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Trophic Level Effects on $^{15}N/^{14}N$ and $^{13}C/^{12}C$ Ratios in Bone Collagen and Strontium Levels in Bone Mineral

This study examines stable isotope ratios of carbon and nitrogen in bone collagen and the elemental concentrations of strontium in the bone mineral of terrestrial vertebrates from a variety of ecosystems. Documentation of the separation of trophic levels by these indices is essential for the assessment of the trophic position of prehistoric humans. Particular emphasis is given to carnivores in this study as they are generally underrepresented in most archeological assemblages. Nitrogen isotope ratios and strontium p.p.m. values can separate herbivores and carnivores depending upon the scale of the analysis. Separation is more pronounced the smaller the geographic area of the sample.

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1. Introduction

Unidirectional changes in stable isotope ratios and trace element concentration along the continuum primary producer, primary consumer, secondary consumer, etc. are referred to as trophic level effects. The effects are, presumably, the result of metabolic processes during uptake, tissue synthesis, or excretion. Such effects have been observed for the $^{15}N/^{14}N$ and $^{13}C/^{12}C$ ratios in various tissues of marine organisms (Miyake & Wada, 1967: McConnaughey & McRoy, 1979; Rau *et al.*, 1983) and in the strontium concentration in various tissues of non-marine organisms from single ecosystems (Ophel, 1963; Elias *et al.*, 1982). The purpose of this study was to determine if the carbon and nitrogen stable isotope ratios in bone collagen and the strontium concentration in bone mineral of terrestrial vertebrates from multiple ecosystems would reflect trophic level effects. If such effects could be documented, these parameters in bone of prehistoric humans could be used to estimate the trophic level at which the people ate. In other words, it would be possible to reconstruct the proportion of meat to vegetables in diet.

In the discussion to follow the stable isotope ratios are presented as delta values as shown below.

$$\delta^{15}N = \left[\frac{(^{15}N/^{14}N)\ \text{sample}}{(^{15}N/^{14}N)\ \text{standard}} - 1\right] \times 1000\,{}^{0}/_{00}$$

$$\delta^{13}C = \left[\frac{(^{13}C/^{12}C)\ \text{sample}}{(^{13}C/^{12}C)\ \text{standard}} - 1\right] \times 1000\,{}^{0}/_{00}$$

The standard for $\delta^{13}C$ measurements is the Peedee belemnite (PDB) carbonate, while that for $\delta^{15}N$ measurements is atmospheric (AIR) nitrogen. The trace element results are presented as a weight percentage, parts strontium per million parts bone.

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2. Nitrogen

As discussed more thoroughly in the introduction to this issue the $\delta^{15}N$ values of an animal's tissues are determined by the stable nitrogen isotope ratios of its diet. Although there is some variation, laboratory experiments indicate that the average $\delta^{15}N$ values of an animal's tissues are about $3^0/_{00}$ more positive than those of an animal's diet (DeNiro & Epstein, 1981; Macko *et al.*, 1982; Minagawa & Wada, 1984). These observations support the existence of a trophic level effect for nitrogen isotopes. Since an animal's tissues are enriched relative to diet, an herbivore's tissues would be expected to have $\delta^{15}N$ values that are $3^0/_{00}$ more positive than the plant it feeds on; a primary carnivore's tissues should have a $\delta^{15}N$ value $3^0/_{00}$ more positive than an herbivore, and so on.

The available field data suggest that this is the case. Marine and freshwater zooplankton have $\delta^{15}N$ values that are, on average, $3^0/_{00}$ more positive than associated phytoplankton (Miyake & Wada, 1967; Wada & Hattori, 1976; Pang & Nriagu, 1977). For organisms collected at higher trophic levels, the data suggest enrichment in ^{15}N through successive levels (Hoering, 1955; Miyake & Wada, 1967; Rau, 1981; Minagawa & Wada, 1984). A recent study (Schoeninger & DeNiro, 1984) of $\delta^{15}N$ values in bone collagen from more than one hundred modern fish, birds, and mammals from multiple food webs strongly supports the existence of a trophic level effect on $\delta^{15}N$ values in marine vertebrates. Further, the average difference in $\delta^{15}N$ values between the bone collagen of terrestrial carnivores and terrestrial herbivores was about $3^0/_{00}$ as expected, but the sample size for terrestrial carnivores was very small ($n = 6$). Thus it was decided that analyses from a larger number of terrestrial vertebrates, especially carnivores, were necessary before any final conclusions could be made concerning the possibility of a trophic level effect on $\delta^{15}N$ values in bone collagen from terrestrial animals representing multiple food webs.

