Africa

	$\delta^{18}O$(‰, V-SMOW)	Average
Turkana Samples		
Zebra (single tooth, bleached)		
BZ2306-A (−1.0 cm)	28.51, 28.67	28.59
BZ2306-B (−0.5 cm)	28.54, 28.34	28.44
BZ2306-C (exterior)	28.04	28.04
BZ2306-D (interior)	27.36, 27.27	27.32
BZ2306-E (exterior)	28.03, 28.00	28.01
BZ2306-F (exterior)	28.03	28.03
BZ2306-G (interior)	27.44, 27.39	27.42
BZ2306-I (exterior)	28.10, 27.97	28.04
BZ2306-J (interior)	27.39, 27.43	27.41
BZ2306-K (exterior)	27.99, 27.95	27.97
BZ2306-L (exterior)	28.26	28.26
BZ2306-M (−1.5 cm)	28.66, 28.89	28.78
Dikdik (single jaw, bleached)		
DD2278-1B (M3)	27.03, 26.97	27.00
DD2278-1E (M1)	28.07, 28.27	28.17
DD2278-1G (P4)	28.96	28.96
DD2278-1J (P2)	29.22	29.22
DD2278-2J (I1)	26.99, 27.03	27.01
Gazelle (single jaw, bleached)		
GG2109-1A (M3)	30.79, 30.56	30.67
GG2109-1C (M3)	30.39, 30.60	30.49
GG2109-1E (M2)	32.60, 31.57	31.58
GG2109-1G (P4)	32.39	32.39
GG2109-1I (P3)	32.21, 32.19	32.20
Nairobi Samples		
Gazelle-1 (single jaw, unbleached)		
M1	23.30, 23.62, 23.67	23.53 ± 0.20
M2	24.35, 24.65	24.50
M3	21.42, 21.91, 21.67, 21.48	21.62 ± 0.22
P3	23.04, 23.13, 22.69, 22.86	22.93 ± 0.20
P4	22.39, 22.44, 22.46, 22.27	22.39 ± 0.09
Gazelle-2 (single jaw, unbleached)		
M1	24.29, 24.13, 23.67, 23.74	23.96 ± 0.30
M2	24.01, 24.16, 24.04	24.07 ± 0.08
M3	25.31, 25.27, 25.01, 25.19	25.20 ± 0.13
P2	23.53, 23.39, 22.98, 23.22	23.28 ± 0.24
P3	23.27, 23.26, 23.11	23.21 ± 0.09
Gazelle-2-M3 (single tooth, bleached)		
a (0 mm)	24.92, 25.06. 24.92	24.97 ± 0.08
b (−3 mm)	25.18, 24.77	24.98
Gazelle-2-M3 (single tooth, bleached)		
c (−5 mm)	25.30, 25.19, 25.31	25.27 ± 0.07
d (−8 mm)	25.44, 25.32, 25.47	25.41 ± 0.08
e (−9 mm)	25.49, 24.83, 25.11, 25.13	25.14 ± 0.27
f (−11 mm)	24.52, 24.53, 24.47	24.51 ± 0.03
g (−12 mm)	23.90. 24.13, 24.05	24.03 ± 0.12
h (−14 mm)	23.57, 23.75, 23.63	23.65 ± 0.09
i (−16 mm)	23.44, 23.34	23.39
j (−18 mm)	22.71, 22.59	22.65
k (−20 mm)	22.63, 22.40	22.52
l (−22 mm)	22.77, 22.87	22.82
m (−24 mm)	22.65, 22.63	22.64
n (−26 mm)	22.45, 22.45	22.45
Gazelle-2-M1 (single tooth, bleached)		
a (0 mm)	23.91	23.91
b (−2 mm)	23.98	23.98
c (−4 mm)	24.05	24.05
d (−6 mm)	24.09, 24.00	24.04
e (−8 mm)	24.05, 24.10	24.08
f (−10 mm)	24.16	24.16
Gazelle-2-M2 (single tooth, bleached)		
a (0 mm inner)[a]	24.23, 24.15, 24.16	24.18 ± 0.04
b (−2 mm inner)[a]	23.79, 24.00	23.90
c (−4 mm inner)[a]	23.98, 23.51	23.74
d (−6 mm inner)[a]	23.71, 23.72	23.71
e (−0 mm outer)	23.68, 23.81	23.74
f (−2 mm outer)	24.06, 24.24	24.15
g (−4 mm outer)	24.16, 24.36	24.26
h (−5 mm outer)	24.79, 24.98	24.88
i (−6 mm outer)	24.75, 24.95	24.85
j (−10 mm outer)	25.11, 25.33	25.22
k (−12 mm outer)	25.03, 24.95	24.99
l (−14 mm outer)	25.01, 25.19	25.10
m (−16 mm outer)	25.33, 25.25	25.29
n (−18 mm outer)	25.40, 25.36	25.38

Normalized to UW standard UWG-2 = 5.8‰ (Valley et al., 1995) and SP3-3 apatite (Farquhar et al., 1993).
'M1'–'M3' refer to molars.
'P2'–'P4' refer to premolars.
'I1' refers to first incisor.
'Interior' and 'exterior' refer to inner and outer convolutions of enamel in the zebra and gazelle molars.
'−0.5 cm' to '−1.5 cm' and '−2 mm' to '−26 mm' are the distances below the zebra and gazelle tooth wear surfaces of samples of (outer) enamel.
'bleached' indicates initial oxidation of organic material in NaOCl.
'unbleached' indicates untreated enamel.
[a]For Gazelle-2 M2 inner enamel means that some dentine was also analyzed.
All dentition was permanent.

