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ORIGINAL PAPER

Elevated $\delta^{15}N$ values in mammoths: a comparison with modern elephants

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Abstract The extinct Pleistocene woolly mammoth bone collagen shows compared with collagen from other contemporaneous large herbivores remarkably high $\delta^{15}N$ values. In order to investigate if the observed discrepancy in $\delta^{15}N$ values between Pleistocene woolly mammoths and coeval large ungulates also exists in modern relatives, we investigated the $\delta^{15}N$ (and $\delta^{13}C$) values in nails of modern proboscideans, rhinoceroses and horses kept in captivity and with a comparable forage. The results of this study show that the nails of the different modern herbivores, supplied with similar diet, have more or less identical $\delta^{15}N$ values, so elephants do not show higher $\delta^{15}N$ values. How to explain the high values in Pleistocene mammoths? Two different options will be discussed.

Keywords Stable nitrogen isotope · Large herbivores · Pleistocene · Controlled feeding

Introduction

Stable isotopes are a powerful tool for archaeologists and ecologists. Depending on which stable isotope is investigated, different kinds of information can be provided. For instance, the $\delta^{13}C$ value informs us about the vegetation consumed, in particular the ratio of C_3 to C_4 plants. Factors that determine the $\delta^{15}N$ value include the trophic level of an organism, the environment (e.g. marine vs. terrestrial) and the diet (e.g. specific plants or plant parts consumed and protein quality) (e.g. Schöninger and Moore 1992; Koch 2007; Gannes et al. 1998; Clementz et al. 2009; Sponheimer et al. 2003; Fox-Dobbs et al. 2008).

The $\delta^{15}N$ value is enriched by about 3 ‰ for each trophic level shift. This means that the bone collagen of an herbivore is enriched in ^{15}N relative to ^{14}N in comparison with the amount of ^{15}N and ^{14}N originally present in the plants consumed, and carnivores have higher $\delta^{15}N$ values than herbivores (Schöninger and Moore 1992; Sealy 2001; Gannes et al. 1998).

However, woolly mammoths (*Mammuthus primigenius*) show a remarkably high $\delta^{15}N$ value in their bone collagen compared with other contemporaneous Pleistocene large herbivores. The $\delta^{15}N$ value is on average about 3 ‰ higher in mammoths than in horses (*Equus* sp.) and rhinoceroses (*Coelodonta antiquus*) (Bocherens 2003; Fox-Dobbs et al. 2008), despite the fact that these animals lived in the same mammoth steppe environments and were all non-ruminant hindgut fermenters. If one would apply the simple trophic level shift theory of $\delta^{15}N$ values, mammoths mistakenly could give the impression of being carnivores. This phenomenon is not the result of a regional effect; a comparable pattern manifests in Europe (Bocherens et al. 1997), Siberia (Bocherens et al. 1996) and Alaska (Bocherens et al. 1994; Bocherens 2003). Although the $\delta^{15}N$ value of mammoths, horses and rhinoceroses varies according to time and region, a discrepancy between the $\delta^{15}N$ values of mammoths and other coeval herbivores remains visible (Bocherens 2003; Bocherens et al. 2011).

In the literature, several possible factors are proposed to explain increased $\delta^{15}N$ values in herbivore body tissues. Amongst these, the aspect of physiological adaptations to handle water and food shortage (e.g. Heaton et al. 1986; Ambrose and DeNiro 1986) or difference in diet, e.g. due to different $\delta^{15}N$ values in vegetation between dry and wet

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environments (Murphy and Bowman 2006; Hartman 2010); feeding on specific plant species or plant parts, e.g. grazing vs. browsing (Sealy et al. 1987; Ambrose 1991) and coprophagy (van Geel et al. 2011; Clementz et al. 2009) are often mentioned. The exact factors determining the high $\delta^{15}N$ values in mammoths are still not understood.