3. Carbon

As described more thoroughly in the introduction, the $\delta^{13}C$ values of an animal's tissues are also determined by the corresponding isotope ratios of its diet. Laboratory experiments indicate that the average $\delta^{13}C$ value of the whole body of an animal is about $1^0/_{00}$ more positive than that of the animal's diet (DeNiro & Epstein, 1978; Bender *et al.*, 1981; Tieszen *et al.*, 1983). Bone collagen appears to be enriched by $3–5^0/_{00}$ over diet depending on the animal studied (DeNiro & Epstein, 1978; Van der Merwe & Vogel, 1978). Van der Merwe (1982) has suggested that a trophic level effect occurs during the step between producers and primary consumers (herbivores) but not in subsequent steps.

The results from field data are mixed. Small increases in ^{13}C content have been observed for animals living at successively higher trophic levels in the open ocean (Fry *et al.*, 1983; McConnaughey & McRoy, 1979; Rau *et al.*, 1983). However, no consistent trend was observed for coastal water species (Rau *et al.*, 1983) or for terrestrial vertebrates (Vogel, cited in Van der Merwe, 1982).

The results of analyses of over one hundred modern fish, birds, and mammals also produced no consistent trends (Schoeninger & DeNiro, 1984). The average difference in $\delta^{13}C$ values of bone collagen from terrestrial herbivores compared with carnivores was less than $1^0/_{00}$. Thus it appears that the trophic level effect on $\delta^{13}C$ values is observed only when animals from single food webs are analyzed. It seems that analysis of individuals from multiple food webs masks any small trophic level effect that may exist. Since very few

terrestrial carnivores were available in the previous study, however, it seemed reasonable to include stable carbon isotope analysis of a larger sample of terrrestrial vertebrates.

4. Strontium

As discussed more thoroughly in the introduction, bone strontium levels reflect diet strontium levels (Comar *et al.*, 1957; Comar & Wasserman, 1963). Results from field studies suggest that within single trophic systems bone strontium levels decrease from herbivore to carnivore (Ophel, 1963; Elias *et al.*, 1982). The phenomenon has been observed in both aquatic (Ophel, 1963) and terrestrial (Elias *et al.*, 1982) systems. Although variations in geographical distribution of strontium have been observed (summarized in Sillen & Kavenaugh, 1982) the effect of this variation on the bone strontium concentration in a large number of known herbivores and carnivores has not been thoroughly investigated. The results of the project outlined here address this problem.

5. Methods and Materials

The animals included in this study and their diets are listed in Table 1. The majority were taken from collections at the Los Angeles County Museum. The majority of animals were obtained by the Museum in Southern California and Kenya (specific area unknown) but other geographic areas are represented as well. As can be seen from the table the emphasis was placed on carnivorous animals. This was done because few carnivores are found in archeological sites and, thus, the variation in $\delta^{13}C$ values, $\delta^{15}N$ values, and strontium concentration at this trophic level is largely unknown.

Bone samples were cleaned mechanically. In the case of very fresh bone, dermestid beetles were used to remove most of the flesh; remaining traces were removed using dissecting scissors and scalpel. Care was taken to analyze only those museum specimens that had been cleaned in the same fashion. The bones were dried, then powdered to less than 0·71 mm.

Collagen was prepared from the bone powder as described previously (DeNiro & Epstein, 1981) with some modifications (Schoeninger & DeNiro, 1984). Collagen samples were combusted using a modified version of the Stump & Frazer (1973) method (Northfelt *et al.*, 1981). The resulting CO_2 and N_2 were separated and purified in a vacuum system by cryogenic distillation prior to determination of their isotope ratios by mass spectrometry.

