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Allometric constraints on Sr/Ca and Ba/Ca partitioning in terrestrial mammalian trophic chains

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Abstract In biological systems, strontium (Sr) and barium (Ba) are two non-essential elements, in comparison to calcium (Ca) which is essential. The Sr/Ca and Ba/Ca ratios tend to decrease in biochemical pathways which include Ca as an essential element, and these processes are termed biopurification of Ca. The quantitative pathway of the biopurification of Ca in relation to Sr and Ba between two biological reservoirs (R_n and R_{n-1}) is measured with an observed ratio (OR) expressed by the $(\text{Sr/Ca})_{R_n} / (\text{Sr/Ca})_{R_{n-1}}$ and $(\text{Ba/Ca})_{R_n} / (\text{Ba/Ca})_{R_{n-1}}$ ratios. For a mammalian organism, during the whole biopurification of Ca starting with the diet to the ultimate reservoir of Ca which is the bone, the mean values for OR_{Sr} and OR_{Ba} are 0.25 and 0.2, respectively. In this study, published Sr/Ca and Ba/Ca ratios are used for three sets of soils, plants, and bones of herbivorous and carnivorous mammals, each comprising a trophic chain, to illustrate the biopurification of Ca at the level of trophic chains. Calculated OR_{Sr} and OR_{Ba} of herbivore bones in relation to plants and of bones of carnivores in relation to bones of herbivores give $\text{OR}_{\text{Sr}}=0.30\pm 0.08$ and $\text{OR}_{\text{Ba}}=0.16\pm 0.08$, thus suggesting that trophic chains reflect the Sr/Ca and Ba/Ca fluxes that are prevalent at the level of a mammalian organism. The slopes of the three regression equations of $\log(\text{Sr/Ca})$ vs. $\log(\text{Ba/Ca})$ are similar, indicating that the process of biopurification of Ca with respect to Sr and Ba is due to biological processes and is independent of the geological settings. Modifications of the logarithmic expression of the Sr/Ca and Ba/Ca relationship allow a new formula of the biopurification process to be deduced, leading to the general equation $\text{OR}_{\text{Ba}}=\text{OR}_{\text{Sr}}^{1.79\pm 0.33}$, where the allometric coefficient is the mean of the slopes of the three regression

equations. Some recent examples are used to illustrate this new analysis of predator-prey relations between mammals. This opens up new possibilities for the utilization of Ba/Ca and Sr/Ca in addition to stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for the determination of the relative contribution of different food sources to an animal's diet.

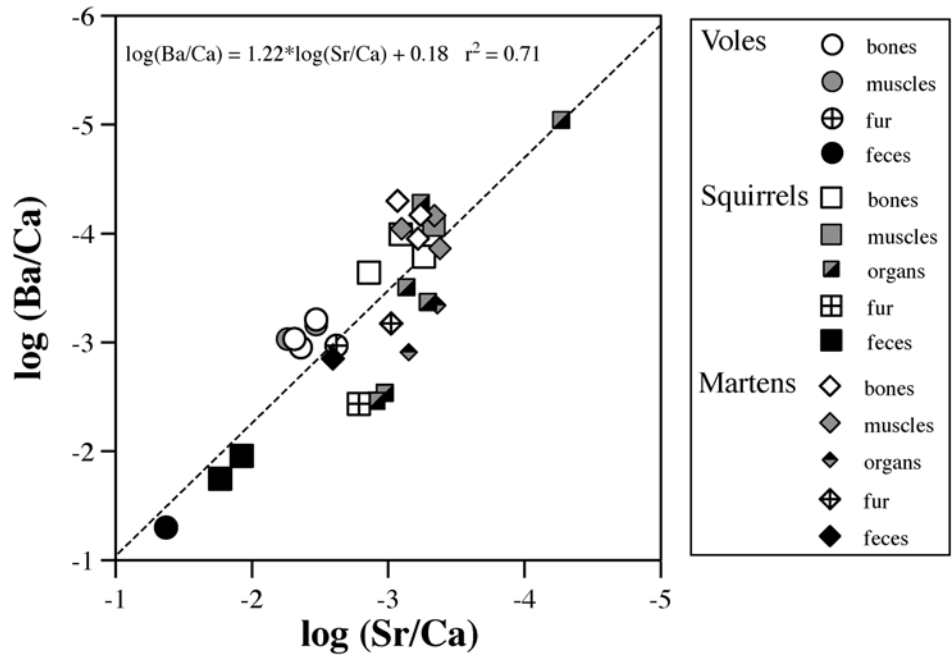
Keywords Calcium biopurification · Strontium · Barium · Diet · Mass balance models