If it is true that the $\delta^{15}N$ values in mammoth bones are higher than in bones of contemporaneous living other large herbivores because of either a physiological adaptation of mammoths to overcome periods of food and water shortage, or by differences in nitrogen content of the diet of the various herbivore species, then one would expect that the $\delta^{15}N$ values of mammoths and other herbivores would be similar in a controlled situation where all animals have a comparable diet and always get all dietary components they need. Controlled feeding studies can provide insight in processes of the stable isotope pathway and, therefore, in the impact of different potential factors on the stable isotope ratio (e.g. Sponheimer et al. 2003; Fuller et al. 2005).

Needless to say, a controlled feeding study would be impossible for woolly mammoths. However, their modern relatives might be appropriate to be subject of a controlled feeding study. Ambrose and DeNiro (1986) showed that the $\delta^{15}N$ value in collagen of an East African elephant (10.6 ‰) is enriched relative to other ungulates which are obligate drinkers and is almost as high as the $\delta^{15}N$ values of the carnivorous species. This pattern shows similarities to that observed in Pleistocene herbivores inhabiting the mammoth steppe environment. In order to get information about the $\delta^{15}N$ values in modern elephantids and other large herbivores living under controlled conditions, stable $\delta^{15}N$ values from modern Indian and African elephants, Indian and white Rhinoceroses and several equids are investigated.

Material and methods

For our investigation, it is important that certain conditions of the animals under study are known and similar, in particular the feeding pattern and the climatological circumstances. Animals living in zoos are obvious sources to sample, since the diets of these animals are well-known and strictly complied with. Many of the stable nitrogen and carbon isotope values of the Pleistocene mammoth, horse and rhinoceros have been measured in bone collagen. Therefore, the initial goal was to measure the $\delta^{13}C$ and $\delta^{15}N$ values of the modern elephant, rhinoceros and horse in bone collagen as well. However, despite the abundant collection of bones of deceased animals from Dutch zoos at the Faculty of Veterinary Science of the University of Utrecht, these bones appeared to be not the best material for measuring stable nitrogen and carbon isotope values because the bones had been all treated with aggressive chemicals to remove associated soft tissues. The treatment affected the collagen and stable isotope ratios.

Turnover time for bones is different than for tissues such as nail and hair. In general, however, the patterns of stable nitrogen and carbon isotope values which are found in bone collagen are comparable with those found in other body tissues such as nail, hair and skin (Sponheimer et al. 2003). Although there might be some enrichment or depletion between the values of nail and bone (O'Connell et al. 2001), the patterns are similar. Since the nails of horses, elephants and rhinoceroses living in captivity have to be trimmed regularly, nails turned out to be an efficient sample material for this study. One has to consider, however, that at the same time of the trimming of the hooves and nails, parts of the dermal tissue associated with the sole of the foot of the animal are removed as well. So in fact, the 'nail' samples are a mixture of keratin and dermis, but in this study, they are regarded and treated as all being nail keratin.

In 2008, samples from the hoofs and nails of 20 equids (*Equus caballus*, *Equus quagga boehmi*, *Equus ferus przewalskii*), six rhinoceroses (*Ceratotherium simum* and *Rhinoceros unicornis*) and 13 elephants (*Elephas maximus* and *Loxodonta africana*) were collected from several Dutch zoos, riding schools and a horse smith. An overview of the samples is given in Table 1.

The diets of these animals are similar in general composition. The most important ingredient of the diets of the elephants, rhinoceroses and horses is fresh grass and hay. Animals living in the same zoo are fed the same hay and/or grass, but the composition of the hay used might differ slightly between zoos. The elephants and rhinoceroses also eat some fruit, vegetables and sometimes branches. Some additional food is special horse or pachyderm pellets which contain nutrients such as proteins and vitamins (Table 2).

The sample preparation and isotope analysis were performed at the Centre for Isotope Research, Groningen University. Each nail sample was cut into pieces varying from 0.5 to 4.0 cm and after that soaked in a solution of 10 % HCl to get rid of carbonates, phosphates and other contaminants. After being rinsed to pH neutral in dH_2O, the samples dried in a stove at a temperature of 100 °C o/n.

