THE ROYAL SOCIETY

Dietary change and stable isotopes: a model of growth and dormancy in cave bears

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In order to discuss dietary change over time by the use of stable isotopes, it is necessary to sort out the underlying processes in isotopic variation. Together with the dietary signal other processes have been investigated, namely metabolic processes, collagen turnover and physical growth. However, growth and collagen turnover time have so far been neglected in dietary reconstruction based on stable isotopes. An earlier study suggested that cave bears (*Ursus spelaeus*) probably gave birth to cubs during dormancy. We provide an estimate of the effect on stable isotopes of growth and metabolism and discuss collagen turnover in a population of cave bears. Based on a quantitative model, we hypothesized that bear cubs lactated their mothers during their first and second winters, but were fed solid food together with lactation during their first summer. This demonstrates the need to include physical growth, metabolism and collagen turnover in dietary reconstruction. Whereas the effects of diet and metabolism are due to fractionation, growth and collagen turnover are dilution processes.

Keywords: stable isotopes; dietary change; dormancy; growth; collagen turnover; lactation

1. INTRODUCTION

Stable carbon and nitrogen isotopes have been used for dietary reconstructions in a variety of different applications, e.g. between and within ecological communities, between and within populations and between individuals (e.g. DeNiro & Epstein 1978; Ambrose & DeNiro 1986; Peterson & Fry 1987; Van der Merwe *et al*. 1990; Vogel *et al*. 1990; Welch & Parson 1993; Angerbjörn *et al*. 1994). There are also studies on isotopic differences within an individual (e.g. Sealy *et al*. 1995). However, in order to identify dietary changes over time between and within individuals by the use of stable isotopes, it is necessary to sort out the processes that can alter the isotopic records. Together with the dietary signal other processes have been investigated, namely metabolic processes (Ambrose 1986, 1991; Ambrose & DeNiro 1986; White & Armelagos 1997; Nelson *et al*. 1998), collagen turnover (Libby *et al*. 1964; Harkness & Walton 1972; Tieszen *et al*. 1983) and growth (Koch *et al*. 1994; Sealy *et al*. 1995).

Metabolic processes such as hibernation, dormancy and starvation (i.e. catabolic processes) can affect both carbon and nitrogen values (Sealy *et al*. 1987; Nelson *et al*. 1998), whereas others will only affect nitrogen (Ambrose 1986, 1991; Ambrose & DeNiro 1986; White & Armelagos 1997). Herbivores in arid areas, for example, have higher δ^{15}N values than herbivores in regions with high rainfall. Ambrose & DeNiro (1986) explained this as an increased urea concentration in water-stressed animals.

In an earlier study (Nelson *et al*. 1998), we discussed cave bears (*Ursus spelaeus* Rosenmüller & Heinroth, 1794) behaving like all their close recent relatives, i.e. going through winter dormancy, giving birth and lactating their offspring during this dormancy. The anomalous isotope values thus obtained in young cave bears probably originated from the specific metabolic circumstances during their neonatal and pre-weaning period while going through dormancy. Since bears, in comparison to other terrestrial mammals, have an exceptionally long lactation period (Oftedal & Gittleman 1989) the adult isotopic value contrasts strongly to that of juvenile individuals. However, changes in isotopic values due to diet or metabolism will also be affected by dilution processes such as growth and collagen turnover.

Although Koch *et al*. (1994) and Sealy *et al*. (1995) mentioned growth as a factor that would influence isotopic values, there is no discussion on how big this effect could be. When growing individuals are included in an analysis, neglecting growth might give the wrong dietary interpretation.

However, dietary signals from different events in an individual's life can be obtained by comparing the isotopic values in several tissues. Such studies of change in diet demand a knowledge of the carbon and nitrogen turnover times in these tissues. In order to study life-history dietary events using bone collagen, it is of interest to separate events early in life, e.g. those caused by lactation or physiological factors, from other dietary changes later in life. The turnover time in tissues with a relatively fast turnover, such as muscle, has been fairly well studied (e.g. Tieszen *et al*. 1983). However, the long-term turnover of bone collagen is not well understood at all. Studies on bone collagen turnover in humans are mainly short-term studies of medical interest where, for example, the focus is on rate differences in collagen synthesis and bone resorption after bone fractures or after the menopause in females (e.g. Langeland 1978; Akesson *et al*. 1993; Sone *et al*. 1995; Ebeling *et al*. 1996; Garnero *et al*. 1996; Ravn