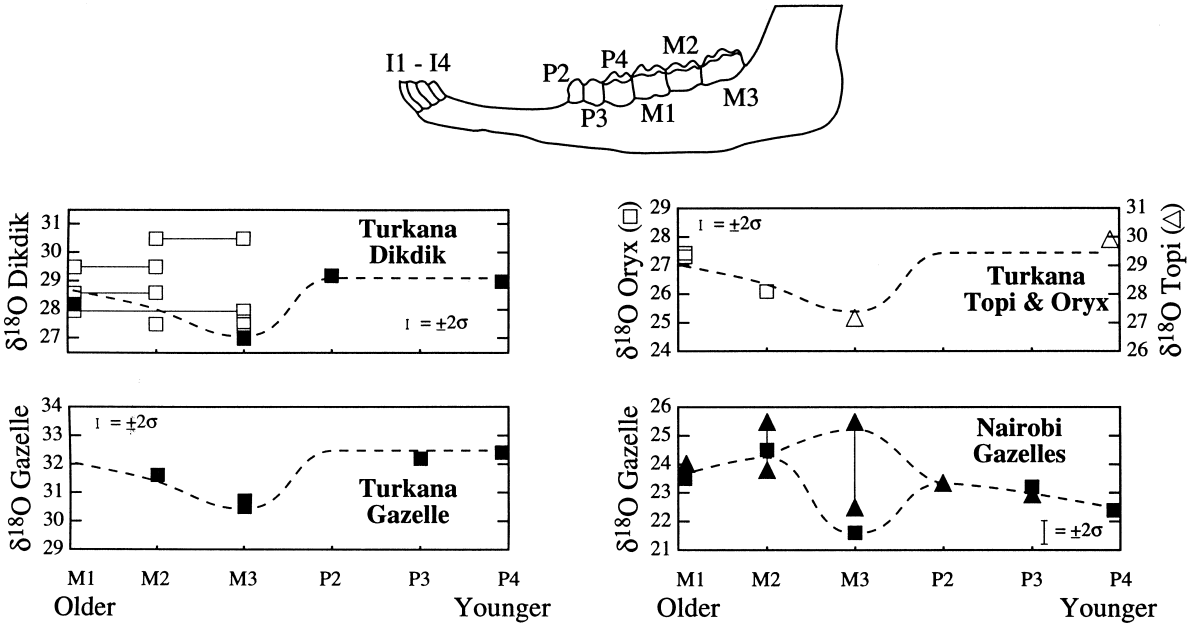

Fig. 2. Sketch of jaw showing locations of different herbivore teeth (after Pérez-Barbería, 1994) and plots of $\delta^{18}O$ vs. tooth identity and time for different animals in the Lake Turkana and Nairobi areas. Solid data are from this study from single jaws, open data are from Kohn et al. (1996). Horizontal lines connecting open squares for Turkana samples indicate that more than one tooth was sampled for the analysis. Two additional data points from Kohn et al. (1996) underlie the M3 solid squares for the Turkana gazelle. For Nairobi samples, squares and triangles correspond to gazelle-1 and gazelle-2, respectively. Vertical lines indicate extent of zoning deduced from detailed analysis of individual teeth from gazelle-2. Despite complications due to intratooth compositional zonation, different genera in the Turkana area display apparently similar isotope patterns (sketched dashed lines).

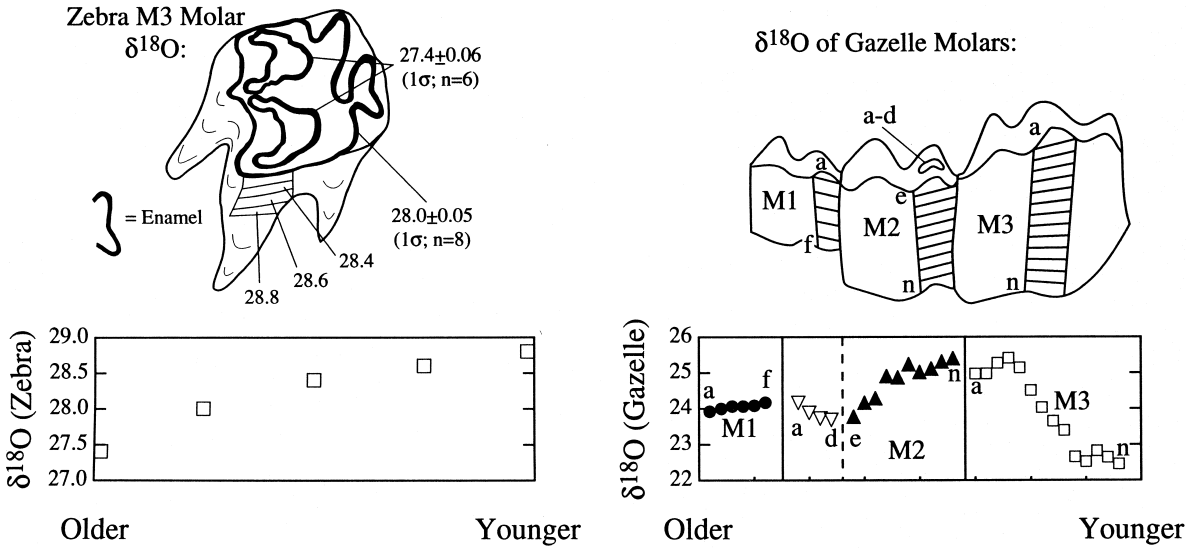

Fig. 3. Values for $\delta^{18}O$ of a zebra M3 molar from the Lake Turkana area and of M1, M2, and M3 molars of a gazelle from near Nairobi showing significant compositional heterogeneity. Vertical lines and open vs. closed symbols separate different teeth or sections of teeth. Although different teeth on average form at different times, there may be temporal overlaps or gaps between the end of mineralization of one tooth and initial growth of another (i.e., at the solid vertical lines).

between 3 and 10 weeks; M2 = 20 to 30 weeks; M3 = 40 to 50 weeks; P2–P4 = 50 to 80 weeks. The range of eruption times reflects natural variability among individuals. These tooth eruption times in gazelles are somewhat earlier than has been determined for wild goats or for other medium-sized antelopes that are related to gazelle (Bullock and Rackham, 1982; Deniz and Payne, 1982; Anderson, 1986; Norton and Fairall, 1991; Pérez-Barbería, 1994). The timing of initial enamel mineralization relative to eruption is not well known for most animals, nor is the duration of the mineralization period. For example, in domestic sheep, M1 enamel is already partially formed at birth (Weinreb and Sharav, 1964), whereas, M1 eruption may not occur in some individuals until 26 weeks after birth (Weinreb and Sharav, 1964; Hillson, 1986). The isotope data for individual gazelle molars suggest that complete precipitation of enamel for a single tooth requires at most 4 months. Therefore, the initial spot sampling of 10–30% of the length of a tooth probably corresponds to 1–6 weeks of enamel production.

