Visualizing the Seasonal Round: A theoretical experiment with strontium isotope profiles in ovicaprine teeth

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Meiggs D. C. 2007. – Visualizing the Seasonal Round: A theoretical experiment with strontium isotope profiles in ovicaprine teeth. *Anthropozoologica* 42 (2): 107-127.

ABSTRACT
The seasonal movements and organization of herds are essential features of pastoral economies. Archaeologists have sought to identify herd mobility using taxa frequencies, osteological measurements, and age profiles. Isotope analysis of faunal tooth enamel and particularly intra-tooth profiles are promising as independent lines of evidence for prehistoric mobility and seasonality. Strontium isotopes ($^{87}Sr/^{86}Sr$) can provide excellent evidence of geographic mobility. However, an understanding of physiological processes which incorporate $^{87}Sr/^{86}Sr$ into tooth enamel is lacking. Based on studies of strontium ecology, calcium metabolism, and amelogenesis, an *a priori* model is presented of $^{87}Sr/^{86}Sr$ ratio profiles in teeth in which animal movement and diet are independent variants. The results of the model show a close and sensitive relationship between movement and observed $^{87}Sr/^{86}Sr$ values, but also a significant effect due to differences in calcium content between components of mixed diets. This presents the possibility that $^{87}Sr/^{86}Sr$ profiles can be used in conjunction with Sr concentrations in enamel as environmental and dietary evidence.

KEY WORDS
Calcium,
strontium,
metabolism,
isotope,
transhumance.

RÉSUMÉ
Visualiser la mobilité saisonnière : un modèle théorique à partir des profils isotopiques du strontium dans les dents de caprinés.
Les mouvements saisonniers et l'organisation des troupeaux sont des éléments essentiels des économies pastorales. Les archéologues ont cherché à identifier la mobilité des troupeaux en utilisant les fréquences des taxons, les mesures ostéologiques et les profils d'âge. L'analyse isotopique de l'émail dentaire des animaux et particulièrement les profils intra-dentaires sont prometteurs comme signes indépendants de la mobilité et de la saisonnalité en Préhistoire. Les isotopes du strontium ($^{87}Sr/^{86}Sr$), notamment, peuvent constituer d'excellents témoins d'une mobilité géographique. Cependant, une bonne compréhension des processus physiologiques menant à l'incorporation du

$^{87}Sr/^{86}Sr$ dans l'émail dentaire fait toujours défaut. Basé sur des connaissances de l'écologie du strontium, du métabolisme du calcium et de l'amélogénèse, un modèle est proposé, prévoyant l'enregistrement des profils de $^{87}Sr/^{86}Sr$ dans les dents, modèle dans lequel la mobilité de l'animal et son alimentation sont des variantes indépendantes. Les résultats du modèle montrent une relation étroite et sensible entre la mobilité et les valeurs de $^{87}Sr/^{86}Sr$ observées, mais aussi un effet significatif des teneurs respectives en calcium des différents composants d'une alimentation mixte. Le modèle suggère que les profils de $^{87}Sr/^{86}Sr$ pourraient être utilisés en conjonction avec les concentrations de Sr dans l'émail comme témoins environnementaux et alimentaires.

MOTS CLÉS
Calcium, strontium, métabolisme, isotope, transhumance.

RESUMEN

Visualizando la estacionalidad : Un experimento teórico con perfiles isotópicos de estroncio en dientes de ovicaprinos.

La programación y organización del aprovisionamiento de los rebaños es un rasgo esencial de las economías pastoriles. Los arqueólogos han tratado de identificar la movilidad de los rebaños empleando frecuencia de taxa, medidas osteológicas y perfiles de edad de los conjuntos. Los análisis isotópicos del esmalte dental de la fauna, y particularmente perfiles intra-dentarios, son promisorios como línea de evidencia independiente para la movilidad y estacionalidad prehistórica. Los isótopos de estroncio ($^{87}Sr/^{86}Sr$) pueden proveer un excelente proxy de movilidad geográfica. Pero todavía falta la comprensión de los procesos fisiológicos de la incorporación del $^{87}Sr/^{86}Sr$ en el esmalte dental. Basado en estudios de ecología del estroncio, metabolismo del calcio y en la amelogénesis, se presenta un modelo *a priori* de perfiles de índices $^{87}Sr/^{86}Sr$ en dientes de animales cuyo movimiento y dieta variaron independientemente. Los resultados del modelo muestra una cercana y sensitiva relación entre movimiento y los valores observados de $^{87}Sr/^{86}Sr$, pero adicionalmente un efecto significativo debido a diferencias en el contenido de calcio entre componentes de las dietas mixtas. Esto plantea la posibilidad de que los perfiles de $^{87}Sr/^{86}Sr$ puedan ser empleados como proxies ambientales y dietarios en conjunto con las concentraciones de Sr en el esmalte dentario.