The means and standard deviations (1 S.D. values) for 27 analyses of a thiourea standard were $-23{\cdot}1 \pm 0{\cdot}3‰$ for $\delta^{13}C$ values, and $-1{\cdot}1 \pm 0{\cdot}2‰$ for $\delta^{15}N$ values. In addition, collagen was prepared from two aliquots of bone powder from each of twelve samples from this and other studies (Schoeninger *et al.*, 1983; DeNiro & Schoeninger, 1983). The results of the isotopic analyses on the paired aliquots were compared. The means and standard deviations (1 S.D. values) of the differences between each pair were $0{\cdot}1 \pm 0{\cdot}2‰$ for $\delta^{13}C$ values and $0{\cdot}2 \pm 0{\cdot}3‰$ for $\delta^{15}N$ values.

Separate aliquots from each bone sample were ashed at 800°C for 24 hours to remove all organic material. Bone ash samples were dissolved following Szpunar (1977) and then prepared for trace element analysis using the standard additions method described

previously (Schoeninger, 1980, 1981). Approximately 0·1 g of bone ash was used for each sample. The dilution used was:

$$\frac{\text{1 pt bone ash}}{\text{25 ml}} \times \frac{\text{2 ml bone ash soln}}{\text{5 ml}} = 1 : 62{\cdot}5$$

In cases where the strontium concentration was higher than the linear range of the atomic absorption spectrometer only 1·0 ml of the solution of dissolved bone ash was used in the second portion of the above equation. This resulted in a dilution of one part bone ash to 125 ml instead of 62·5 ml. The concentration of strontium in the solution was determined by flame atomic absorption spectrometry with nitrous oxide as oxident. The concentration in the solution was multiplied by the dilution and then divided by the sample weight. Results are given as parts strontium per million parts bone ash.

The mean and standard deviation (1 S.D. value) for results of analyses of 19 aliquots of ground cow bone was 252 ± 18 p.p.m. Sr (range 221,278). These aliquots were prepared and analyzed over the course of several months, thus this amount of variation is higher than would be expected within a single period of machine use and best represents inherent variation for all samples analyzed in this study. Two bone ash standards were provided by Dr Douglas Price at the University of Wisconsin. Analyses of four aliquots of the first standard (BO126) had a mean and standard deviation of 290 ± 17 p.p.m. Sr (range = 274, 300). Analyses of five aliquots of the second standard (5407) had a mean and standard deviation of 199 ± 5 p.p.m. Sr (range = 195, 206). These concentrations are within 10% of the sample values measured by the Health and Safety Laboratory of the U.S. Atomic Energy Commission (1965).

6. Results

Collagen $\delta^{15}N$ values and $\delta^{13}C$ values and strontium concentration in bone ash of all the animals sampled are listed in Table 1 and plotted in Figures 1, 2, and 3. In these figures, the animals are grouped as carnivorous mammals, carnivorous birds, and herbivorous mammals. Means, standard deviations (1 S.D. values), and ranges of the $\delta^{15}N$ and $\delta^{13}C$ values in bone collagen and strontium concentration in bone ash for these different groups of animals are presented in Table 2. These statistics are presented in order to illustrate the variation within each group. No statistical tests for difference between means were performed because neither the samples analysed nor the populations from which they were drawn can be assumed to be normally distributed. For example, the sample of herbivores does not represent all types of diets and certain species are represented by more individuals than are other species.

7. Discussion

Nitrogen—$\delta^{15}N$ values

From the results presented in Table 2 and Figure 1 it appears that bone collagen $\delta^{15}N$ values of carnivorous animals and carnivorous birds are enriched by 1·3–1·6‰ relative to herbivorous mammals. This difference is smaller than the 3‰ difference in means that was observed in previous studies (DeNiro & Epstein, 1981; Macko *et al.* 1982; Minagawa & Wada, 1984; Schoeninger & DeNiro, 1984). Based on distribution of results in the present

Table 1 **Diet, collection site, bone collagen $\delta^{15}N$ and $\delta^{13}C$ values, and Sr concentration for specimens analyzed in this study**