Introduction

The process of Ca biopurification vs. Sr and Ba in mammalian communities was discovered during the 1950s and the 1960s, during the period of above-ground nuclear testing and the subsequent fallout of radioactive Sr and Ba (Comar et al. 1957; Wasserman et al. 1957). In biological systems Sr and Ba are not essential elements and tend to mimic Ca as trace constituents in metabolic pathways due to their similar atomic properties. Sr/Ca and Ba/Ca ratios diminish during metabolic processes involving Ca, a process termed biopurification of Ca. In healthy adult mammals, biopurification of Ca occurs via two main reactions: first, at the level of the digestive tract where Sr and Ba are discriminated with respect to Ca (Sips et al. 1997; Leggett 1992), and second at the level of the kidneys (Kobayashi and Suzuki 1990; Leggett 1992) where the excretion of Sr and Ba is more efficient than that of Ca (Fig. 1). Sr/Ca and Ba/Ca ratios are thus lower in the body in comparison to those of the diet. This reduction is quantified by calculating an observed ratio (OR), an ecological equivalent of a partition coefficient. It is given by the ratios $(\text{Sr/Ca})_{R_n} / (\text{Sr/Ca})_{R_{n-1}}$ and $(\text{Ba/Ca})_{R_n} / (\text{Ba/Ca})_{R_{n-1}}$ where R_n and R_{n-1} are the Ca reservoirs after and before the metabolic reaction (Comar et al. 1956). By reviewing the literature, Sillen and Kavanagh (1982) calculated a value of 0.23 ± 0.05 ($\pm\text{SD}$) for the OR_{Sr} between bone and diet. A single reference suggests a value of 0.2 for OR_{Ba} (Leggett 1992).

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Fig. 1 Distribution of $\log(\text{Sr}/\text{Ca})$ vs. $\log(\text{Ba}/\text{Ca})$ values of soft tissues, bones and excrements of several mammals (data from Elias et al. 1982). Composition of soft tissues are variable within an organism, but Sr/Ca and Ba/Ca ratios for muscles and bones are similar. Discrimination of Sr and Ba by the mammalian metabolism is illustrated by the strong systematic enrichment of feces



Materials and methods

The compilation of available data concerning three terrestrial trophic chains (Fig. 2) allows calculation of OR_{Sr} and OR_{Ba} between bones of herbivores and plants and between bones of carnivores and herbivores. Considering that the Sr/Ca and Ba/Ca ratios of bones are similar to those of muscles (Fig. 1), these ratios in bones of herbivorous mammals are a valid estimate of those of the diet of carnivorous mammals. The results are $OR_{Sr} = 0.30 \pm 0.08$ and $OR_{Ba} = 0.16 \pm 0.08$, which are in accordance with values prevailing

within a mammalian organism according to Sillen and Kavanagh (1982) and Leggett (1992). This shows that Sr/Ca and Ba/Ca fluxes within a mammalian organism are reflected at the level of the trophic chain due to the predator-prey relationships which act as a chemical pathway for nutrients.

For two successive trophic levels, $n-1$ and n , the slope (α) of the regression line of logarithmic values of Sr/Ca vs. Ba/Ca is given by:

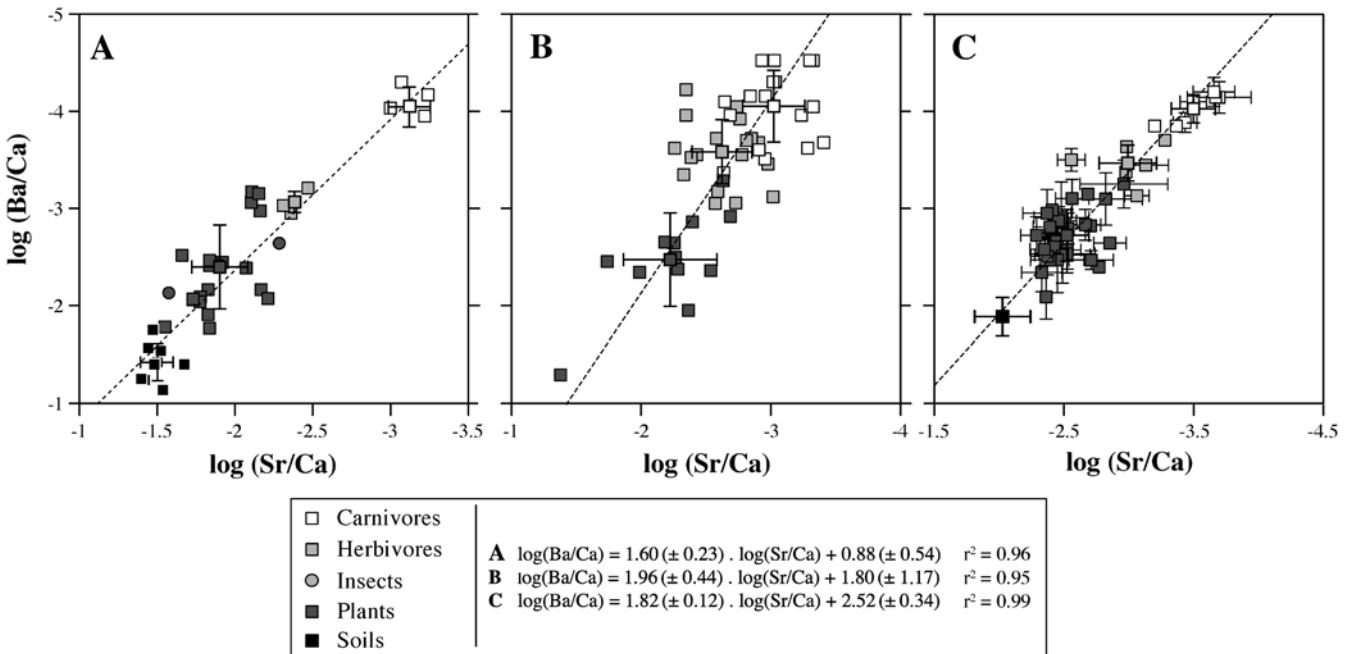


Fig. 2A–C Distribution of $\log(\text{Sr}/\text{Ca})$ vs. $\log(\text{Ba}/\text{Ca})$ values of soils, plants, bones of herbivores and carnivores for three trophic chains. **A** Data from Elias et al. (1982) including values for small grazing mammals and insects (shaded circles) sampled in a remote subalpine ecosystem in the Yosemite National Park (California, United States). **B** Data from Gilbert et al. (1994) reporting values of

an ungulate food chain located in the southwestern Cape (South Africa). **C** Data from Burton et al. (1999) of a mammalian food chain sampled along the Wisconsin/Michigan border (United States). The total dataset summarizes >1,000 samples, representing 41, 14 and 13 species of plants, herbivores and carnivores, respectively

$$\alpha = \log \frac{[(Ba_n/Ca_n) - \log (Ba_{n-1}/Ca_{n-1})]}{[\log (Sr_n/Ca_n) - \log (Sr_{n-1}/Ca_{n-1})]} \quad (1)$$

which leads to:

$$\alpha = \log \frac{[(Ba_n/Ca_n)/(Ba_{n-1}/Ca_{n-1})]}{\log [(Sr_n/Ca_n)/(Sr_{n-1}/Ca_{n-1})]} \quad (2)$$

Considering the definition of an OR, one obtains:

$$\alpha = \log (OR_{Ba}) / \log (OR_{Sr}) \quad (3)$$

which is equal to:

$$OR_{Ba} = OR_{Sr}^\alpha \quad (4)$$

The value of the intercept is thus eliminated with this relation which describes the inherent biological process of Ca purification. By calculating the average for the three regression equations, i.e. 1.60 ± 0.23 , 1.96 ± 0.44 , and 1.82 ± 0.12 for trophic chains A, B, and C respectively, we obtain $OR_{Ba} = OR_{Sr}^{1.79 \pm 0.33}$. The existence of such a relationship has several implications. First, the power coefficient is an allometric coefficient, which predicts for $\alpha > 1$ (1.79 ± 0.33) the relationship $OR_{Ba} < OR_{Sr}$, i.e. a greater efficiency of the biological discrimination of Ba in comparison to Sr. This phenomenon was recognized by Marcus and Wasserman (1965), but this is the first time that it has been demonstrated that the response curve of the concomitant partitioning of Sr and Ba vs. Ca in biological systems follows a power law. This allometric constraint is also valid for other non-essential trace elements. Elias et al. (1982) published Pb values which are in agreement with this assumption (Fig. 3). The relationship between $\log(Pb/Ca)$ and $\log(Ba/Ca)$ gives $\log(Pb/Ca) = 0.97(\pm 0.27) \cdot \log(Ba/Ca) - 1.55(\pm 0.77)$ ($r^2 = 0.88$). Following the rearrangement from Eqs. 1–4, this leads to $OR_{Pb} = OR_{Ba}^{0.97 \pm 0.27}$. However, the Pb/Ca ratio is similar between herbivores ($8.4 \times 10^{-6} \pm 1.3 \times 10^{-6}$) and carnivores ($1.8 \times 10^{-5} \pm 3.0 \times 10^{-5}$) leading to aberrant OR_{Pb} values. This is due to the presence of some anthropogenic Pb which overrides the natural low abundance in a high trophic level (Hirao and Patterson 1974). Scarce results of Rb/K and Cs/K ratios from soils to martens and from seawater to tuna also suggest that the relative abundance of Rb and Cs vs. K is controlled by such a relationship (Burnett et al. 1976). However, the metabolism of Rb and Cs and their Ca substitution in bones as monovalent cations, remains to be investigated. Second, since the Sr/Ca and Ba/Ca ratios in mammalian bones are currently used to reconstruct past trophic chains (e.g. Balter et al. 2002; Burton et al. 1999; Sillen and Lee-Thorp 1994), the relation between OR_{Sr} and OR_{Ba} places new constraints on the identification of predator/prey relationships. Various cases are illustrated in the following sections. They show how the relation between OR_{Sr} and OR_{Ba} could be used to trace the general pathways of Ca, Sr and Ba in biological terrestrial systems and to reassess the biogeochemistry of Sr/Ca and Ba/Ca for ecological and paleodietary investigations.

Results and discussion

Biopurification of Ca along a single nutrient pathway:
laboratory experiments

Feeding experiments using laboratory rats were carried out by Lambert and Weydert-Homeyer (1993) in order to clarify how bone chemistry is affected by diet. Several diets with high and low contents of Sr, Ba and Ca were tested during the lifetime of the rats. Moreover, the phytate content of the different diets was measured. Phytates, or hexaphosphoric esters, are present in plant biomass

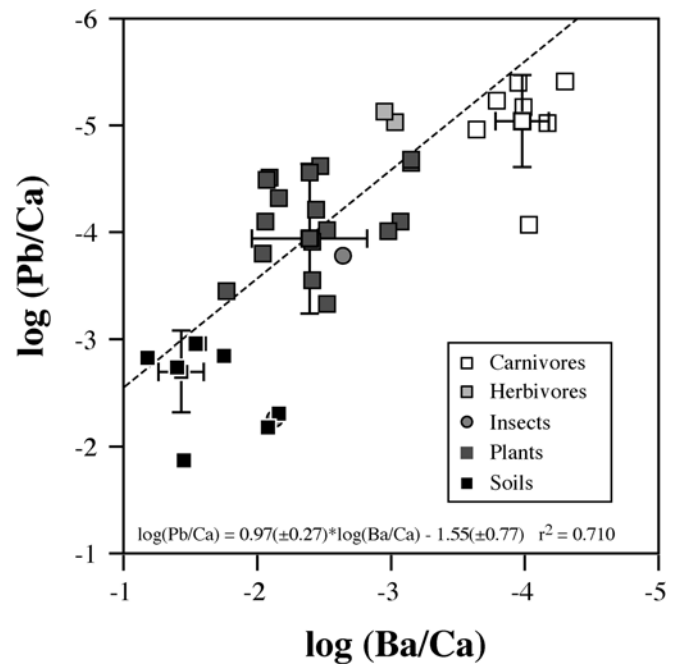


Fig. 3 Distribution of $\log(Ba/Ca)$ vs. $\log(Pb/Ca)$ values in soils, plants, bones of herbivores and carnivores for the trophic chains. Data from Elias et al. 1982). see Fig. 1 for details

(Knudsen et al. 1996) and possess a strong affinity for Ca (but also for other major cations) with which they form insoluble complexes (Taylor 1990). This set of data may be used to test the hypothesis that the OR_{Sr} vs. OR_{Ba} plots (from diet to bone) match the relation $OR_{Ba} = OR_{Sr}^{1.79 \pm 0.33}$. The OR_{Sr} and OR_{Ba} values obtained largely fall within the bounds of the predicted relationship (Fig. 4). Phytate-corrected values of OR_{Sr} and OR_{Ba} , despite their very low values, also mostly fall within these limits. It is thus clear that taken together, OR_{Sr} and OR_{Ba} enable one to identify unambiguously nutrient-to-consumer relationships.