PALABRAS CLAVE
Calcio, estroncio, metabolismo, isótopos, trashumancia.

INTRODUCTION

Herd mobility plays a central role in pastoral economies, both past and present. As a result, elucidating the nature of herding strategies in prehistoric societies has been a focus of much archaeological research (*e.g.* Halstead 1981, 1996; Geddes 1983, Levy 1983, Cribb 1991, Bar-Yosef & Khazanov 1992, Bernbeck 1992, Köhler-Rollefson 1992, Greenfield 1999, Martin 1999, Arnold & Greenfield 2004). How flocks were provisioned in prehistory has important implications for basic social structures. Ethnographic studies document relationships between different herding strategies and the organization of labor and production, group interaction and sharing, and patterns in resource exploitation and residential mobility (Bates 1973, Bates & Lees 1977, Hole 1978, Ingold 1986, Casimir 1988, 1992; Agrawal 1999, Salzman 2002). Addressing these issues, however, based on species representation, mortality profiles, and other osteological data has been difficult, as they cannot fully address the seasonal and geographic character of herd management (*cf.* Halstead 2005). Isotope measurements of faunal tooth enamel have been used to adduce evidence for palaeoenvironments, diet and migration in prehistoric animal populations (Delgado Huertas *et al.* 1995, Gannes *et al.* 1998, Hobson 1999, Sponheimer & Lee-Thorp 1999, Schoeninger *et al.* 2000, Zazzo *et al.* 2000, Hoppe 2004, Hoppe *et al.* 2006). Specifically, due to the time-progressive nature of enamel formation (amelogenesis), analysis of intra-tooth enamel samples allows reconstruction of seasonal and annual changes during the life of the individual (Hoppe *et al.* 1999, Wiedemann *et al.* 1999, Balasse *et al.* 2000, Bocherens *et al.* 2001, Balasse 2002, 2003; Balasse *et al.* 2002, Balasse *et al.* 2003, Sponheimer *et al.* 2006). Isotope analyses provide an advantageous perspective as independent proxies of these aspects of an animal's life. Isotope values in teeth do not, however, necessarily bear an obvious or simple relationship to the animal's environment or behavior. In an effort to discern processes by which the isotopes of particular elements become incorporated into enamel, research using carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) isotopes has investigated sources of environmental variation, and how these are transformed by mammalian metabolism and amelogenesis into biogenic signatures (*e.g.* Ambrose & Norr 1993, Bryant *et al.* 1996, Fricke & O'Neil 1996, Kohn *et al.* 1996, Gannes del Rio *et al.* 1998, Lee-Thorp 2002, Passey & Cerling 2002).

Unlike lighter isotopes, variability in strontium isotope ratios ($^{87}Sr/^{86}Sr$) arises from geochemical factors. Thus it is particularly well-suited to investigate the geographic extent of herding strategies such as the emergence of transhumant pastoralism. Strontium isotope ratios have been usefully applied to a variety of archaeological situations to investigate human residential mobility and migration, as well as to the migration and habitat of animal populations (Vogel *et al.* 1990, Hoppe, Koch *et al.* 1999, Price *et al.* 2000, Balasse, Ambrose *et al.* 2002, Schweissing & Grupe 2003, Hodell *et al.* 2004, Hoppe 2004, Knudson *et al.* 2005, Price *et al.* 2006). Biological processes do not significantly fractionate strontium isotopes, and diagenesis does not seem to have a substantial effect on biogenic values in dental enamel (Budd *et al.* 2000, Hoppe *et al.* 2003, Dauphin & Williams 2004, Sponheimer & Lee-Thorp 2006). A natural presumption therefore has been that values observed in tooth enamel faithfully record geography — as it is expressed in geological variability in space. But the scale of sensitivity at which this is physiologically expressed is poorly understood. How much will dietary values be attenuated and/or averaged during amelogenesis? Strontium substitutes for calcium in skeletal hydroxyapatite, and strontium *concentrations* in the body depend on dietary calcium (Comar 1963), which is under tight biological control. Mixing of strontium isotopes has been considered in the context of bone turnover and Sr residence time (*e.g.* Beard & Johnson 2000, Schweissing & Grupe 2003, Bentley 2006), but unlike bone, enamel does not remodel once formed. An understanding of specific physiological processes is critical if sequential samples of tooth enamel from an animal are to be translated into mobility patterns, particularly at small scales.