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Table 1. *Age classes, estimated weight and juvenile growth of cave bears, based on Kurtén (1976)*

	age		weight				
age class	range (years)	mean (years)	class	kg	δ^{15}N	s.d.	*n*
neonates (0)	0.0	—	rat	1	—	—	—
neonates first winter (1)	0.0–0.3	—	—	10[a]	7.1	0.48	4
cubs first summer (2)	0.3–0.9	—	—	25[a]	—	—	—
cubs second winter (2)	0.9–1.4	—	wolf	32	4.3	0.41	4
yearlings (3)	1.4–2.4	2.2	hyena	65	2.8	0.54	5
juveniles (4)	2.4–3.4	3.2	lion	150	4.2	0.28	2
subadults (5)	3.4–5.4	4.2	—	210	2.5	1.23	4
adult (6)	5.4–7.4	6.4	—	250	1.9	0.70	11
adult (6)	7.4–20	13.2	—	270	—	—	—

[a]Based on Gittleman & Oftedal (1987).

et al. 1996). The only two studies discussing the total turnover time in bone collagen (i.e. cartilage) concluded that the turnover time is very long (10–30 years; Libby *et al.* 1964; Stenhouse & Baxter 1979). Both studies based their estimates on a few elderly human individuals either suffering from illnesses that are known to affect metabolism or having some other physiological status with the same effect (Langeland 1978; Okazaki *et al.* 1997).

In this paper we have a well-defined population of the extinct cave bear and will discuss dietary changes in connection to a specific metabolism and growth as seen in δ^{15}N in bone. We will present a quantitative estimate on how growth and lactation patterns in the cave bear affect the isotope values. We will also discuss the possible effects of collagen turnover in bone.

2. MATERIAL AND METHODS

Despite cave bears belonging to the order Carnivora, they have been described as herbivores, which can be seen from their heavy molars and skull morphology (Kurtén 1976). This has been confirmed isotopically, where it was also shown that their diet was C3 based (Bocherens *et al.* 1990, 1991*a*,*b*, 1995; Nelson *et al.* 1998).

Kurtén (1958, p. 7) noted that 'One of the most striking features of every larger cave bear collection which I have studied is the clear-cut separation of the younger individuals into a series of discrete stages of development, identical or nearly so for all the samples'. This led to the conclusion that caves were inhabited only during the dormancy season, resulting in growth stages separated by one year. Kurtén (1958) based this conclusion on the size of the teeth, progression of tooth replacement, deposition of dentine in the pulp cavities and initiation of wear of the tooth crowns. The youngest specimens found are the neonates, equal in size to newborn cubs of the brown bear *Ursus arctos*, followed by various age stages up to the adults.

As a base for this study, we used the δ^{15}N-values from a cave bear population in the Divje Babe Cave, northern Slovenia, published by Nelson *et al.* (1998). Here, stable carbon and nitrogen isotopes were measured on a set of bones from individuals of known age ranging from neonates to adults (table 1). In order to avoid interbone variability, the bone chosen was in most possible cases the tibia ($n=18$), otherwise it was the femur ($n=3$), cranium ($n=2$), radius ($n=2$), ulna, fibula and one unknown bone. Collagen was extracted according to Brown *et al.* (1988). High molecular (>30 kDa) remnants were selected for and the samples were measured on a VG Isotech (Micromass, Manchester, UK) mass spectrometer with a measurement uncertainty of <0.1‰ (Nelson *et al.* 1998).

Cave bears probably gave birth in caves from November to February during dormancy (Kurtén 1976; Nelson *et al.* 1998). Due to recycling of nitrogen from urea in the dormant bear mother (Barboza *et al.* 1997), there should be a 3‰ higher value in the neonate's tissue compared to its mother (Nelson *et al.* 1998). A lactation effect has been detected in humans and other mammals, where δ^{15}N-values in infants became *ca.* 3‰ more positive than their breast-feeding mothers (Fogel *et al.* 1989; K. Lidén, A. Olsson, G. Eriksson and A. Angerbjörn, unpublished data). However, since Steele & Daniel (1978) found no differences in cow's milk from that of the cow's flesh, we would like to emphasize that the so-called lactation effect is a trophic-level effect albeit caused by lactation. Based on this we assumed a similar lactation effect in cave bears which should be added to the 3‰ dormancy effect, thus giving a value for bear cubs 6‰ higher than their mothers (Nelson *et al.* 1998). During the winter, cubs were fully lactated in both the modern brown bear (Oftedal & Gittleman 1989) and cave bears (Kurtén 1976—based on tooth eruption). Although lactation in modern bears continues during their first summer and second winter, cubs start to eat solid food during their first summer (Oftedal & Gittleman 1989). Based on initiation of wear of the tooth crowns in cave bear cubs, Kurtén (1976) inferred a similar pattern in cave bears with consumption of solids during their first summer, but a final weaning in their second spring.