Gazelle births are generally semi-annual, with a high narrow peak in June and July, and a low broad peak between November and March (Spinage, 1986a). Within a few days or weeks after birth, young gazelle and dikdik begin to eat plants, and final weaning ordinarily occurs within 2–4 months (Hendrichs and Hendrichs, 1971; Kingdon, 1982; Spinage, 1986b; Estes, 1991). Studies of water turnover in juvenile domestic animals and behavioral observations indicate that milk consumption steadily decreases until weaning (e.g., Hendrichs and Hendrichs, 1971; Bailey and Lawson, 1981). That is, a progressive change in the proportion of milk to plant intake occurs within the first few weeks to months, so that M1 and possibly M2 compositions are potentially affected by mother's milk and weaning, but subsequent teeth (M3 and P2–P4) are not.

For zebra, the timing of tooth eruption is somewhat different. From oldest to youngest, the time of eruption is: M1, M2, P2, P3, M3 + I1 + P4 (Levine, 1982). Because fewer data were collected for zebra, less detail concerning the specific tooth eruption times is required. However, the duration of mineralization is important, which is assumed to be at least 6 months based on dental data for other animals (Hillson, 1986), and the isotope trends found for gazelle (this study).

4. Inter-tooth isotope variations

Compositional heterogeneity among different teeth is significant in both the Turkana and Nairobi areas. In the Turkana region, teeth from individual jaws show compositional variability of 1.7‰ for the gazelle and 2.2‰ for the dikdik. Additional analyses collected from isolated teeth for dikdik, Grant's gazelle, topi, and oryx support similar intratooth variations among all genera (Fig. 2; data from Kohn et al., 1996), and possibly increased heterogeneity. For example, the total range of dikdik tooth compositions is nearly 4‰. Much of this variability is centered on M2/M3 compositions, and as described below for individual gazelle molars, M2 and M3 are particularly heterogeneous. If other teeth are compared (e.g., M1 or the premolars), then compositional scatter among individuals of the same genus is much smaller, $\sim \pm 0.2$–0.3‰. In the Nairobi area, the two gazelles analyzed also illustrate significant isotope heterogeneity, with a variation exceeding 3‰.

5. Intra-tooth isotope variations

For the single zebra M3 molar, a total range of 1.4‰ was found (Fig. 3; Table 1). Values of $\delta^{18}O$ increased from the crown towards the root by 0.8‰, and the $\delta^{18}O$ of the inner enamel convolutions (the infundibula) was 0.6‰ lower than the outer enamel margins. Because teeth mineralize from the crown towards the root (e.g., Hillson, 1986), as the Turkana zebra M3 was growing, the body water composition was thus becoming progressively enriched in ^{18}O. The time over which this $\delta^{18}O$ increase occurred is unknown. The single M3 molar of the Nairobi gazelle shows a crown to root initial increase in $\delta^{18}O$ from $\sim$25.0‰ to $\sim$25.4‰ followed by a decrease to $\sim$22.5‰ (Fig. 3; Table 1). Two areas of M2 were analyzed. The first 4 samples (a–d), from an infundibulum, were not pure enamel as their oxygen yields were only $\sim$65–70%. The small decrease in $\delta^{18}O$ indicated by these analyses from $\sim$24.2 to

~23.7‰ should be viewed as preliminary. The remaining pure enamel analyses (e–n) from the side of the tooth show a strong increase in $\delta^{18}O$ towards the root from 23.7 to 25.4‰. The final composition trend near the base of the tooth from ~25.0 to ~25.4‰ is the same within uncertainty as the initial trend shown by the crown of M3. In contrast to M2 and M3, the single M1 molar analyzed from the same gazelle shows little if any compositional variation: its $\delta^{18}O$ may increase slightly from ~23.9 to ~24.2‰ from crown towards root, but the differences are within analytical uncertainty.

Knowing that the molars grow in the order M1–M2–M3, these variations indicate that, following a period of nearly static isotope composition, the $\delta^{18}O$ of the Nairobi gazelle first decreased (M1–M2), then increased (M2, M3) and finally decreased again sharply (M3). The 2–3‰ composition range measured for individual gazelle M2 and M3 molars explains much of the apparent compositional variability in Fig. 2. For example, the low $\delta^{18}O$ M3 composition for one Nairobi gazelle was obtained from the base of the tooth (the crown was missing), whereas, the higher $\delta^{18}O$ Nairobi M3 compositions were obtained from the crown. Large changes in intratooth compositions and compositional reversals for sheep, bison, and equid teeth were also found by Fricke and O'Neil (1996), and by Bryant et al. (1996a,b).

6. Discussion

6.1. Modeling of isotope compositions

Because migration is impossible in the circumscribed areas from which the gazelle teeth were collected, there are only two reasonable interpretations of the observed ontogenetic isotope variations: seasonality or developmental physiology. By seasonality, we mean changes of food and water isotope composition resulting from seasonal changes of water and plant composition and/or seasonal changes of diet of a mature individual. This is considered independently of developmental physiology, by which we mean ontogenetic changes of what a young herbivore consumes (i.e., milk vs. leaves) or in the proportions of oxygen fluxes as an animal matures. If the observed inter- and intratooth isotope variations in part reflect developmental physiology, then physiologies of now-extinct species may possibly be inferred from isotope studies of fossil materials. If, instead, the isotope variations only reflect seasonality, then past yearly climate may be inferred from fossils.

Although both seasonality and developmental physiology have been modeled by Bryant et al. (1996a,b), their generalized body mass-dependent model (Bryant and Froelich, 1995) and assumed dietary fractionations may not be applicable to the specific animals studied or their food (Kohn, 1996; Kohn et al., 1996). There are large differences at the genus-level in diet, the amounts of fecal and urinary water loss, the proportions of panting to sweating, and the ratio of water turnover to total daily energy requirements. Because liquid water output has a different isotope composition from water vapor output, and because ingested water has a different composition from other oxygen sources, a knowledge of genus-specific physiology is critical for accurate modeling. Consequently, the genus-specific modeling approach of Kohn (1996) was adopted, but a comparison to the simpler Bryant and Froelich (1995) and Bryant et al. (1996a,b) models is also described.