As a step in this direction this paper considers an *a priori* model of strontium isotope incorporation into ovicaprine tooth enamel as a first step to illuminate how physiology, environment, diet and movement may affect observed $^{87}Sr/^{86}Sr$ isotope ratios. The goal of the model is to explore the relationship between animal life history and measured strontium isotope profiles, as well as laying the groundwork to refine inferences possible from these data.

MODELING STRONTIUM ISOTOPES FROM DIET

The model consists of five elements (Fig. 1). It is based in an idealized landscape divided by a gradient between two arbitrary strontium isotope ratios, A and B, in which a hypothetical sheep travels in specific patterns over a time period equivalent to tooth formation (Fig. 2) — in this

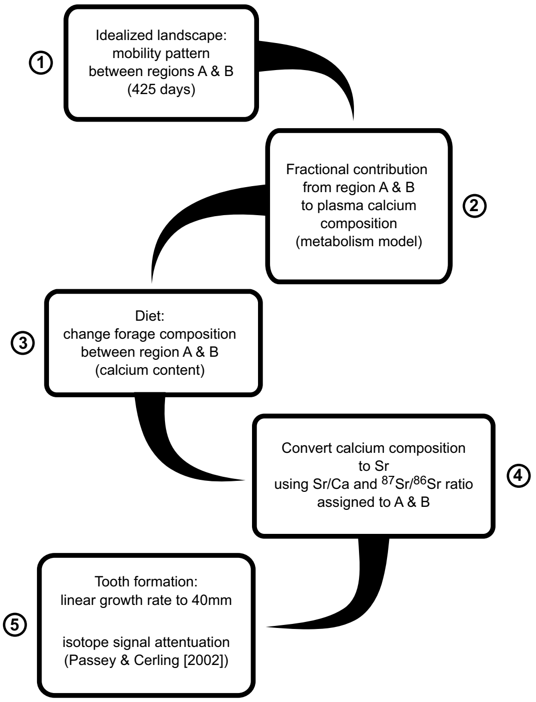

FIG. 1. – Flowchart summarizing the components of the *a priori* model.

study, 425 days for the permanent third molar (M3). To investigate the effect of diet, different forage is available in each region. Four pairs of forage combinations were used, covering a spectrum of calcium content (NRC 1985, Table 1).

A compartmental model of calcium (Ca) metabolism (Fig. 3), based on data from veterinary studies, was developed to generate fractional contribution to plasma Ca from each region iterated daily for the movement cycle. The amount of biologically available strontium is assumed to be the same across the entire landscape, making the amount of strontium incorporated through the diet a function of forage calcium content and Sr/Ca ratio for the part of the plant consumed (Elias *et al.* 1982). This allowed calculation of intermediate Sr isotope values. Lastly, time was converted to distance along the crown of the tooth, and following the technique described by Passey and Cerling (2002) to mathematically estimate attenuation during amelogenesis, model enamel Sr isotope profiles were created. In these modeled profiles movement and diet could be independently varied. The results show, within the constraints of the model, a close relationship

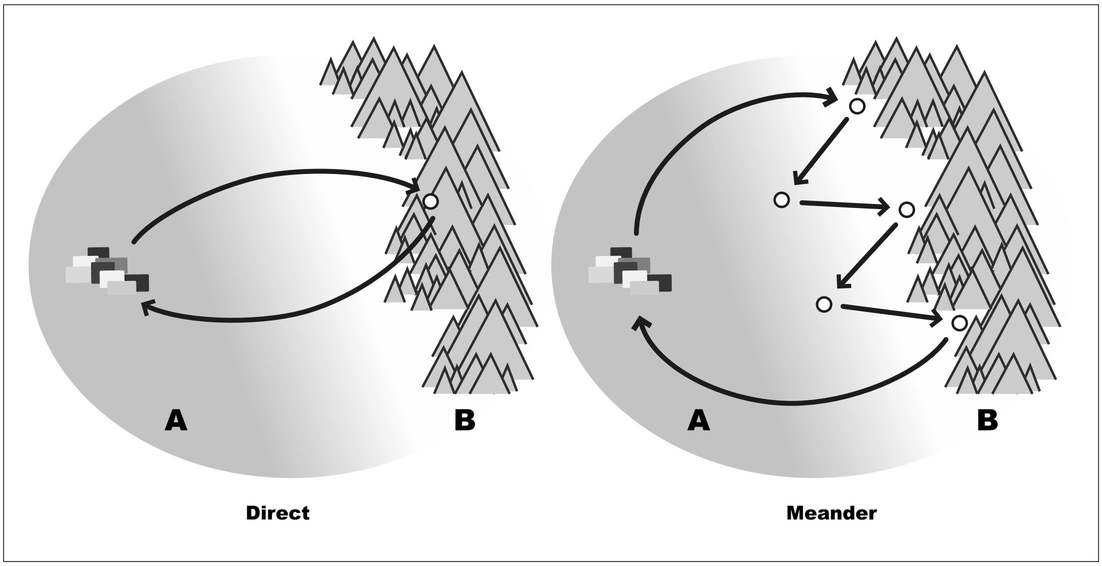

FIG. 2. — Idealized landscape and indicative movement patterns. Shaded gradient represents $^{87}Sr/^{86}Sr$ isotope change from region A to B.