3. THE MODEL

The nitrogen isotope values are mostly expressed as relative values between the ratio of ^{15}N and ^{14}N in the sample in relationship to a standard ratio in the atmosphere, such as

$$\delta^{15}\mathrm{N} = \frac{^{15}\mathrm{N}/^{14}\mathrm{N}\text{ in sample}}{^{15}\mathrm{N}/^{14}\mathrm{N}\text{ in the atmosphere}} - 1 \times 1000. \quad (1)$$

We are, however, interested in how the isotopic values could change over time. In this model we have equated the amount of protein, i.e. nitrogen, assimilated in the body with growth, since we are working with growing individuals. If the isotope values in the body and diet are body δ^{15}N and diet δ^{15}N, respectively, the body weight at time t is W_t, the growth between t and $t-1$ is thus $W_t - W_{t-1}$ and the fractionation coefficient is f, then the isotopic signature for a growing individual will be

$$\delta^{15}\mathrm{N} = \frac{f \times (W_t - W_{t-1}) \times \text{diet } \delta^{15}\mathrm{N} + W_{t-1} \times \text{body } \delta^{15}\mathrm{N}}{W(t)}. \quad (2)$$

There are many studies suggesting that the ordinary fractionation coefficient for δ^{15}N between trophic levels is *ca.* 3‰ (see e.g. Wada 1980; Minagawa & Wada 1984; Schwarz & Schoeninger 1991); we therefore assumed that $f=3$‰. For a lactating cub, milk will be just like any other diet and, thus, will have the same fractionation function as any other food. However, this will be dependent on whether the milk has been produced directly

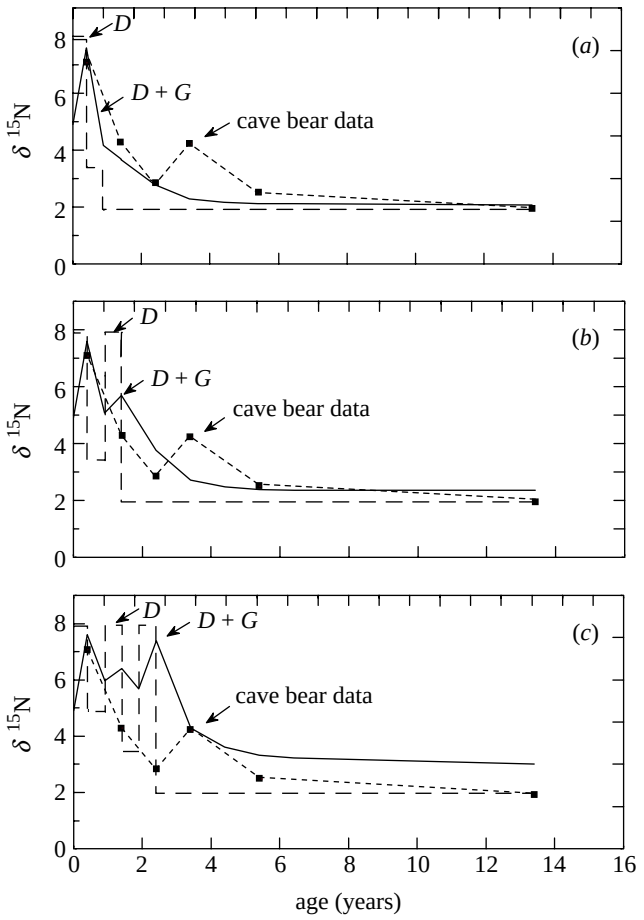

Figure 1. Theoretical δ^{15}N-values plotted against age for a dietary change D (···) in a hibernating lactating cave bear population, including growth $D + G$ (—). Empirical Slovenian cave bear data, with δ^{15}N-values plotted against age (- - -). (*a*) Model 1. Cubs weaned after their first summer. (*b*) Model 2. Cubs weaned after their second summer. (*c*) Model 3. Cubs weaned after their third summer.

from the blood or via an extra metabolic step due to dormancy or hibernation. The fractionation coefficient for dormancy and hibernation is so far unknown. However, the only study that has treated this problem (Nelson *et al.* 1998) indicated that for cave bears it is *ca.* 3‰ as well. We have therefore assumed a similar fractionation coefficient for both processes. Future studies will hopefully provide better estimates of this.