Biopurification of Ca along a single nutrient pathway:
simple food chains

The grazing food chain composed of sedges, voles and martens in the survey published by Elias et al. (1982) has been considered to be the simplest “natural” example available of the biopurification of Ca. Voles are the principal herbivore living in the meadow community of the Thompson Canyon, and are in turn the principal component of the diet of martens, the ultimate carnivores in this food chain. Moreover, this study presents data concerning insects that could be considered as the single nutrient pathway of Ca, Sr and Ba for shrews. The Sr/Ca and Ba/Ca values of voles/sedges, martens/voles and shrews/insects ratios match the power law defined by $OR_{Ba} = OR_{Sr}^{1.79 \pm 0.33}$. The trophic step from plants to voles is characterized by higher values and SD of OR_{Sr} and OR_{Ba} (0.3 ± 0.09 and 0.17 ± 0.08 , respectively) in comparison to the trophic step involving voles and martens (0.17 ± 0.04 and 0.09 ± 0.04 , respectively). Concerning absolute

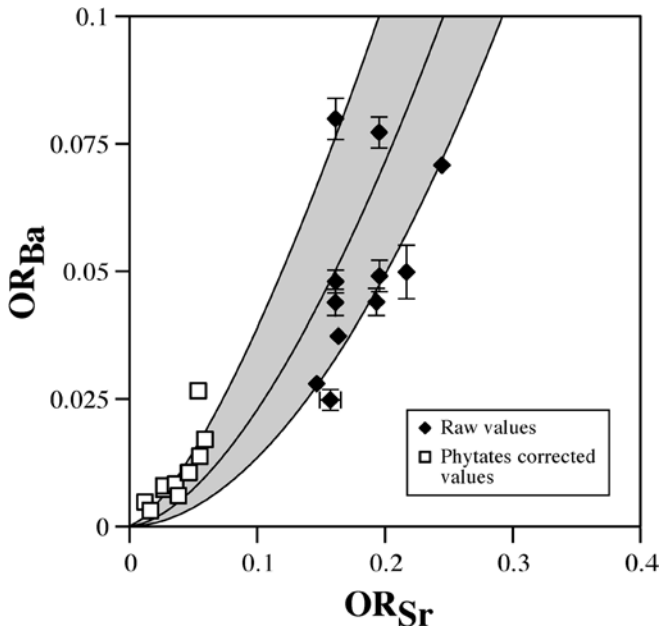


Fig. 4 Calculated OR_{Sr} and OR_{Ba} for diet-to-bone transfers with experimental rats. The equation $OR_{Ba} = OR_{Sr}^{1.79 \pm 0.33}$ is shown by the shaded area. Assuming that phytates have no sizeable influence upon Sr and Ba ingestion in the gastro-intestinal tract, corrected Sr/Ca and Ba/Ca ratios of diets with phytates were performed by dividing Ca content by the phytate content, inducing higher Sr/Ca and Ba/Ca ratios and in turn, lower OR_{Sr} and OR_{Ba} . Data from Lambert and Weydert-Homeyer (1993)

OR values, these results are quite surprising since voles and martens are both mammals and were thus expected to have similar OR_{Sr} and OR_{Ba} values with respect to their diets. However, the higher OR_{Sr} and OR_{Ba} ratios from sedges to voles can be explained by the presence of phytates in the leaves of sedges, which may induce less efficient ingestion by the digestive tract. The decrease in variability at a higher trophic level is due to the progressive impoverishment of the Sr and Ba abundance and to the consequently narrower variability of the Sr/Ca and Ba/Ca ratios (Burton et al. 1999). Nevertheless, this “natural” predator-prey example exhibits a greater scattering of the OR_{Sr} and OR_{Ba} ratios in comparison to the experimental data. As levels in a whole bone indicate the diet of the last 2–4 years of the organism, the migration of the animals and/or seasonal fluctuations could be sources of variation in the Sr, Ba and Ca inputs. Otherwise, ontogeny is known to influence the calcemetry of mammals and thus these ratios (e.g. Sillen and Kavanagh 1982). In the absence of further data, this case illustrates the minimal variability which can exist in a mammalian food chain with regard to a single-nutrient pathway.