TABLE 1. – Four forage pairs available forage in region A and B used with shift in Ca content indicated.

Change in forage Ca content from A to B	Region A	Region B
lower → higher	barley grain barley hay	clover, fresh mid-bloom intermountain meadow
approx. 1:1	clover hay	alfalfa hay
higher → lower	barley grain + vetch hay	intermountain meadow

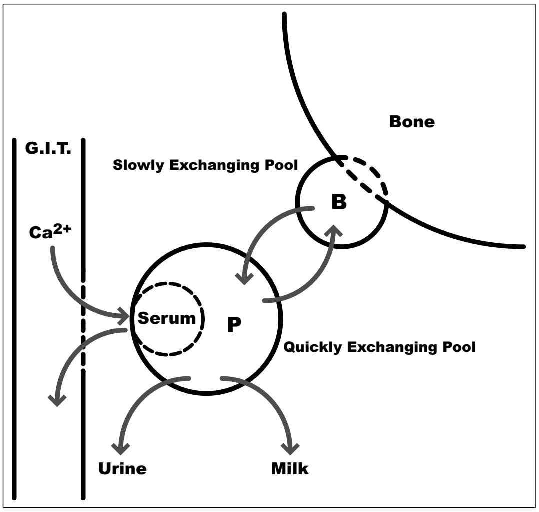

FIG. 3. — Schematic diagram of Ca compartments and flow as used in the metabolism model (No. 2 from Figure 1).

in time between dietary fluctuations and strontium isotope profiles that would be measured in enamel. Biases resulting from diet-dependent effects and parameters of amelogenesis significantly affect the profiles, however. The implications these data have for the application of strontium isotope ratios to the investigation of prehistoric herding strategies will be considered. Following the numbered boxes in Figure 1, the subsequent sections describe each portion of the model in greater detail.

NO.1. IDEALIZED LANDSCAPE: CHARACTERISTICS, MOVEMENT AND FORAGE

A hypothetical landscape was created consisting of two regions with distinct, arbitrary strontium isotope ratios. The scenario presented here arbitrarily assigns a $^{87}Sr/^{86}Sr$ value of 0.7080 to region A and 0.7070 to region B; this modest difference of 0.001 is a good starting point as a reasonable upper boundary for intra-regional variation (*cf.* Price *et al.* 1998, Price *et al.* 2002, Bentley & Knipper 2005a). Although each region has a distinct $^{87}Sr/^{86}Sr$ value, the boundary between them is not; it bisects the landscape and grades over some distance. It is indistinct and the $^{87}Sr/^{86}Sr$ ratio will change gradually as it is crossed. To make this hypothetical situation less abstract, one can imagine a small village in region A from which a herd moves toward the mountains in region B, as in Fig. 2.

The third permanent molar (M3) was chosen as the tooth modeled in the study. Therefore its formation time determines the period over which the model is evaluated. Based on eruption times (Weinrab & Sharav 1964) and radiographic study (Milhaud & Nezit 1991), a reasonable estimate is that this tooth forms beginning at 10 months of age and is completely formed and in occlusion by 24 months, or approximately 425 days. Two types of schedules were investigated, so-called 'direct' and 'meander' (Fig. 2) to encapsulate differences in movement behavior. The 'direct' pattern — analogous to a seasonal transhumant pattern — is one in which the sheep move from region A to region B over a 21-day travel period. The sheep stay in region B for 120 days before returning to region A in a similar fashion. Characteristic of this pattern is that movement is roughly *perpendicular* to the isotope boundary. Thus, the herd is moving in the most direct manner across this boundary and the shift in isotope values from region A to region B will be the most abrupt. This contrasts with a 'meander' schedule, in which movement is both across *and* along the boundary. Several stops can be made after the herd initially moves from region A, some of them firmly in region B and some to a greater or lesser degree in region A. This schedule type, depending on its periodicity, could perhaps be analogous to a horizontal transhumance pattern (Bernbeck 1992) but other alternatives are possible. Two variants in the periodicity of the "meander" schedule were examined (Fig. 4). The variant with only one period fully in region B is somewhat similar to the 'direct' pattern but with more gradual movement across the isotope boundary. Within the metabolism model (discussed below), each of these three cases of mobility were represented by a mathematical expression, and the gradient expressed by the fractional contribution of calcium from each region.