Group and order	Scientific and common names	Diet*	Site†	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	Sr (p.p.m. ash)
Mammals						
Carnivora						
	621. *Leo pardus* Leopard	M	KY	−13·3	+10·8	1142
	622. *Leo pardus* Leopard	M	KY	−13·9	+11·0	139
	623. *Leo pardus* Leopard	M	KY	−14·5	+12·3	878
	627. *Leo tigris* Tiger	M	IN	−17·9	+7·4	195
	628. *Leo tigris* Tiger	M	IN	−11·8	+8·6	214
	629. *Leo tigris* Tiger	M	—			223
	715. *Leo leo* Lion	M	KY	−5·7	+10·2	291
	716. *Leo leo* Lion	M	KY	−7·4	+10·7	195
	626. *Felis caracal* Caracal	M	KY	−18·3	+12·7	320
	630. *Felis concolor* Mountain lion	M	AR	−7·5	+10·4	178
	633. *Felis concolor* Mountain lion	M	SC	−17·8	+7·3	242
	634. *Felis concolor* Mountain lion	M	SC	−18·4	+5·5	173
	631. *Alopex lagopus* Arctic fox	M	AK	−20·6	+5·9	114
	632. *Martes pennanti* Fisher	M	BC	−20·9	+6·7	195
	635. *Lynx rufus* Bobcat	M	SC	−17·1	+11·4	263
	636. *Lynx rufus* Bobcat	M	NC	−16·0	+9·2	325
	638. *Canis latrans* Coyote	M	SC	−19·3	+8·0	167
	639. *Canis latrans* Coyote	M	NC	−18·6	+5·7	237
	640. *Canis latrans* Coyote	M	MX	−11·7	+18·8	665
	614. *Hyaena hyaena* Striped hyaena	M, i	KY	−8·9	+9·9	199
	615. *Hyaena hyanena* Striped hyaena	M, i	KY	−6·5	+10·1	434
	616. *Hyaena hyaena* Striped hyaena	M, i	KY	−17·8	+6·9	285
	617. *Canis* sp. Jackal	M, i	KY	−8·8	+6·4	95
	618. *Canis* sp. Jackal	M, i	KY	−9·2	+10·3	90
	624. *Mellivora capensis* Honey badger	M, i, p	KY	−14·3	+13·4	698
	625. *Fennecus zerda* Fennec	M, i, p	KY	−9·0	+7·8	831
	637. *Urocyon cinereoargenteus* Grey fox	M, i, p	SC	−15·8	+6·7	242

Table 1 *continued*

Group and order	Scientific and common names	Diet*	Site†	$\delta^{13}C$(‰)	$\delta^{15}N$(‰)	Sr (p.p.m. ash)
Primates						
	706. *Cercopithecus aethiops* Vervet monkey	p	KY	−17·8	+4·5	169
	707. *Cercopithecus aethiops* Vervet monkey	p	KY	−18·0	+7·6	195
Lagomorpha						
	708. *Lepus* sp. Hare	p	KY	−11·1	+5·6	171
Artiodactyla						
	709. *Gazella* sp. Gazelle	p	KY	−8·9	+8·5	307
	710. *Gazella granti* Grant's gazelle	p	KY	−14·2	+7·1	351
	711. *Gazella* sp. Gazelle	p	KY	−8·0	+8·1	230
	712. *Aepyceros vendilis* Impala	p	KY	−12·1	+7·9	259
	713. *Ourebia ourebia* Oribi	p	KY	−8·5	+7·8	283
	714. *Madoqua* sp. Dik-dik	p	KY	−21·0	+6·1	361
Birds						
Falconiformes						
	641. *Buteo lagopus* Rough legged hawk	M	SC	−16·9	+6·8	91
	644. *Buteo lineatus* Red shouldered hawk	M	SC	−19·9	+8·1	358
	645. *Buteo lineatus* Red shouldered hawk	M	SC	−20·6	+8·7	178
	649. *Buteo jamaicensis* Red tailed hawk	M	SC	−17·9	+7·4	198
	650. *Buteo jamaicensis* Red tailed hawk	M	SC	−20·0	+7·9	171
	651. *Buteo jamaicensis* Red tailed hawk	M	SC	−19·1	+7·0	122
	652. *Falco sparverius* Kestrel	M	SC	−17·5	+10·6	
	653. *Falco sparverius* Kestrel	M	SC	−17·1	+8·8	
	654. *Falco sparverius* Kestrel	M	SC	−19·3	+8·7	
Strigiformes						
	642. *Bubo virginiarus* Great horned owl	M	SC	−21·2	+5·3	130
	643. *Bubo virginiarus* Great horned owl	M	SC	−17·7	+10·0	83
	646. *Tyto alba* Barn owl	M	SC	−21·5	+7·8	214
	647. *Tyto alba* Barn owl	M	SC	−20·0	+9·0	
	648. *Tyto alba* Barn owl	M	SC	−21·2	+9·7	