Identification of multiple sources of nutrients

By analogy with stable isotope ratios (e.g. see the discussions: Ben-David and Schell 2001; Phillips 2001; Koch and Phillips 2002; Phillips and Koch 2002; Robbins et al. 2002), the diet of an animal could be considered in a

first approximation as a mixture of several foods with distinct Sr, Ba and Ca values. Considering two foods to have end-member values of Sr/Ca and Ba/Ca, there is only one combination of the foods that matches the OR_{Sr} vs. OR_{Ba} power law between nutrients and consumer. In other words, one can replace $(Sr/Ca)_{n-1}$ and $(Ba/Ca)_{n-1}$ in Eq. 2 by:

$$(Sr/Ca)_{n-1} = x_1 \cdot (Sr/Ca)_{n-1}^{f1} + x_2 \cdot (Sr/Ca)_{n-1}^{f2} \quad (5)$$

$$(Ba/Ca)_{n-1} = x_1 \cdot (Ba/Ca)_{n-1}^{f1} + x_2 \cdot (Ba/Ca)_{n-1}^{f2} \quad (6)$$

with $x_1 + x_2 = 1$, where f1 and f2 are two foods with distinct Sr/Ca and Ba/Ca ratios and x_1 and x_2 the proportion of f1 and f2. By varying the value of x_1 or x_2 between 0 and 1, there is one solution for which the equation verifies the value of the coefficient as 1.79 ± 0.33 . However, two assumptions must be met before using elemental ratios in such mixing equations. First, as for $\delta^{13}C$ and $\delta^{15}N$ mixing models which are based on the $^{12}C/^{13}C$ and $^{15}N/^{14}N$ ratios, the ratio of the heavier element (i.e. Sr and Ba) to the lighter one (i.e. Ca) must be low enough that it closely approximates the abundance in atom percents of the heavier element. In the case of Sr and Ba in the mineral fraction of the bones (composed of hydroxylapatite) the Sr/Ca and Ba/Ca ratios are typically in the range 10^{-2} – 10^{-4} , so that the Sr/Ca and Ba/Ca ratios range from 1/99 to 1/9,999 whereas the proportions of Sr and Ba in atom percent range from 1/100 to 1/1,000. Second, the Ca content in the different foods must be similar because a high Ca content in one of the foods will override the Sr/Ca and Ba/Ca of the mixture. Field studies of the Southwestern Cape (South Africa), first published by Sealy and Sillen (1988), and then by Gilbert et al. (1994) and Sillen and Lee-Thorp (1994) documents this approach well. At the time of these studies, only the Sr/Ca ratio was used to reconstruct trophic relationships and, based upon an established average value of 0.2 for OR_{Sr} (Sillen and Kavanagh 1982), these authors claimed that hyraxes were the preferred prey of leopards ($OR_{Sr} = 0.29$). By considering both OR_{Sr} and OR_{Ba} (Figs. 5, 6), it becomes evident that this assumption should be reviewed. Antelopes, comprising here elands, springboks, steenboks and grysboks, constitute one component of the diet of leopards which is at least as important as hyraxes. Note that the Sr/Ca values are equal to $1.6 \times 10^{-3} \pm 5.1 \times 10^{-4}$, $3.7 \times 10^{-3} \pm 1.3 \times 10^{-3}$ and $1.3 \times 10^{-3} \pm 6.9 \times 10^{-4}$ and the Ba/Ca values are equal to $4.7 \times 10^{-3} \pm 3.0 \times 10^{-4}$, $2.6 \times 10^{-4} \pm 1.9 \times 10^{-4}$ and $1.2 \times 10^{-4} \pm 1.2 \times 10^{-4}$ for antelopes, hyraxes and leopards, respectively, which are in the range of the classic values given for Sr and Ba abundance in biogenic hydroxylapatite. Taking an average $\log(Sr/Ca)$ value of -2.81 , -2.43 and -2.88 and an average $\log(Ba/Ca)$ value of -3.33 , -3.59 and -3.92 for antelopes, hyraxes and leopards, respectively, the allometric coefficient α (1.79 ± 0.33) is verified for a consumption of $58 \pm 17\%$ antelopes by leopards, a feature supported by classic ethological considerations. However, this is a rough estimate of the