The $\delta^{15}N$ values are measured in duplicate. For each measurement, 1.20 mg of sample material was required. To measure the $\delta^{13}C$ value, 5 mg sample material was extracted from each sample. The measurement is executed by an elemental analyzer/isotope ratio mass spectrometer.

Results

All samples yielded both a $\delta^{13}C$ and $\delta^{15}N$ value, as shown in Table 1. In this table, the atomic C/N ratios

Table 1 Stable isotope ($\delta^{13}C$ and $\delta^{15}N$) and C/N ratios of nails and hoofs for all animals investigated

Source	Species	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C/N
Zoo C	*Elephas maximus*	−26.92	5.30	*4.50*
Zoo B	*Elephas maximus*	−26.85	7.94	3.97
Zoo B	*Elephas maximus*	−26.44	8.04	3.82
Zoo B	*Elephas maximus*	−26.07	7.95	3.55
Zoo A	*Elephas maximus*	−25.96	6.65	3.29
Zoo A	*Elephas maximus*	−26.48	6.40	*4.54*
Zoo A	*Elephas maximus*	−26.14	6.89	*5.76*
Zoo A	*Elephas maximus*	−26.20	6.61	*4.14*
Zoo A	*Elephas maximus*	−26.88	6.66	*4.83*
Zoo A	*Elephas maximus*	−27.03	6.52	*4.55*
Zoo B	*Elephas maximus*	−26.65	7.67	*4.15*
Zoo B	*Elephas maximus*	−26.20	7.80	*4.50*
Zoo A	*Elephas maximus*	−27.11	6.15	*4.49*
Zoo A	*Elephas maximus*	−26.29	6.19	*4.01*
Zoo A	*Elephas maximus*	−25.66	6.54	3.48
Zoo A	*Elephas maximus*	−25.89	7.01	3.85
Zoo A	*Elephas maximus*	−26.17	6.36	*4.38*
Zoo A	*Elephas maximus*	−26.35	6.71	*4.49*
Zoo C	*Elephas maximus*	−27.22	5.96	*4.49*
Zoo F	*Elephas maximus*	−26.91	5.81	*4.20*
Zoo F	*Elephas maximus*	−26.02	5.92	*4.26*
Zoo D	*Loxodonta africana*	−25.75	5.98	*4.70*
Riding school J	*Equus caballus*	−25.86	7.42	3.44
Riding school K	*Equus caballus*	−25.49	7.61	3.36
Riding school G	*Equus caballus*	−25.57	7.30	3.86
Riding school G	*Equus caballus*	−26.41	7.75	3.37
Riding school G	*Equus caballus*	−25.27	7.56	3.66
Riding school G	*Equus caballus*	−26.01	7.47	3.56
Horse smith H	*Equus caballus*	−26.88	8.09	3.34
Horse smith I	*Equus caballus*	−24.96	6.90	3.43
Horse smith I	*Equus caballus*	−23.68	7.75	3.50
Riding school G	*Equus caballus*	−25.96	7.53	*4.07*
Riding school G	*Equus caballus*	−25.15	8.24	3.36
Riding school G	*Equus caballus*	−25.91	6.81	3.27
Riding school G	*Equus caballus*	−26.17	9.81	3.44
Riding school G	*Equus caballus*	−26.58	7.63	3.60
Riding school G	*Equus caballus*	−25.82	8.39	3.63
Riding school G	*Equus caballus*	−26.68	7.48	3.61
Riding school G	*Equus caballus*	−26.06	7.30	3.62
Zoo D	*Equus ferus przewalskii*	−26.05	7.77	3.29
Zoo A	*Equus quagga boehmi*	−26.27	5.83	3.73
Zoo A	*Equus quagga boehmi*	−26.16	5.61	3.38
Zoo D	*Ceratotherium simum*	−23.00	6.30	3.42
Zoo A	*Ceratotherium simum*	−26.04	6.33	3.19
Zoo A	*Ceratotherium simum*	−26.82	5.93	3.37
Zoo A	*Ceratotherium simum*	−25.54	6.57	3.60
Zoo B	*Rhinoceros unicornis*	−25.22	7.12	3.22
Zoo C	*Rhinoceros unicornis*	−25.47	5.56	3.43