6.2. Theoretical seasonality

Accurate modeling of seasonality requires assigning several different physiological and dietary parameters, as well as seasonal signals such as humidity, temperature, and surface water composition. The focus of this paper is on changes of isotope composition, and these are less susceptible to errors in the value assigned to any particular parameter. However, for accuracy we attempted to account for geographically-dependent surface water compositions. We restricted modeling to Grant's gazelle because it is the most extensively studied isotopically of our samples, and because the isotope trends observed mimic those found in other species (Fig. 2). Physiological and dietary parameters were based on several detailed studies of gazelles (Taylor, 1968, 1972; Macfarlane and Howard, 1972; Spinage et al., 1980), and with one exception are tabulated by Kohn (1996). As noted by Kohn (1996), transcutaneous water vapor losses strongly impact modeled $\delta^{18}O$ values, and in

hot dry areas, such as in Kenya, this loss can be four times higher than measured in cooler, wetter settings (e.g., Grice et al., 1971, 1972). To better account for the Kenyan climate, the amount of transcutaneous water vapor loss was doubled in the gazelle models over 'standard' water loss estimates (Kohn, 1996). Seasonal variations in temperature and humidity were based on tabulations of 22 years of meteorological observations (Meteorological Office, London) for Nairobi, and for Lodwar, which is just west of Lake Turkana (Table 1).

Because most animals drink water and because plant $\delta^{18}O$ is affected by rainwater $\delta^{18}O$, meteoric and surface water isotope compositions are important for evaluating seasonal isotope effects. Unfortunately, assigning monthly surface water compositions is non-trivial, because they are not routinely monitored at either Lake Turkana or Nairobi. For the Lake Turkana area, we assumed that surface water $\delta^{18}O$ varied from +5‰ to +7‰ during the year based on direct measurements of lake water composition (Cerling et al., 1988; Cerling, pers. comm., in Johnson et al., 1991). This range is smaller than that observed for rainwater on the Ethiopian plateau (+1.5‰ to −3.5‰ for Addis Ababa; IAEA, 1992), which supplies Lake Turkana's water, but is similar to that observed for rainwater in the nearby Sudan desert (−1‰ to −3‰ for Khartoum for months with significant rainfall; IAEA, 1992), and is larger than that predicted from worldwide correlations between temperature and meteoric water $\delta^{18}O$ (+6‰ to +7‰; Dansgaard, 1964). Thus, we believe the modeled range is reasonable. For Nairobi, isotope compositions were based on data collected at Entebbe, Uganda (IAEA, 1992) because it has a similar seasonal periodicity to its rainfall and temperature. Unfortunately, Entebbe is more humid than Nairobi and receives twice the rainfall. Because the data for East African stations show a general correlation of increasing average $\delta^{18}O$ with decreasing precipitation amount, the $\delta^{18}O$ at Nairobi must be higher than in Entebbe. Based on correlations between measured $\delta^{18}O$ and precipitation amount for Entebbe, we uniformly increased the model $\delta^{18}O$ of Nairobi surface water over the Entebbe measurements by 0.9‰. This change increases modeled gazelle $\delta^{18}O$ by ~0.6‰.

Results of these calculations (Table 3, Fig. 4) show that Lake Turkana gazelle should have a significantly higher $\delta^{18}O$ than Nairobi gazelle. This geographic difference occurs largely because surface water at Lake Turkana is enriched in ^{18}O compared to Nairobi surface water, but also because of differences in humidity. The lower humidity at Lake Turkana increases the $\delta^{18}O$ of plant water and cellulose over surface water compositions there more strongly than near Nairobi [i.e., Δ(plant − surface water) is larger at Turkana than at Nairobi]. For gazelle, the total predicted range in enamel $\delta^{18}O$ is in reasonable agreement with the measurements:

Table 3
Selected results of seasonality modeling

Month	Surface water $\delta^{18}O$ (‰)	Leaf water $\delta^{18}O$ (‰)	Enamel $\delta^{18}O$ (‰)
Nairobi			
January	−0.9	9.6	23.7
February	0.5	11.7	25.0
March	−1.9	7.8	22.6
April	−2.3	5.4	21.3
May	−2.4	4.8	21.0
June	−0.8	6.9	22.4
July	−0.6	7.1	22.6
August	−0.6	7.7	22.8
September	−0.9	8.8	23.4
October	−2.2	8.0	22.7
November	−3.4	4.5	20.7
December	−1.7	7.0	22.3
Year average	−2.0	6.7	23.7
Lake Turkana			
January	6.5	20.9	30.5
February	7.0	21.4	30.8
March	6.0	19.4	29.6
April	5.5	17.2	28.3
May	5.5	17.4	28.4
June	6.5	18.9	29.4
July	6.5	18.7	29.3
August	6.5	18.9	29.4
September	6.5	20.1	30.1
October	5.5	19.4	29.5
November	5.0	18.4	28.9
December	6.0	19.9	29.9
Year average	6.0	19.2	29.5

Compositions are all relative to V-SMOW.
Surface water compositions for Nairobi are based on IAEA measurements at Entebbe, Uganda.
The composition of surface water at Lake Turkana assumes a 2‰ seasonal variation, based on measurements of lake water compositions (+5‰ to +7‰; Cerling pers. comm., in Johnson et al., 1991).