composition of a leopard's diet because OR_{Sr} and OR_{Ba} were calculated with mean leopard, antelope and hyrax Sr/Ca and Ba/Ca values. Considering Sr/Ca and Ba/Ca values for each sample, there is a clear overlap between leopards and herbivores and it becomes evident that the consumption of about 60% antelope by leopards is not systematic (Fig. 7). This scattering is partly due to the geological heterogeneity of the studied area (situated around 19°E and between 32° and 34°S; Gilbert et al. 1994) which is composed of magmatic (Nieuwoudtville dolerite) and sedimentary rocks (Gifberg and Table Mountain sandstones). Unfortunately, these authors do not report the locality for each sample, and it is not possible to examine specific trophic relationships at the regional level. Thus, this global pattern exhibits extreme and sometimes surprising predator/prey relationships. An example is the UCT#1892 leopard which is characterized by a Sr/Ca ratio higher than that of all the antelopes and hyraxes. It is likely that this leopard did not eat antelopes or hyraxes from the areas mentioned above. Other examples are the UCT#1890 and UCT#1893 leopards which could not have consumed most of the antelopes and the UCT#1891 leopard which was enriched in Ba in comparison to the four most log(Ba/Ca)-negative hyraxes. The lack of information concerning the leopards' habitat, sex, and age-at-death does not allow one to quantify precisely the individual diet of the leopards.

However, this calculation is valid because it has been assumed that the diet of the leopards is mostly composed of meat of which the Ca content can be considered constant (i.e. 100 µg/g, Balter et al. 2001). In cases of omnivorous diets, this modelling should take into account the Ca content of each foodstuff and Eqs. 5 and 5' become Eqs. 6 and 6', respectively: $(Sr/Ca)_{n-1} = [(1-x) \cdot (Sr)_{n-1}^{f1} + x \cdot (Sr)_{n-1}^{f2}] / [(1-x) \cdot (Ca)_{n-1}^{f1} + x \cdot (Ca)_{n-1}^{f2}]$ (Eq. 6); $(Ba/Ca)_{n-1} =$

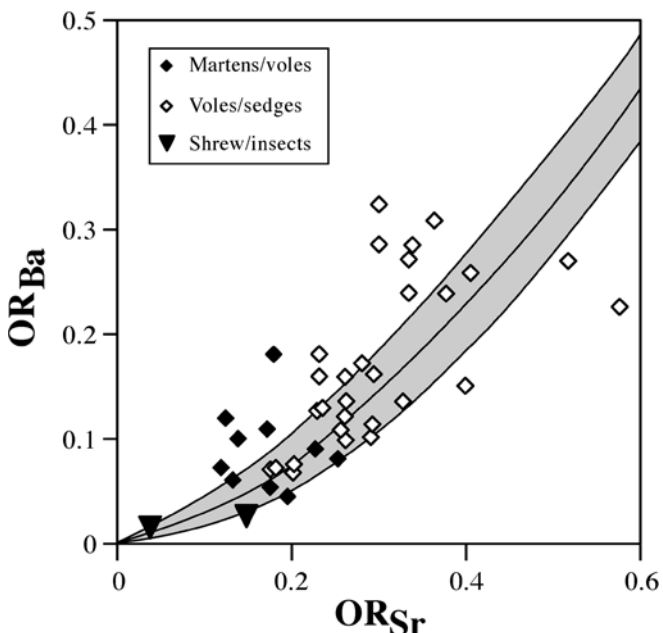


Fig. 5 Calculated OR_{Sr} and OR_{Ba} values for diet-to-bone transfers for several mammals. The equation $OR_{Ba} = OR_{Sr}^{1.79 \pm 0.33}$ is shown by the shaded area. All the diets are assumed to be mono-specific. Data from Elias et al. (1982)

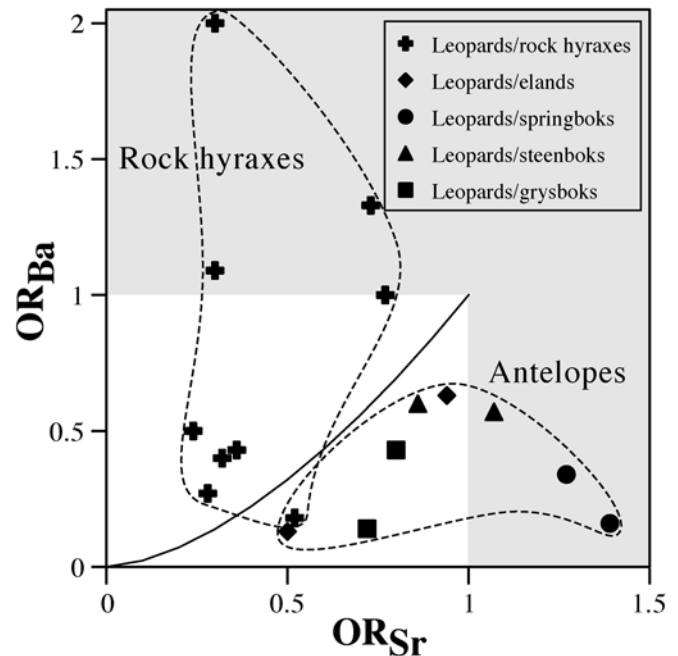


Fig. 6 Calculated OR_{Sr} and OR_{Ba} values for diet-to-bone transfers for leopards ($n=9$) of the Southwestern Cape. The equation $OR_{Ba} = OR_{Sr}^{1.79}$ is shown and the shaded areas represent $OR_{Sr} > 1$ and $OR_{Ba} > 1$. Data from Gilbert et al. (1994)