* Diets are abbreviated as follows; M, meat; p, plants; i, insects (taken from Walker, 1975).

† Sites are abbreviated as follows: AK, Alaska; AR, Arizona; BC, British Columbia; IN, India; KY, Kenya; MX, Mexico; NC, Northern Californa; SC, Southern California.

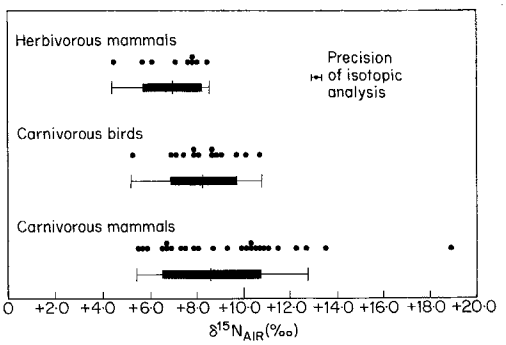

Figure 1. Bone collagen $\delta^{15}N$ values for terrestrial vertebrates included in this study. Each point represents a sample from one individual. All animals were collected in their natural habitats. For the indicated groups, the means are given by the central vertical bars, the standard deviation by the heavy horizontal bars, and the ranges by the narrow horizontal bars.

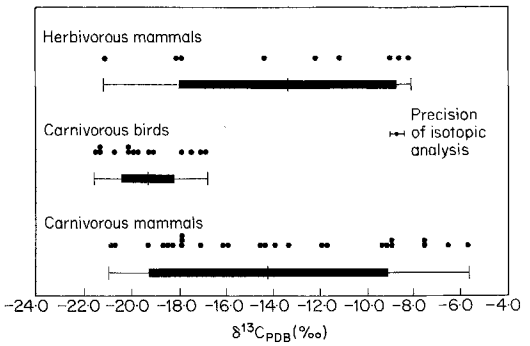

Figure 2. Bone collagen $\delta^{13}C$ values for terrestrial vertebrates included in this study. Each point represents a sample from one individual. All animals were collected in their natural habitats. For the indicated groups, the means are given by the central vertical bars, the standard deviation by the heavy horizontal bars, and the ranges by the narrow horizontal bars.

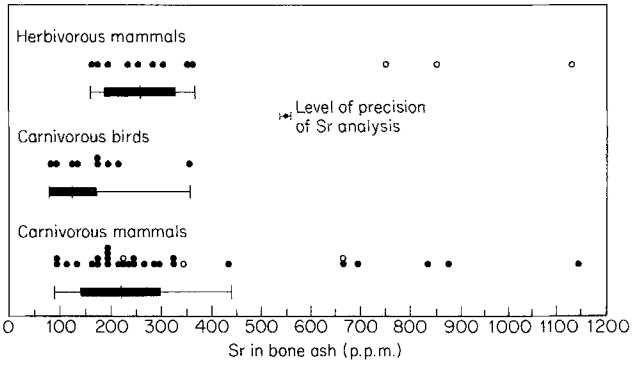

Figure 3. Strontium concentrations in bone ash for terrestrial vertebrates included in this study. Each point represents a sample from one individual (○: Turkana, Kenya; ●: world wide). All animals were collected in their natural habitats. For the indicated groups, the means are given by the central vertical bars, the standard deviation by the heavy horizontal bars, and the ranges by the narrow horizontal bars. Within carnivorous mammals the five samples with the highest bone strontium concentrations were not included in the calculation of mean and standard deviation. Within carnivorous birds the sample with the highest bone strontium concentration was not included in the calculation of mean and standard deviation although it is included in the range. See text for explanation.