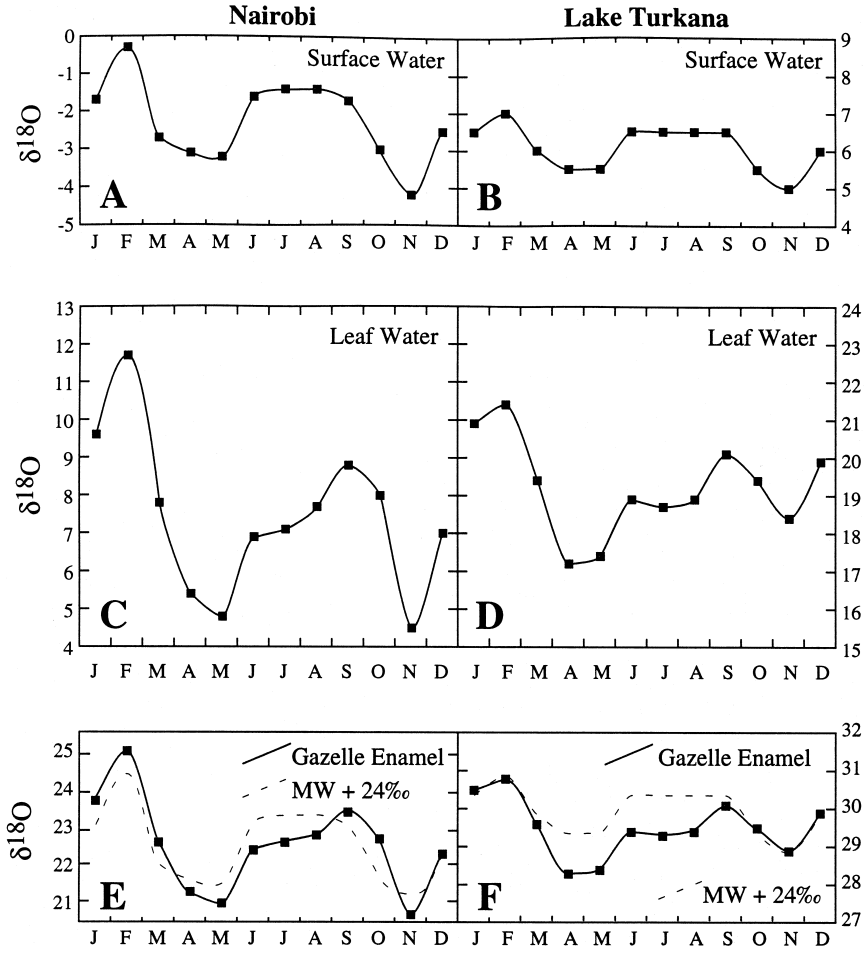

Fig. 4. Combined with meteorological data (Table 1), seasonal variations in meteoric water compositions for Nairobi (A) and the Turkana area (B) allow modeling of seasonality in oxygen isotope compositions for plants (C, D) and gazelle enamel (E, F). Leaf water composition was calculated according to the Craig–Gordon equation of isotope enrichment (Craig and Gordon, 1965), which is appropriate for mixed feeders like gazelles. Enamel compositions were determined for gazelle; different animals would likely have a similar seasonality trend, but offset to higher or lower $\delta^{18}O$ values depending on specific diet and physiology. Seasonality in Nairobi is greater than at Lake Turkana, as reflected in the greater variability in modeled isotope compositions for Nairobi. Plant isotope compositions generally follow surface water trends (with a large offset), but are magnified and modified by seasonal humidity effects. Variations in enamel compositions are not simply offset from meteoric water signals (solid vs. dashed lines, E and F), but have components of both the surface water and plant signals.

~4‰ predicted vs. ~3.5‰ measured for Nairobi and ~2‰ vs. ~1.5‰ for Turkana. However, the total range of dikdik compositions at Turkana (4‰) suggests that either dikdik are more sensitive to seasonality, or predicted seasonality is underestimated. The actual predicted values for gazelle enamel $\delta^{18}O$ at Lake Turkana are systematically 1–2‰ too low (predicted compositions = 28.3 to 30.8‰; measured compositions = 30.5 to 32.5‰). Although the range of predicted compositions at Nairobi better matches the measurements (predicted compositions = 21.0 to 25.0‰; measured compositions = 21.6 to 25.4‰), a detailed comparison with seasonality (see below) suggests that a similar underestimate of compositions by ~1‰ occurs. Predicted $\delta^{18}O$ may be too low because of an underestimate in the isotope fractionation between transcutaneous water vapor and body water, which is very poorly known (Bryant and

Froelich, 1995; Kohn, 1996), or because the $\delta^{18}O$ of surface water was underestimated.

Considering that systematic uncertainties in the genus-specific physiological models and in the assigned surface water compositions are respectively ± 1–2‰ (Kohn, 1996) and at least ± 1‰, the agreement between the measurements and our theoretical calculations to within 1–2‰ is reasonably good. If the Bryant and Froelich (1995) model is applied, however, then predicted $\delta^{18}O$ is systematically $\sim$ 4‰ lower than measurements in both areas, a deviation which significantly exceeds their stated model uncertainties ($\sim \pm 0.5$‰). Substantial changes in assumed water and plant $\delta^{18}O$ values could perhaps rectify the predictions of the Bryant and Froelich (1995) model with measured compositions for gazelle, but if such changes are made, then discrepancies between models and measurements for other coexisting animal families (e.g., for zebra) increase to several permil. That is, the Bryant and Froelich (1995) modeling approach cannot simultaneously match the oxygen isotope data found for the physiologically diverse herbivores inhabiting East Africa (e.g., Kohn et al., 1996). One simple explanation is that the specific physiologies of some animals (e.g., gazelle) deviate significantly from the generalized equations used by Bryant and Froelich (1995), and that more specific models are required for accurate modeling.

Despite the fact that the ~ 8‰ difference in gazelle tooth enamel $\delta^{18}O$ between Turkana and Nairobi mimics the ~ 8‰ difference in surface water composition between the two areas, it is important to note that enamel composition does not simply track surface water. For example, as described by Kohn (1996), a 1‰ change in meteoric water composition should change gazelle composition by only 0.7‰, because a significant fraction of an animal's input oxygen is derived from air, which has a constant $\delta^{18}O$ value. The isotope enrichment in gazelle enamel between Nairobi and Turkana instead reflects differences not only in meteoric water but also in humidity, in that the lower humidity near Turkana causes additional increases in plant $\delta^{18}O$ and hence in gazelle enamel $\delta^{18}O$ there. More generally for interpreting isotope zoning trends, because humidity does not simply correlate with rainfall (Table 1), plants do not directly track surface water compositions (Fig. 4C, D), and this leads to differences in the trends of meteoric water and tooth enamel compositions (Fig. 4E, F). Although the predicted seasonal trend in tooth enamel $\delta^{18}O$ is strongly tied to surface water changes, it is further modified and enhanced by humidity effects on food compositions, and simultaneously damped by isotopically less variable air oxygen.