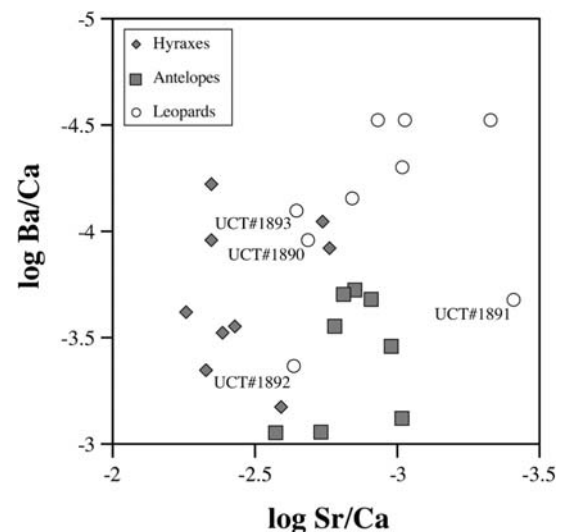


Fig. 7 Distribution of $\log(Sr/Ca)$ vs. $\log(Ba/Ca)$ values for bones of herbivores and carnivores of the Southwestern Cape. Data from Gilbert et al. (1994)

$[(1-x) \cdot (Ba)_{n-1}^{f1} + x \cdot (Ba)_{n-1}^{f2}] / [(1-x) \cdot (Ca)_{n-1}^{f1} + x \cdot (Ca)_{n-1}^{f2}]$ (Eq. 6'), which are similar to those given by Phillips and Koch (2002) for $\delta^{13}C$ and $\delta^{15}N$ stable isotope mixing when C and N concentrations are incorporated. The scattering of the Sr/Ca and Ba/Ca values in the Southwestern Cape trophic chain is also probably due to the fact that leopards break the bones of antelopes to extract their marrow, thus digesting one fraction which is highly rich in Ca.

However, as suggested by Burton et al. (1999), the present work confirms that the statistical relationship between Sr/Ca and Ba/Ca along trophic chains may be used in archaeological studies to detect possible diagenetic effects (Balter et al. 2002). This is based on the fact that it

is unlikely that diagenesis affects bones of herbivores and carnivores in such a way that the relative biological discrimination between Sr and Ba remains unchanged. However, the variability of the Sr and Ba discrimination and thus the influence of a mixed diet with a high or low Sr, Ba and Ca content, needs to be investigated either with experimentally controlled diets or with analyses of mammals sharing known predator/prey relationships.

It is likely that other non-essential trace elements could be discriminated in favour of Ca. If this were so, the other elements may indicate some additional nutrient pathways within mammals. This could thus improve our knowledge of elementary fluxes at the scale of the trophic chain which are controlled by each organism and in turn by the whole community structure.

Conclusions

This study shows how the Sr/Ca and Ba/Ca ratios concomitantly decrease in terrestrial trophic chains. It demonstrates that the positive degrees by which Sr and Ba are discriminated in favour of Ca within mammals are linked by an allometric law with the form $OR_{Ba} = OR_{\alpha Sr}$ where $\alpha = 1.79 \pm 0.33$ and where OR_{Ba} and OR_{Sr} are the partition coefficients (observed ratio) between two trophic positions. The relevance of this relation was strengthened by using experimental data and examining several cases of a single nutrient pathway in different natural contexts. The existence of such an equation allows one to quantify mixed diets with two components with distinct Sr/Ca and Ba/Ca ratios. However, this requires several assumptions to be made which may constitute some limitations for the application of the mass balance equations in ecological studies. It is likely that biopurification of Ca could be depicted by means of its allometric relations with other trace elements (e.g. heavy alkaline earth elements). This would extend the possibility of studying complex predator/prey relationships within mammals in addition to $\delta^{13}C$ and $\delta^{15}N$ stable isotope ratios. In the present circumstances, the results highlight the need to carry out further experimentally controlled dietary studies and field surveys.

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