Table 2 **Sample size, mean, and standard deviation of $\delta^{15}N$, $\delta^{13}C$, and bone strontium values in the dietary groups included in this study**

	Herbivorous mammals	Carnivorous mammals	Carnivorous birds
$\delta^{15}N$ (‰)			
sample (n)	9	21	14
mean	+7·0	+8·6	+8·3
S.D.	1·3	2·1	1·4
range	+4·5, +8·5	+5·5, +12·7	+5·3, +10·6
$\delta^{13}C$ (‰)			
sample (n)	9	21	14
mean	−13·3	−14·1	−19·3
S.D.	4·7	5·1	1·6
range	−18·0, −8·0	−10·9, −5·7	−21·5, −16·9
PPM Sr			
sample (n)	9	22	8
mean	258	219	148
S.D.	73	81	49
range	169, 361	90, 434	83, 214

study, it would be possible to predict carnivory in a terrestrial animal with a bone collagen $\delta^{15}N$ value of $+9‰$ or more positive. This is the same value reported for terrestrial animals in an earlier paper (Schoeninger & DeNiro, 1984). Using this value, somewhat less than 50% of the animals could have been identified as carnivores based on $\delta^{15}N$ values. It would also be possible to predict herbivory in animals with bone collagen $\delta^{15}N$ values less than $+5‰$. In the case of the samples analyzed for this study only one herbivore had a bone collagen $\delta^{15}N$ value less than $+5‰$. Thus eight of nine herbivores could not be identified as such based on the $\delta^{15}N$ values of bone collagen.

If the study area is restricted from world-wide to Kenya, the trophic level effect appears to be more apparent (Table 3). The average difference in bone collagen $\delta^{15}N$ values between carnivorous mammals and herbivorous mammals from Kenya is $\sim 4‰$ and there is no overlap between the two distributions. This difference of means is similar to that observed between trophic levels in the marine system (Schoeninger & DeNiro, 1984) although in that study there was more overlap. The lack of overlap in the present study may reflect the small number of samples included from Kenya.

In any case, these results suggest that it may be possible to reconstruct the proportion of meat to vegetable materials in prehistoric human diet based on the $\delta^{15}N$ values of bone collagen. The human skeletons should originate from a restricted geographical area. The effective size of this area could be determined by the analysis of faunal bone collagen from known herbivores and carnivores to establish the difference in $\delta^{15}N$ values between the two groups.

Carbon—$\delta^{13}C$ values

When the bone collagen $\delta^{13}C$ values of all of the samples included in this study are considered, no obvious trophic level effect is apparent (see Figure 2 and Table 2).

Table 3 **Sample size, mean, and standard deviation of $\delta^{15}N$, $\delta^{13}C$, and bone strontium values in the dietary groups from Kenya**

	Carnivorous mammals		Herbivorous mammals
$\delta^{15}N$ (%)			
Sample (n)	6		9
Mean	+11·3		+7·0
S.D.	1·0		1·3
Range	+10·2, +12·7		+4·5, +8·5
$\delta^{13}C$ (%)			
Sample (*n*)	6		9
Mean	−12·2		−13·3
S.D.	4·7		4·7
Range	−18·3, −5·7		−18·0, −8·0
Sr (p.p.m.)			
Sample (*n*)	6	4	9
Mean	494	236	258
S.D.	413	84	73
Range	139, 1142	139, 320	169, 361

If the bone collagen $\delta^{13}C$ values of only those animals collected in Kenya are considered (Table 3), however, a small trophic level effect is indicated. The mean for the carnivorous animals is enriched by 1·2‰ relative to herbivorous animals. This is an enrichment of similar magnitude to that observed between trophic levels in the open ocean (McConnaughey & McRoy 1979; Fry *et al.* 1983; Rau *et al.*, 1983).