6.3. Comparison of specific compositional variations with seasonality models

For many animals, relating specific tooth compositions to specific seasons is complicated by the potentially long duration of tooth enamel production and the difficulties of sampling exactly the same location on each tooth. Some of these difficulties are illustrated by the large compositional differences among M2 and M3 molars (Fig. 2). These differences could reflect seasonal composition variations coupled with either different birth times during the year or different rates of maturing, so that M3 teeth mineralize in different months in different individuals. Alternatively, because M3 is compositionally heterogeneous by up to 3‰, even if all individuals grew their M3 teeth at the same time, vagaries in sampling due to differences in preservation would inevitably lead to apparent heterogeneity. Despite these shortcomings, a first order comparison of the models and data clearly supports the hypothesis that teeth encode isotope seasonality. There is a strong correspondence between the magnitudes of the predicted seasonal isotope shifts and measured intertooth variability, and furthermore the reversal in $\delta^{18}O$ exhibited in the Nairobi gazelle M3 molar and the opposite trends in M2 vs. M3 are difficult to explain physiologically.

If seasonality is in fact recorded by some teeth, then specific intratooth composition changes should be quantitatively relatable to the theoretical predictions of seasonality models. Furthermore, if a reconciliation between measurements and models is possible within the uncertainties of the models and of tooth mineralization times, then the timing of mineralization of gazelle teeth can be inferred. In order to evaluate these implications, the intratooth isotope variations measured for the Nairobi gazelle were compared with the theoretical predictions. The com-

positional trend for the M3 molar was first used to deduce the rate of enamel production. Then knowing the general eruption times of M1–M3 relative to birth, and the likely seasonal variation, we identified the gazelle's birth month and attempted to match measured tooth compositions to predicted seasonal changes (Fig. 5). For this analysis, it is important to recognize that the theoretical models are temporally accurate, but compositionally uncertain, whereas, the measured data are compositionally accurate, but temporally uncertain. Thus, attempts at reconciling the model with the data must account for the possibility of systematic errors in the composition placement of the theoretical models (Fig. 5A), as well as in the time placement of the measured compositions (Fig. 5B).

The M3 molar has the highest $\delta^{18}O$ measured for all gazelle teeth in the area, as well as a significant drop to one of the lowest $\delta^{18}O$ values, with no intervening reversals. Because M3 production occurs while gazelles are adults, these compositions and trends are not likely affected by developmental changes, and are therefore most consistent with the seasonal transition from dry to wet conditions between February and May (Fig. 4). More specifically, comparing M3 values with the predicted curve sug-

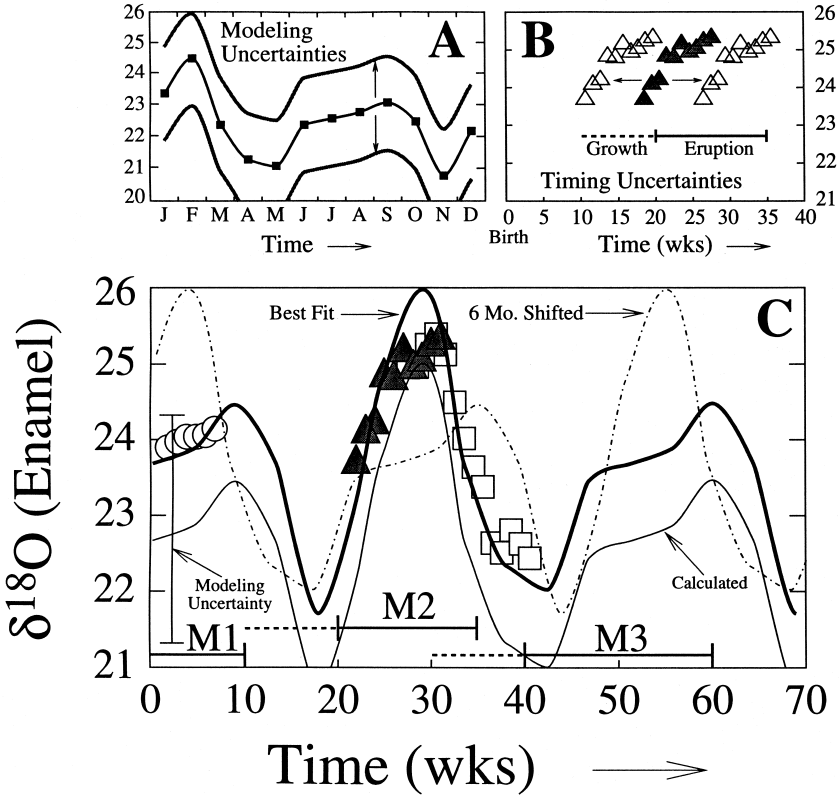

Fig. 5. Effects of uncertainties in placement of theoretical models and measured data, and best-fit match of models and data. Note different composition and time scales. (A) Theoretical models can be shifted up or down in composition by 1–2‰, but not distorted or shifted in time. (B) Example of how measured data for M2 can be shifted in time. The solid tooth formation bar is based on the observed range of tooth eruption times. Teeth may continue to mineralize during eruption, but must be completely formed by the end of eruption. Dashes account for 10 weeks of initial mineralization prior to eruption. (C) Comparison of measured data for Nairobi gazelle-2 with the theoretical model for seasonal changes of gazelle enamel $\delta^{18}O$ in the Nairobi area. Temporal scaling of data (2 mm enamel produced per week) was based on M3 measurements, assuming that the M3 compositional wavelength reflects a partial seasonal isotope signal. The thin solid line is the independent prediction of gazelle tooth enamel composition from Fig. 4; the thick solid line is the same curve shifted upward by ~1‰ to better match the measured compositions. The dash–dot curve shows the expected compositions for an alternative December birth.

gests that the M3 molar started to grow in ~January and was fully formed by late April or early May (Figs. 4 and 5). For a total apparent growth period of 14 ± 2 weeks for this molar and an enamel length of 27 mm, on average 1.9 ± 0.3 mm of enamel per week is produced. This rate is somewhat faster than has been empirically determined by Fricke and O'Neil (1996) from the isotope zoning of teeth from wild bison (~0.8 mm/week) and domestic sheep (~0.4 mm/week).