Herd mobility strategies are designed to take advantage of ephemeral, seasonal forage resources. Such geographic movement is bound to include different plant communities and soil conditions, which may affect both the amount of calcium and strontium consumed. Calcium concentrations can vary widely between different plants, and parts of plants, and regions (NRC 1958, NRC 1985, Khan *et al.* 2004). Therefore, in addition to an isotope value, each region has a distinct forage. The suite of forage chosen represents a range of plant parts and Ca contents (Table 2). Four pairs of forage were investigated, with the change in Ca content from A to B being either lower to higher, of equivalent Ca content, or higher to lower (Table 1).

No. 2. Calcium metabolism in sheep: characteristics and compartment model

Interest in the nature of nutritional dynamics in domestic stock (*e.g.* Hacker & Ternouth 1987) has generated a substantial body of veterinary research on Ca metabolism in sheep. Reflecting its crucial biological functions, Ca is tightly regulated (Moodie 1975, Underwood & Suttle 1999) and its absorption, retention and excretion in sheep have been related to a variety of factors, such as: pregnancy, lactation, age, dietary phosphorus, vitamin D, protein and total food intake (Braithwaite *et al.* 1969, Braithwaite & Riazuddin 1971, Braithwaite 1982, 1983a, 1983b; Field *et al.* 1985, Chrisp *et al.* 1989, Fredeen 1990, Rajaratne *et al.* 1990, Liesegang & Risteli 2005). Homeostasis in sheep is maintained either by adjustment in the absorption of Ca from the gastrointestinal tract (GIT) or by resorption of bone (Braithwaite 1974, Fredeen & van Kessel 1990), so it is best "…from a physiological and nutritional standpoint to consider what proportion of Ca requirement will be furnished by the diet and the skeleton at different levels of Ca demand […]" (Chrisp, Sykes *et al.* 1989: 54-5). Efficiency of absorption from the GIT decreases with age, and in mature animals is independent of dietary intake (Braithwaite & Riazuddin 1971). It has been shown that during pregnancy and lactation, bone resorption

Table 2. – Calcium content (% as fed, not dry basis) for all forages included in this study (data from NRC 1985). Sr/Ca ratios calculated from Elias *et al.* (1982, table 2). Value for 'seeds' used for all except clover, where Sr/Ca for 'leaves' was used.

Forage	Ca (% mass, as-fed)	Sr/Ca
Alfalfa hay (*Medicago sativa*)	1.27	
Barley hay (*Hordeum vulgare*)	0.20	0.014575
Barley grain	0.04	
Clover, fresh mid-bloom (*Trifolium pretense*)	0.46	0.014866
Clover hay	1.24	
Intermountain meadow plants	0.58	0.014575
Vetch hay (*Vicia spp.*)	1.05	

increases regardless of dietary Ca content (Braithwaite 1983a, Fredeen 1990). These studies form a basis with which to model flux in the plasma Ca pool available for amelogenesis.

In order to physiologically quantify the flow of Ca in animals, researchers have used isotope tracer techniques coupled with compartment analysis. Animal metabolism can be considered a collection of pools, or 'compartments', composed of identical particles in exchange with each other. A compartment is therefore a *kinetically distinct* pool in the body which tends to remain a constant size while undergoing turnover, *i.e.* equal rates of input and output (see *e.g.* Takagi & Block 1991). Compartment analysis assumes that these pools can be identified using isotope tracers and described by exponential equations (Aubert *et al.* 1963; Shipley & Clark 1972). The flows between body pools, then, can be described by relatively simple differential equations and their parameters, incorporating mass balance calculations. The kinetic model of Ca metabolism used here was constructed using software (ModelMaker, Cherwell Scientific) capable of easily calculating the multiple flows in a physiological system. The model necessarily assumes a steady-state metabolism over time, although the Ca demand of an animal changes throughout its life (Underwood & Suttle 1999).