Relatively high C/N ratios (>4.00) are shown in italic. In order to stay anonymous, the different sources (zoos, riding schools, horse smith) are indicated with a letter (A–K)

are given too. A nail should generally have a C/N ratio of about 3.4 (O'Connell and Hedges 1999; O'Connell et al. 2001). The mean C/N ratios for rhinoceros and horse are 3.37 and 3.53, respectively; many elephants,

Table 2 Contents of special horse or pachyderm pellets which contain nutrients such as proteins and vitamins

	Zoo A (horse 0.5♀/1♂ kg/day)	Zoo A (elephant 5♀/8–10♂ kg/day) (rhinoceros 6 kg/day)	Zoo B (elephant 4 kg/day)	Zoo B (rhinoceros 4 kg/day)	Zoo C (elephant 2 kg/day)	Zoo C (rhinoceros 3 kg/day)	Zoo D (elephant 4 kg/day)	Zoo D (rhinoceros 4 kg/day)	Riding school E (horse 2–6 kg/day)
Protein	7.5 %			8.5 %	9.65 %	14.56 %			
Crude protein	10.7 %	15 %	166.38 g/kg	11.7 %			11.9 %	16.0 %	15.0 %
Crude fat	2.5 %	7.8 %	44.89 g/kg	4.5 %	3.02 %	3.90 %	2.8 %	5 %	4.0 %
Crude fibre	9.0 %	10 %	101.17 g/kg	4.5 %			9.1 %	9 %	5.5 %
Crude ash	7.2 %	13 %	134.03 g/kg	8.0 %	10.52 %	8.00 %	6.9 %	14 %	8.5 %
Ca	9.0 g/kg	1.5 %	15 g/kg	10.0 g/kg	0.59 %	0.73 %	10.0 %	1.62 %	1.37 %
P	4.0 g/kg	0.5 %	3.26+6.5 g/kg	4.7 g/kg	0.26 %	0.49 %	5.1 %	0.65 %	0.55 %
Mg	3.7 g/kg		3.98 g/kg	4.3 g/kg			2.9 g/kg	0.40 %	0.48 %
Na	4.1 g/kg		18 g/kg	7.3 g/kg			4.1 g/kg	1.77 %	0.45 %
Vit A	14,200 IU/kg	32,000 IU	30,000 IU/kg	18,800 IU/kg	2.25 IU/g	9.97 IU/g	14,000 IU/kg	30,000 IU/kg	28,000 IU/kg
Vit D3	2,525 IU/kg	7,400 IU	6,000 IU/kg	3,325 IU/kg	0.42 IU/g	2.23 IU/g	2,000 IU/kg	6,000 IU/kg	4,200 IU/kg
Vit E	150 mg/kg	400 mg/kg	500 mg/kg	500 mg/kg	161.32 IU/kg	166.31 IU/kg	150 IU/kg	195 mg/kg	200 mg/kg
Biotine (mcg/kg)	760	5,000	5,000	1,000			200	1,250	940
Cu (mg/kg)	25		9.98	33			30	10	150

however, have remarkably high C/N ratios (between 3.29 and 5.76) with a mean C/N ratio of 4.27. All samples have been included in the analyses. Those with C/N ratios higher than 4.00 are shown in Table 1 in italic.

Figure 1 shows that the mean $\delta^{13}C$ values of the elephants (−26.41 ‰), horses (−25.85 ‰) and rhinoceroses (−25.35 ‰) are quite similar. However, the extent of the range of $\delta^{13}C$ values of each animal group does differ: The elephants have a range of 1.32 ‰, whilst the rhinoceroses and the horses have a range of 3.82 ‰ and 3.20 ‰, respectively.