For the gazelle M1 and M2, a constant rate of enamel production of ~2 mm per week implies total formation times of ~1 1/2 months (M1) and ~3 months (M2). From these durations and the known general times of tooth eruption, and assuming that the high $\delta^{18}O$ values observed for M2 and M3 correspond to a February dry season, the most likely birth time of the gazelle is identified as June or July, which also corresponds to the major narrow birth peak. Assuming a July birth is correct, the predicted seasonal signal and the tooth formation times were then plotted (thin solid curve and tooth formation bars in Fig. 5C). Finally, the measured data for each tooth were shifted in time (but not composition) within the limits imposed by the tooth formation periods, and the theoretical model was adjusted in composition (but not time) within modeling uncertainties to maximize the quality of fit between data and model (thick solid curve). We reiterate that the intention in this analysis is not to independently derive a detailed, accurate seasonal curve based on the tooth compositions. Such an attempt would be unadvisedly speculative given the uncertainties in the timing of tooth mineralization, actual meteoric water compositions, and modeling. Rather, the intent was to see whether the isotope zoning data were consistent with the hypothesis that tooth enamel encodes seasonal variations in its $\delta^{18}O$ values, within the stated uncertainties of the model compositions and tooth eruption times.

Within uncertainty, the data (symbols, Fig. 5C) can be reconciled quite well with a seasonal model (thick solid line, Fig. 5C). There is consistent offset of ~1‰ between the data and the independent theoretical model (thin solid line), but this is within the modeling uncertainties ($\pm$1–2‰; Kohn, 1996; Fig. 5A), and could be caused by errors in assumptions about either gazelle physiology or meteoric water compositions. An offset between predicted and measured compositions of similar magnitude and direction was also found for gazelles in the Lake Turkana area. The similarity of the model predictions to both the measured shapes of the composition trends and the relative differences between months supports the hypothesis that teeth preserve a compositional record of seasonality. Growth of M2 and M3 probably occurred at 25–37 and 34–48 weeks after birth respectively, whereas M1 likely formed relatively early, prior to 10 weeks.

A significantly different birth time is more difficult to reconcile with the data. The only reasonable alternative birth peak is in November–January, which implies a seasonal isotope variation corresponding to the dash–dot curve in Fig. 5C. The magnitudes and rates of composition changes in M3 and M2 and the compositional homogeneity of M1 are less consistent with this alternative birth-time hypothesis.

Interestingly, the measured isotope compositions do not quite reach the highest $\delta^{18}O$ values predicted by the model (for February). The models incorporate month-to-month meteorological data that were averaged over 22 years. The ~1‰ discrepancy during February (~30 weeks after birth) could simply reflect a difference in the February weather during the specific year in which the gazelle was growing M3 compared to the 22 year average. For example, a slightly rainier February that year would likely depress meteoric $\delta^{18}O$ and increase humidity, decreasing plant and enamel $\delta^{18}O$.

Because fewer analyses were possible for the Turkana zebra, interpretation of its isotope trend is necessarily less specific. The data for the Nairobi gazelle and the late timing of M3 formation in zebras supports a seasonal signal to the isotope zoning in the zebra molar. The increase in $\delta^{18}O$ during M3 growth may correspond to a shift from the low $\delta^{18}O$ wet season (either April–May, or November) to the high $\delta^{18}O$ dry season (June–September or December–January). That is, the period sampled probably spans 3–6 months. Because final production of enamel and eruption for M3 teeth varies by as much as 2 years in equids (Levine, 1982), it is not possible to relate the isotope shift temporally to the known zebra birthing peak, and hence to more specific wet and dry seasons. Based on crown height measurements, the zebra was at least 10 years old, and over

half its tooth must have been worn away (Spinage, 1972). Analysis of younger equids with less worn teeth could potentially allow an entire year's seasonal signal to be extracted (Bryant et al., 1996a,b).

6.4. Developmental physiology

An alternative explanation for the isotope differences observed among M1, M2, and M3 teeth involves developmental changes in diet, metabolism, or water turnover. Such changes occurring in the first year include a shift from milk as the predominant food source to vegetation, a decrease in water turnover, and a decrease in metabolic rate. Data for different animal classes and orders suggest that the decrease in water turnover occurs more quickly than the decrease in metabolic rate (e.g., data in Macfarlane and Howard, 1972; data in Schoeller, 1988; Williams et al., 1993). The modeling approach of Kohn (1996) can be used to explore the isotope effects of ontogenetic changes in both diet and water turnover (Fig. 6).

Models of ontogenetic dietary changes from milk to plant consumption were constructed by assuming a typical milk composition as the major food and water source, with a $\delta^{18}O$ appropriate to its derivation from a mature parent, and a sufficient increase in water turnover to account for the high water content of the ingested milk (85%). It is not clear how the extra water intake is subsequently expelled from the young gazelle, but we assume it is in liquid (urine or moister feces) rather than vapor form. Vapor loss would cause substantial cooling, which would in turn cause energy balance problems. For these assumptions, the $\delta^{18}O$ of a newborn nursing gazelle is predicted to be not more than 0.5‰ lower than an adult (Fig. 6A and B, at 0 weeks). Given the uncertainties in the theoretical calculations (± 1–2‰), this difference is not statistically significant. Such a compositional difference should also decrease rapidly with age, as many wild herbivores progressively substitute plants for milk starting almost immediately after birth.

Models of ontogenetic decreases in the ratio of water turnover to metabolic rate as an animal matures were also constructed, but are again complicated by an imperfect knowledge of how the additional water is gained and lost in a juvenile. The most likely process is that younger animals eat more but either digest less than adults or are less capable of salt concentration, so that they obtain more water from plants but lose more as liquid in their feces and/or urine. If so, a juvenile gazelle is predicted to have an isotope composition ~ 0.5‰ higher than an adult (Fig. 6A and B, at ~ 15 weeks). Although this result is again statistically indistinguishable from the composition of an adult, it is interesting that the two ontogenetic effects most readily identified in young animals (nursing and changes in the ratio of water turnover to metabolism) may well compensate for each other isotopically.