The studies cited above indicate the most significant physiological effects on calcium metabolism are pregnancy/lactation and age. Parameters of calcium metabolism in four physiological 'states' were used, based on metabolism data for three-year old lactating and non-lactating ewes (Braithwaite, Glascock *et al.* 1969), and 6-month and 16-month-old wethers (Braithwaite & Riazuddin 1971). The structure of the metabolism simulation followed Braithwaite *et al.*'s (1969: 829-30) inference of a quickly exchangeable pool of calcium (P) — which is partly composed of serum plasma Ca — and a slowly exchangeable pool (B). It is important to recognize, however, that this pool does not represent the Ca pool of bone itself, but one intermediate between bone *sensu stricto*, and the more quickly exchanging P (Fig. 3). A reasonable estimate is 99% of a sheep's total Ca is stored in bone mineral (Braithwaite 1975: 322; MacFarlane 1975, Moodie 1975) which exchanges with this slow pool (B). The behavior of the quick pool (P) in each of the four physiological 'state' cases is not significantly different (Figs 5 and 6), but there are differences in the behavior of the slow pool (B) between each case. Because the behavior of the quick pool (P) is similar — this is considered to be the pool from which Ca for amelogenesis is drawn — differences between these physiological cases are not further considered in the construction of the model. Further work should, however,

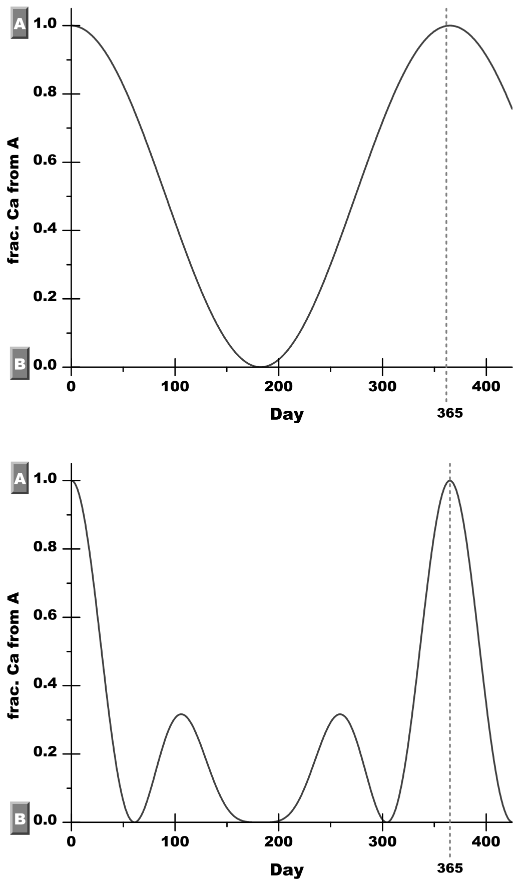

FIG. 4. – Variations in 'meander' movement schedule used, shown as fraction of contribution of region A to plasma Ca over tooth formation time.