Even so, the distribution of $\delta^{13}C$ values of carnivorous animals almost completely overlaps that for herbivorous animals. Thus, it would be impossible to predict trophic level based on the $\delta^{13}C$ value of the animal's bone collagen. In application to the prehistoric human record, this means that the $\delta^{13}C$ values of human bone collagen would not be useful in estimating the proportions of meat to vegetable material used by humans throughout the prehistoric record. This conclusion is not surprising since the proportion of C_3 to C_4 plants in the diet of humans or in the diet of animals eaten by humans will have an effect on the $\delta^{13}C$ of bone collagen that is larger than a 1‰ trophic effect.

Strontium Concentration in Bone Ash

When the bone strontium levels of all of the animals in this study, except those from Turkana, Kenya, are considered, the carnivorous animals (mammals and birds) have lower bone strontium levels, on average, than do herbivorous animals. Five bone samples were not included in the calculation of mean and standard deviation because the values were separated from the rest of the distribution by 200 parts strontium per million parts bone ash. Based on results from previous studies it is clear that this amount of variation is far too large for a single dietary regime (Schoeninger, 1981). This plus the fact that the distribution is not continuous argued that the five samples should not be included in calculation of mean and standard deviation. Even with the removal of these five samples, however, the distributions of carnivorous and herbivorous mammals overlap completely. No predictions about diet could be made based on bone strontium level. The same is true between carnivorous birds and herbivorous mammals. The mean for carnivorous birds is

very low because the outlyer was eliminated for the reasons discussed above. A larger sample would have to be analyzed before it could be concluded that the outlyer is actually part of the distribution. Even so, it would be difficult to separate the herbivorous and carnivorous animals using only their bone strontium concentration.

If only animals from Kenya are considered (see Table 3) the bone strontium levels descriminate less well between herbivores and carnivores than within the sample as a whole. If all samples are considered (six carnivorous mammals, nine herbivorous mammals), the mean for carnivorous animals is 200 p.p.m. higher than for herbivorous animals. With two outlyers removed from the calculation of mean and standard deviation (for the same reasons as those discussed above) the herbivorous animals are, on average, only 20 p.p.m. higher in strontium concentration and the two distributions overlap almost completely.

The bone samples from animals collected east of Lake Turkana in Kenya are the only group that show a discrete separation between herbivores and canivores in bone strontium concentration (see Figure 3). The two dietary groups are separated by 100 p.p.m. and there is no overlap. The mean bone strontium level for herbivorous animals is 500 p.p.m. higher than the mean for carnivorous animals. These results suggest that bone strontium levels can be used to estimate the dietary dependence on meat and vegetable material when the animals to be analyzed are collected within a very restricted geographic area. In this case, the animals were collected from one drainage basin (K. Behrensmeyer, pers. comm.). Other sample sets in which bone strontium concentrations have been shown to reflect known diet differences (Schoeninger, 1982; Elias *et al.*, 1983) were also collected from restricted geographic areas. Obviously, more samples of animals representing several trophic levels from a single drainage basin must be analyzed before a firm conclusion can be reached. Even so, in estimating prehistoric human diet it appears that bone samples must be chosen from restricted geographical areas. As a test, bone from known herbivores and known carnivores should be analyzed to ascertain whether the bone strontium concentrations separate the two groups (as previously suggested by Sillen, 1981).

Most bone samples were provided by D. McIntyre of the Los Angeles County Museum of Natural History. The samples from near Lake Turkana in Kenya were collected and provided by K. Behrensmeyer of the Smithsonian Institution. Assistance in preparing collagen and bone ash samples and in their analysis was provided by K. Katrak, H. Agie, and D. Winter of U.C.L.A., and T. Vetters of the Johns Hopkins University School of Medicine. Stable isotope analysis was done at U.C.L.A.; trace element analysis was done at the Johns Hopkins University School of Medicine. D. McIntyre provided the founders of the dermestid beetle colony. The figures were drawn by J. Guenther of U.C.L.A. Typing was done by B. Coe of the Johns Hopkins University School of Medicine. Support for the project was provided by NSF Grants BNS 79-24756 and ATM 79-24581 to Michael DeNiro of U.C.L.A., and NIH Biomedical Research Support Grant #RR 5378 to Margaret Schoeninger.

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