It is probably not justified to estimate isotope variations during the early life of a gazelle by com-

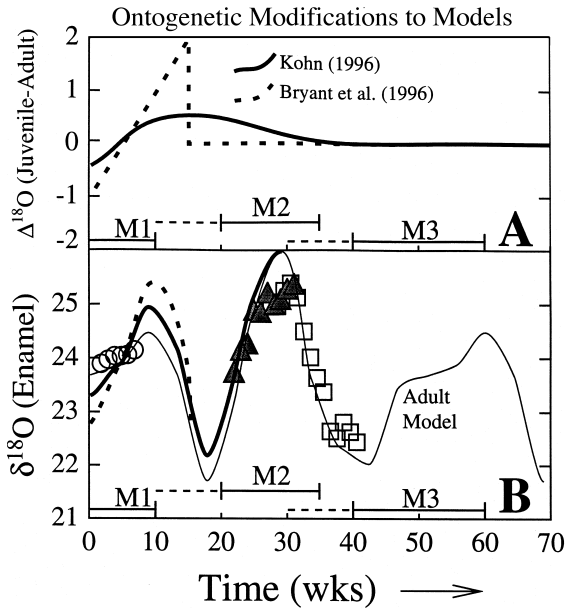

Fig. 6. Effects of ontogenetic models on predicted isotope trends. (A) Predicted deviation between juvenile and adult gazelle, using models developed in this study (based on the approach of Kohn, 1996) and the model of Bryant et al. (1996b). Both models predict an initial depletion in neonate gazelle ^{18}O followed by an enrichment as the animal progressively consumes more plants and less milk, but the magnitude of the isotope effect is greater in the Bryant et al. (1996b) model and changes more suddenly. The predicted compositional differences are much smaller than the uncertainties in the models themselves. (B) Combining ontogenetic and seasonal models (thick solid and dashed lines) substantially degrades the quality of fit between models and data for M1, although the average predicted composition for M1 remains the same.

bining ontogenetic models for juveniles with seasonal models for adults, because the large uncertainties in the models overwhelm the small modifications to predicted trends. Nonetheless, combined models with maximized isotope effects (Fig. 6B) indicate no change in average $\delta^{18}O$ of young gazelles in East Africa, but do suggest a more rapid change of isotope composition than predicted for adults. This modified trend is not supported by the measurements, and the disparity could reflect either deficiencies in the models or possibly a very different seasonal signal in East Africa during the months the gazelle was maturing compared to the 22-year averaged seasonal signals.

In comparison to these results, the models of Bryant et al. (1996b) for horses (Fig. 6A) predict that neonate foals should have a $\delta^{18}O \sim 1‰$ lower than mares, similar to but larger than our estimate of the compositional differences between nursing gazelles and their parents. Bryant et al. (1996b) further predict that foal $\delta^{18}O$ increases relative to adults until weaning, at which time foal $\delta^{18}O$ abruptly drops by nearly 2‰ onto the adult trend. That is, their predicted trends are similar to but larger than our models discussed above. Combining their predicted isotope effects of ontogeny for horses with our adult gazelle models causes an even greater disparity between models and measurements (Fig. 6B). Clearly, differing model assumptions about developmental physiology have yielded disparate isotope models that poorly reflect the few extant measured data. Predictive accuracy will only be improved with additional detailed physiological information on water turnover and energy expenditure in developing animals.

Can ontogenetic dietary changes cause significant isotope shifts? Our models do imply that such shifts might attain 0.5‰, but because this value falls within modeling uncertainties, and because simultaneous changes in physiology during development may have compensating isotope effects, it is unclear whether any isotope difference between immature and adult animals is expected. Until much more sensitive studies are conducted, estimation of the actual shifts attending physiological development is necessarily indefinite. Even given this uncertainty, the fact that seasonal variations already account for all measured compositional changes implicates seasonality as the most important cause of the observed isotope systematics. Furthermore, our data for the gazelle M1 molar, which should have formed while the gazelle was still consuming milk, has an isotope trend that is completely consistent with that predicted for an adult. Thus, at present there does not appear to be any reason to ascribe observed isotope variations to ontogenetic effects.

7. Conclusions

As suggested for East African herbivores (this study) as well as for sheep, bison, and equids (Bryant et al., 1996a,b; Fricke and O'Neil, 1996) compositional differences are substantial for different teeth in the same jaw and within a single tooth. For East African herbivores these inter- and intratooth variations approach 4‰. Despite this variability, comparisons of the same tooth from different individuals suggest that compositions can be internally consistent to $\pm 0.2–0.3‰$. This consistency among individuals and the consistency of isotope trends among genera suggests that similarly aged individuals of the same genus have similar compositions. Sampling care concerning tooth identity and location will be required for any quantitative paleoclimate research using fossil teeth, but conversely more detailed interpretation concerning seasonality is possible.

Overall, seasonality rather than developmental physiology seems the most likely explanation for the tooth composition differences. In East Africa, the 1–3‰ temporal trends towards higher and lower $\delta^{18}O$ for gazelle, dikdik, and zebra can be explained by seasonal shifts from the lower $\delta^{18}O$ wet seasons to the higher $\delta^{18}O$ dry seasons. Detailed comparison of measured data to theoretical seasonality models for the Nairobi area demonstrates that the observed gazelle enamel $\delta^{18}O$ trends can be reconciled with the predicted seasonal changes of animal isotope compositions quite precisely. There is little indication from the measurements that the composition of gazelle M1 is strongly affected by nursing or changes in water turnover. This conclusion is consistent with models of nursing gazelles, which within modeling uncertainties resolve no difference between juvenile and adult $\delta^{18}O$. Any compositional difference should also rapidly diminish as the young gazelle progres-

sively increases plant consumption, and by the time M1 formation is complete, milk is probably a less important part of the young gazelle's diet. Ontogenetic changes in water turnover are also predicted to have a small effect on isotope compositions.

Animal compositions do not simply track either surface water or plant compositions, but rather contain components of both signals. Knowledge of animal physiology and modeling of genus-specific oxygen isotope mass balance (e.g., Kohn, 1996) is required to identify those genera with the greatest sensitivities to plant and surface water compositions, which in turn reflect contributions from seasonal rainfall and humidity. Once the dependence of animal oxygen isotope compositions on present day climate is verified through both modeling and measurements, as was done in East Africa, then analysis of the isotope composition of fossils of these same genera within the geologic record should allow quantitative determination of past changes of surface water composition, humidity, and seasonality.

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