The mean $\delta^{15}N$ values for different species are quite similar: elephants 6.64 ‰, horses 7.51 ‰ and rhinoceroses 6.30 ‰. As for $\delta^{13}C$ values, the ranges of the $\delta^{15}N$ values for the different animal groups vary considerably. The horses cover a range of 4.20 ‰, the elephants 2.31 ‰ and the rhinoceroses only 1.55 ‰. The values of the different animal groups (elephant, rhinoceros and horse) are clustered. The $\delta^{15}N$ and $\delta^{13}C$ values of the rhinoceroses and elephants do not differ significantly. The $\delta^{15}N$ and $\delta^{13}C$ values for the horses differ from the elephants and rhinoceroses, according to the Mann–Whitney statistics test. A much larger sample would be needed to fully quantify our experiment.

Discussion and conclusions

The $\delta^{15}N$ values of elephant, horse and rhino living in Dutch zoos are quite similar. So, in a situation where all animals get roughly the same diet providing all nutritional components they need, the $\delta^{15}N$ values of elephants are not elevated relative to those of other large herbivores. How to explain the relative high $\delta^{15}N$ values in woolly mammoths? Differences in diet and different physiological adaptations might cause the observed discrepancies.

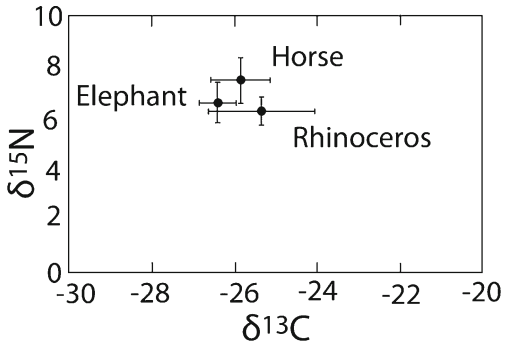

Fig. 1 Modern captive elephants have, in contrast to Pleistocene mammoths, $\delta^{15}N$ values similar to other herbivores

Diet

Animals obtain nitrogen by consuming plants or, indirectly, by consuming herbivorous species. Drought, marine environments, salinity and high grazing pressure cause relative high $\delta^{15}N$ values in plants (e.g. Britton et al. 2008; Bocherens 2003). It is also known that grasses and sedges have higher $\delta^{15}N$ values than shrubs. The values in trees are even lower than those in shrubs (Bocherens 2003; Fox-Dobbs et al. 2008). Several studies on fossil mammoth dung and on stomach contents of well-preserved mammoths showed that the diet of mammoths consisted predominantly of grass (Ukraintseva 1993; Agenbroad 2005; van Geel et al. 2008; Guthrie 1990), the major component of the vegetation of the mammoth steppe. Therefore, it is to be expected that mammoth bones show relative high $\delta^{15}N$ values.

However, this applies not only to mammoths but also to some other herbivores that lived on the mammoth steppe. Several botanical analyses on stomach contents of carcasses found in the permafrost and in molar cusps indicate that the diets of woolly mammoth, horse and woolly rhinoceros were quite similar and that these species should be considered as grazing specialists predominantly feeding on grasses, but with small amounts of browsing (Guthrie 1990, 2001; Vereshchagin and Baryshnikov 1982; Ukraintseva 1993; Boeskorov et al. 2011). Based on these results, a difference in diet between Pleistocene horse, woolly mammoth and woolly rhinoceros does not seem to be the major trigger for the discrepancy in $\delta^{15}N$ values between woolly mammoth and the other species. However, in modern terrestrial ecosystems, the cohabitation of species with similar dietary habits (e.g. monogastric large herbivores in the present case) leads to niche differentiation to avoid competition. Did the mammoth steppe diverge from this general rule in modern ecosystems?

In contrast to the studies mentioned in the part above, the results of various recent studies based on dental wear patterns (e.g. Rivals et al. 2010) and stable isotope measurements (Fox-Dobbs et al. 2008; Bocherens et al. 2011) indicate diversity amongst diets of Pleistocene large herbivores, especially between time and regions, and show that recourse partitioning really existed within the mammoth steppe (Fox-Dobbs et al. 2008; Bocherens et al. 2011). These studies make dietary variance as major cause for the discrepancy in $\delta^{15}N$ values between woolly mammoth and the other ungulates more plausible. These results do not explain, however, why the discrepancy in $\delta^{15}N$ values between woolly mammoths and rhinoceroses and horses is larger than the divergence in $\delta^{15}N$ values between for instance horses and rhinoceroses.