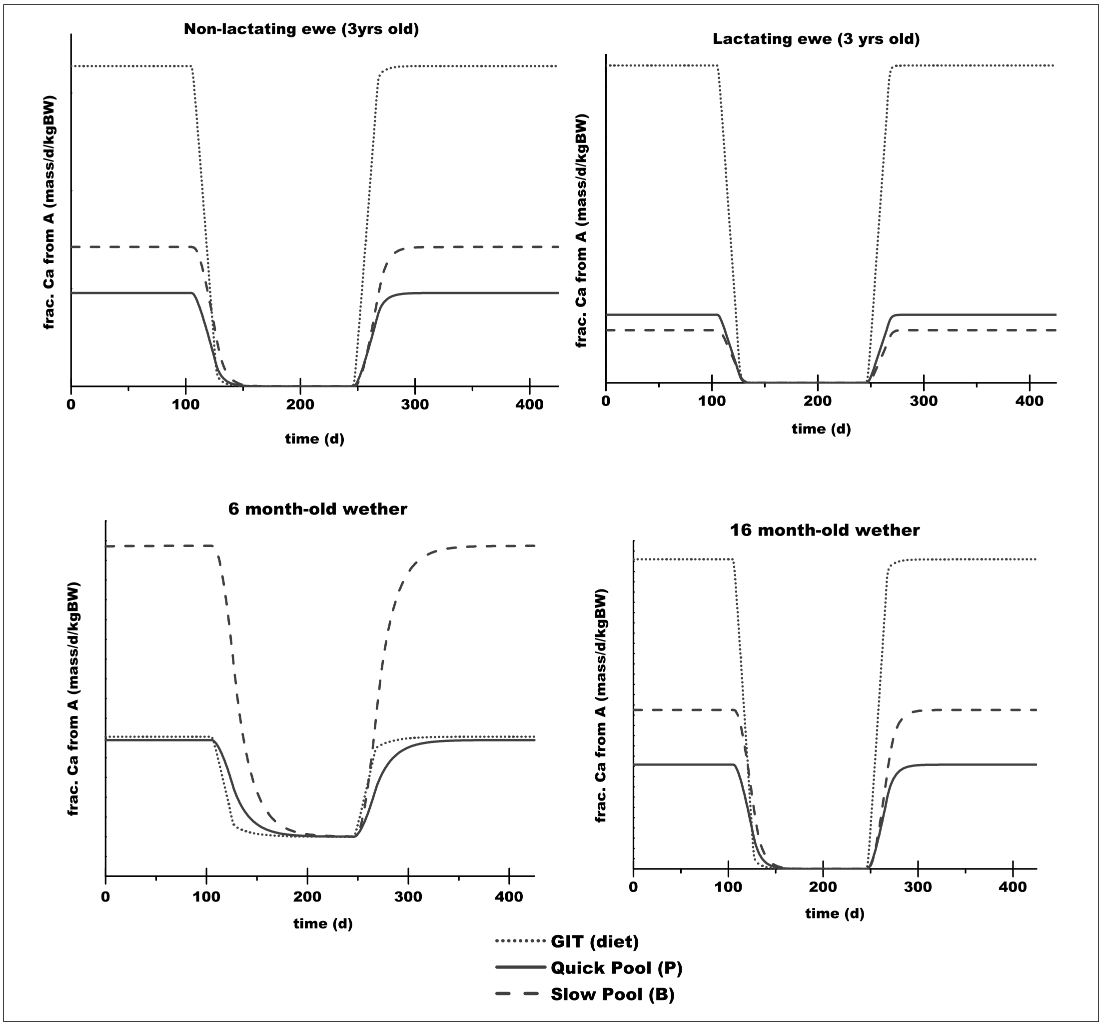

FIG. 5. – Output of Ca metabolism simulation for the 'direct' movement pattern of four physiological 'states' (clockwise from upper left: non-lactating and lactating 3 yr-old ewe [parameter data from Braithwaite *et al.* 1969, Table 3]; 16 mo. and 6 mo. old wether [Braithwaite and Riazuddin 1971, Table 3]). Solid line, P, represents fluctuations in serum Ca over time based on changes in diet input source (prop. of region A, dotted line). Dashed line represents changes in slow pool (B) values.

particularly consider the effect of large rates of bone resorption, which makes up Ca deficits in late-term and early lactating ewes (Braithwaite 1983a).

Dietary input is modeled as a fraction of Ca from region A through time according to the idealized movement schedules described above (*i.e.* 100% Ca from region A equal 1 and 100% Ca from region B equal 0). The effect on the quickly exchangeable pool (P) over 425 days was then tabulated in a spreadsheet. This produced values for each movement schedule and metabolic state (lactating, mature, etc.) over the formation time of the tooth. These data were then converted into effective or composite strontium isotope values by applying each of the dietary forage pairs and the chosen ratios for region A and B as described in the next section.