This gave us a general model of how isotope values vary in relation to variation in diet and growth, but there is no time-lag included. In the model we quantify how cave bear growth and three different patterns of lactation, partly during dormancy, could affect the stable nitrogen isotope values. We made assumptions regarding body size at different ages and how weaning could interact with dormancy in cave bears. The data on body size for different age classes were based on Kurtén (1976): 'newborn (the size of a rat); one-year-olds (the size of a wolf); two-year-olds (the size of a hyena); three-year-olds (the size of a lion)' (pp. 110–111). We accordingly assumed body sizes of 1, 32, 65 and 150 kg, respectively (table 1). For body sizes after the first winter we based our estimates on growth in brown bears of $100\,\mathrm{g\,d^{-1}}$ during lactation and during the first summer growth of $50\,\mathrm{g\,d^{-1}}$ (Gittleman & Oftedal 1987; Oftedal & Gittleman 1989), reaching 10 and 25 kg, respectively (table 1). The size of adult cave bears is more difficult to estimate but not so important in the current study. Since cave bears were highly sexually dimorphic in size and we have no knowledge of the sex in our samples, we assumed moderate mean adult body sizes of 250–270 kg (table 1).

The three quantitatively different isotope models (figure 1) were based on data on lactation length in modern bears, which varies from brown bears (60–560 days) to polar bears, *Ursus maritimus* (210–870 days) (Gittleman & Oftedal 1987). In model 1, we assumed that the cubs were fully lactated until four months of age (a diet of +6‰ δ^{15}N compared to the mother; Nelson *et al.* 1998) during their first winter while mothers were in dormancy and then completely weaned after their first summer (figure 1). In model 2, the most realistic model, we assumed 100% lactation from birth to four months of age (+6‰) and 50% lactation with 50% solids during the first summer (= +1.5‰ compared to the mother), with 100% lactation during their second winter (+6‰) and then complete weaning the second spring (figure 1). Finally, in model 3 we assumed 100% lactation from birth to four months of age (+6‰), 100% lactation during the cub's first summer (+3‰), 100% lactation during their second winter (+6‰), 50% lactation and 50% solids during the cub's second summer (+1.5‰) and 100% (+6‰) lactation during their third winter and then completely weaned (figure 1).

4. RESULTS

The three different models, presented in figure 1 were based on different assumptions regarding weaning time in cave bears but similar growth. For each model, the first curve is the dietary change for the lactating cub compared to that of its mother (D) assuming that the mother's dormancy and lactation were the only processes affecting the isotopic value. The second curve is the same dietary change but the growth of the cub is also included ($D + G$), causing a dilution effect in the δ^{15}N-value. The third curve in the figure is the empirical data from the Slovenian cave bears (Nelson *et al.* 1998). By comparing the models with empirical data from the Slovenian cave bear population, we found the best fit with model 2. All three models showed a similar peak in isotopic value after the first winter, demonstrating the increase in δ^{15}N due to lactation and that the cubs were formed during the mothers dormancy. However, in model 1 there was no second peak but only a gradual depletion towards adult values contrary to the empirical data. Model 3, on the other hand, produced two more peaks at very high levels, the third approximately as high as the first peak. Further, the isotopic value in model 3 never came down to the observed adult values of *ca.* 1.9‰. Model 2 produced two peaks and thereafter a gradual depletion towards the adult value, just like the empirical cave bear data. Model 2 with the best isotopic fit also had the best support in Kurtén's (1976) morphological cave bear studies. Based on model 2, we hypothesize that the cave bear cubs were fully lactated in their first and second winters during dormancy, which includes them having their first solids during their first summer and being fully weaned by their second summer.