Physiology

Besides dietary variety, a possible explanation for the discrepancy in $\delta^{15}N$ values might be related to digestion

coefficiency of the animals. Water uptake and excretion patterns in the modern horse, rhinoceros and elephant are similar (Clauss et al. 2005). The animals are all obligate drinkers (Ambrose 1991; Ambrose and DeNiro 1986; Sealy et al. 1987). Furthermore, the digestive system of horses, rhinoceroses and elephants is quite comparable (Wittemyer et al. 2009; Sealy et al. 1987; Sponheimer et al. 2003). However, there are some physiological dissimilarities amongst these animals. Elephants in particular differ in some respects. Amongst others, the digestive tract of elephants is relatively much shorter compared to that of other herbivores (Clauss et al. 2007). This causes considerably lower digestion efficiency for the elephant when compared to horse and rhinoceros (Clauss et al. 2005; Clauss and Hummel 2005). For elephants, the time during which the food consumed is digested ('ingesta retention time') is short due to their relatively short digestive tract. In general, the digestive tract, and therefore ingesta retention time, increases with increasing body size: Food needs more time to pass through a longer digestive tract (Olivier 1982; Clauss and Hummel 2005).

Since rhinoceroses have a much larger body and longer ingesta retention time than horses, they can achieve similar digestion coefficients as horses (Clauss et al. 2005; Clauss and Hummel 2005). In contrast, although the elephant's body is much bigger than that of a horse, the digesta retention time of elephants is similar to that of horses (Clauss et al. 2005; Clauss and Hummel 2005). Therefore, elephants have lower digestion coefficients than horses and rhinoceroses: The percentage of ingested food that is excreted in faeces is high relative to the part of food that is digested and absorbed (Clauss and Hummel 2005; Martin 1982).

Due to this digestive inefficiency, in times of food scarcity, elephantids might have to rely, more than horses and rhinoceroses, on the recycling of their own nitrogen resources, leading to increased $\delta^{15}N$ values in elephantids. Due to seasonal fluctuations, mammoths must have been subject to food scarcity during their lifetime for several times, but since the mammoth has been a successful species during thousands of years, they must have had access to enough nutrients during most of the year. Whether the $\delta^{15}N$ enrichment in tissues is (only) the result of a temporal increase of $\delta^{15}N$ values that is 'strong' enough to be reflected in bone collagen with a turnover time of years is doubtful.

Another possible explanation for enriched $\delta^{15}N$ values in mammoths, related to both diet and digestive inefficiency, is coprophagy (van Geel et al. 2008, 2011; Clementz et al. 2009). Investigations by van Geel et al. (2011) on frozen mammoth dung from Alaska indicated that coprophagy (faecal consumption), which leads to $\delta^{15}N$ enrichment, might have been a routine amongst woolly mammoths because the dung contained many fruit bodies of coprophilous fungi. Since dung is enriched in ^{15}N values relative to the original food, coprophagy leads to enriched $\delta^{15}N$ values in body tissues.

From the zoos which provided the sample material of the elephants in the current study, it is known that the young elephants occasionally eat dung, mainly from their mother as well as from other elephants of their group. The nail samples come from adult elephants that had never been observed eating any dung at an advanced age. Therefore, coprophagy was not a consideration in the analysis.

The results of the present investigation do not explain the discrepancy of $\delta^{15}N$ values between Pleistocene herbivores, however indicate that the three options (diet, physiology, as well as coprophagy) are possible. Captive elephantids, rhinoceroses and horses, which do not have to cope with competition for sources and niche partitioning leading to dietary differences nor have to rely on their own nitrogen recourses due to nutritional stress, show similar $\delta^{15}N$ values.

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