5. DISCUSSION

In this study we used a cave bear population with well-known diet and age distribution (Kurtén 1976; Nelson *et al*. 1998) to estimate the different processes that can influence δ^{15}N-values, namely metabolic processes and growth in bone. The cave bear had a very special physiology during dormancy, like most other extant bears. It was periodically in a catabolic state and burned fat body mass; bears only rarely lose lean body mass during dormancy (Folk 1974; Nelson 1980; Nelson *et al*. 1983; Barboza *et al*. 1997). The dormant mother recycled nitrogen from urea (Barboza *et al*. 1997), produced proteins to produce a cub and lactated the cub, which resulted in the double trophic-level shift in nitrogen values in bear cubs (Nelson *et al*. 1998). Further, our model supports the view of Kurtén (1976) that cave bears lactated their cubs during their first two winters. This could be tested on extant bear species, where we hypothesize a similar double trophic-level effect in isotopes with respect to growth.

Growth has been discussed in earlier studies, but not necessarily been considered to affect the isotopic signature (Koch *et al*. 1994; Sealy *et al*. 1995). However, during periods of fast growth, our model showed that it will have a large effect on isotopic changes and trends of decreasing or increasing isotopic values will be less pronounced. This growth effect is particularly important to note in studies of lactation and weaning.

The large and long-lived cave bear provides an opportunity for studying collagen turnover time. Bears have extremely long lactation periods and a special metabolism, which confer high nitrogen values with two nitrogen peaks early in life for the cubs, which are strongly contrasting to the adult nitrogen values. This gave us an opportunity to discuss the time-lag between the predicted and observed peak values. There was a clear time difference between the second peak in the empirical data set and the same peak in model 2. In model 2 it appeared at the age of two years, whereas in the Slovenian data set it did not appear until four years of age. Since collagen turnover was not accounted for in the models, this might be due to a time-lag of two years in collagen turnover in this cave bear population at this specific age. The difference in height between the two peaks can also be explained by the turnover time, which will affect the isotopic signature in a negative manner. However, the first peak occurred at the same age (six months) in all three models, as well as in the empirical data set, indicating a considerably faster turnover time at that age. Further, with no turnover the values would not reach the adult standard level which can be seen in all three models. Consequently, in this specific case the turnover time was estimated to be two years in an individual at age four years. However, it is probable that turnover time increases with age, at least during the juvenile stage, probably due to changes in metabolism. This was supported by a study of 57 pubertal boys, where an increase in collagen metabolism was found in the very last stage of puberty (Sorva *et al*. 1997). A positive correlation between overall metabolic rate and collagen metabolism was found in a study on the effect of exercise (i.e. increased metabolism) and collagen metabolism in young women (Thorsen *et al*. 1997). One would also expect to find a faster turnover time in different types of bones, e.g. bones with high proportions of cancellous bone, such as the ribs, than in bones with a higher proportion of compact bone (Sealy *et al*. 1995). Further, it is possible that, for example, bears, which go through dormancy and, thus, lower their metabolic rate, will also have a temporarily reduced collagen turnover during dormancy, which in this case indicates that our obtained value on collagen turnover should be higher. This demonstrates the need for both better measurements of turnover in several tissues and models that quantify different effects.

We would like to stress the differences between processes that can alter the isotopic signature. Diet and metabolism can affect the isotopic ratio through fractionation processes. Dormancy and hibernation are examples of catabolic states where nitrogen can be recycled in the body and, thereby, cause fractionation. On the other hand, during growth and with protein turnover, the isotopic value will be diluted in relation to a change in diet, e.g. the weaning process.

Other animals can also be in a catabolic state during winter without the ability to hibernate or go through dormancy, e.g. reindeers (*Rangifer tarandus*) and badgers (*Meles meles*). Under these circumstances they might use lean body mass in order to maintain normal metabolism. This will then show up in isotopic records as enriched nitrogen values. It should thus be possible to trace other mammals and humans under periodic and/or seasonal starvation or during anorectic behaviour in increased nitrogen values (Nelson *et al*. 1998). This method of using stable isotopes to study lactation and weaning processes could be valuable, particularly in studies of extinct or marine mammals where such information is otherwise difficult to obtain.

We conclude that, in order to use stable isotopes in studies of dietary change in both prehistoric and extant populations, the underlying processes must be understood. Of main importance are metabolism, growth and collagen turnover in bone.

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