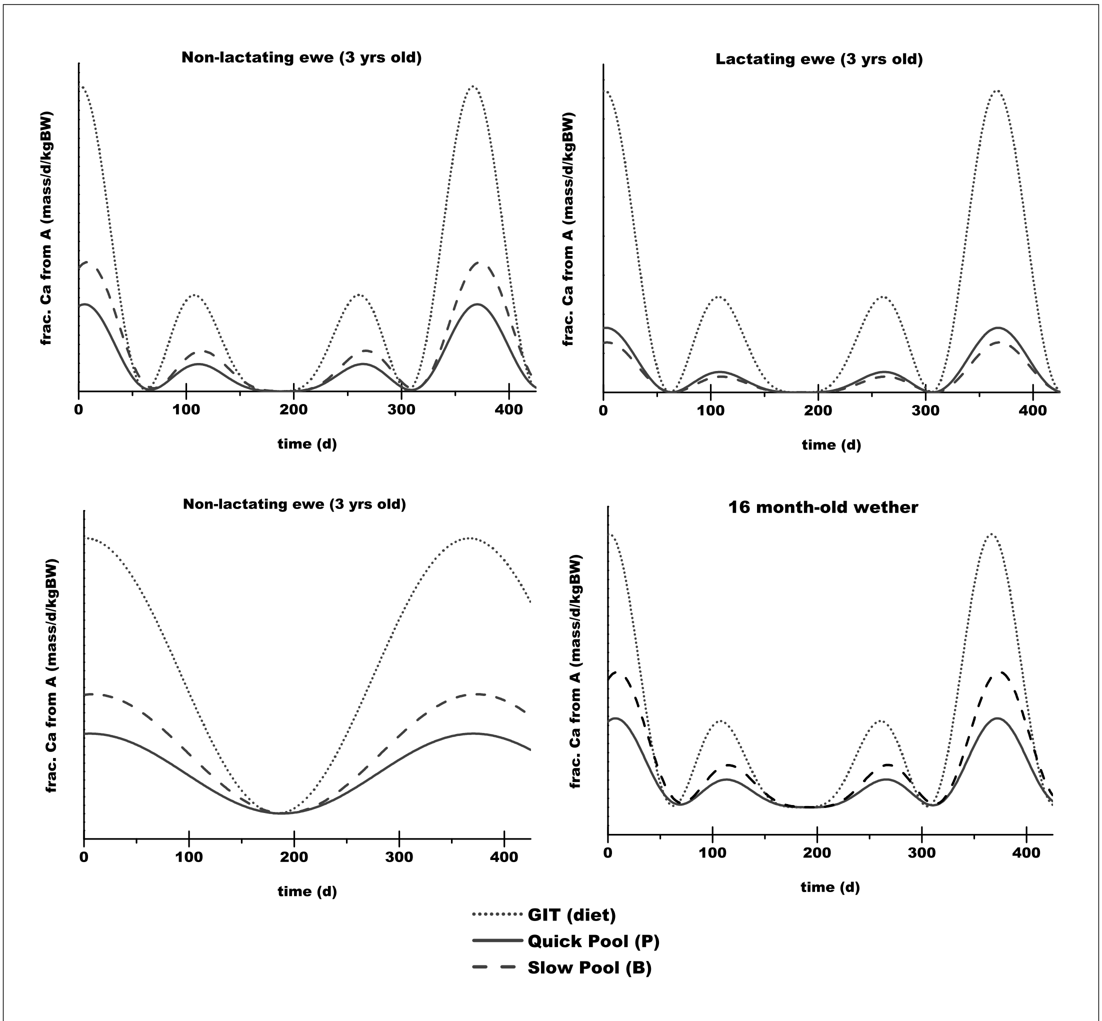

FIG. 6. – Output of Ca metabolism simulation for one and three-stop 'meander' movement pattern (clockwise from upper left: non-lactating and lactating 3yr-old ewe; three-stop cyclical pattern for 16 mo. wether and one-stop pattern for non-lactating ewe), as in Figure 5.

NOS. 3 AND 4. DIET, BIOPURIFICATION OF CALCIUM, AND STRONTIUM ISOTOPES

In order to investigate the behavior of strontium isotopes in sheep, a quantitative model of calcium metabolism is a necessary starting point. Calcium is a crucial component in skeletal tissue. Strontium behaves in a chemically similar fashion, and is nearly ubiquitous in the environment. More specifically, it can substitute for Ca in skeletal hydroxyapatite. Early investigation of the effect of nuclear fallout led to the recognition of biological discrimination against strontium progressively through the food chain from the soil (*e.g.* Comar 1963), or 'biopurification' of calcium (Elias, Hirao *et al.* 1982). In general, this translates into a trophic-level effect in the Sr/Ca ratio, but critically, "[within] normal dietary ranges the stable strontium to calcium ratio…will be directly related to the ratio that exists in the diet" (Comar & Wasserman 1964: 530) in a given biological system. This characteristic discrimination factor against ingested strontium may be constant, but this applies to the *whole* diet, and in mixed diets both the strontium and calcium content (and Sr/Ca ratio) of *all* components in the diet must be taken into account. In this experiment, the strontium content was held constant, *i.e.* it's biological representation only changes as a function of changing dietary Ca —not as function of changing Sr availability (*cf.* Capo *et al.* 1998, Crout *et al.* 1998, Price, Burton *et al.* 2002). Since dietary Ca intake can vary over orders of magnitude, the amount of strontium which enters the body pool can similarly vary (*cf.* Ericson 1989). Different species of plants, and parts of plants, will display different Sr/Ca in the same environment, for example (Bowen & Dymond 1955, Vose & Koontz 1959, Elias, Hirao *et al.* 1982, Runia 1987). This linkage between dietary calcium and absorbed strontium can create a strongly non-linear relationship in mixed diets — either between component representation, or as in this experiment between geographic source — particularly when calcium content differs greatly between dietary components (Burton & Wright 1995). The Sr/Ca ratio of a range of dietary combinations can be strongly non-linear, and will only be linear if the Ca content of the mixture is equivalent (Fig. 7 and Table 1).

Although the amount of Sr present in the diet is affected by biopurification, its isotopes are not. In particular, the ratio $^{87}Sr/^{86}Sr$ depends on the geochemical composition and age of a particular geologic formation, and the small relative difference in the masses between the isotopes leaves

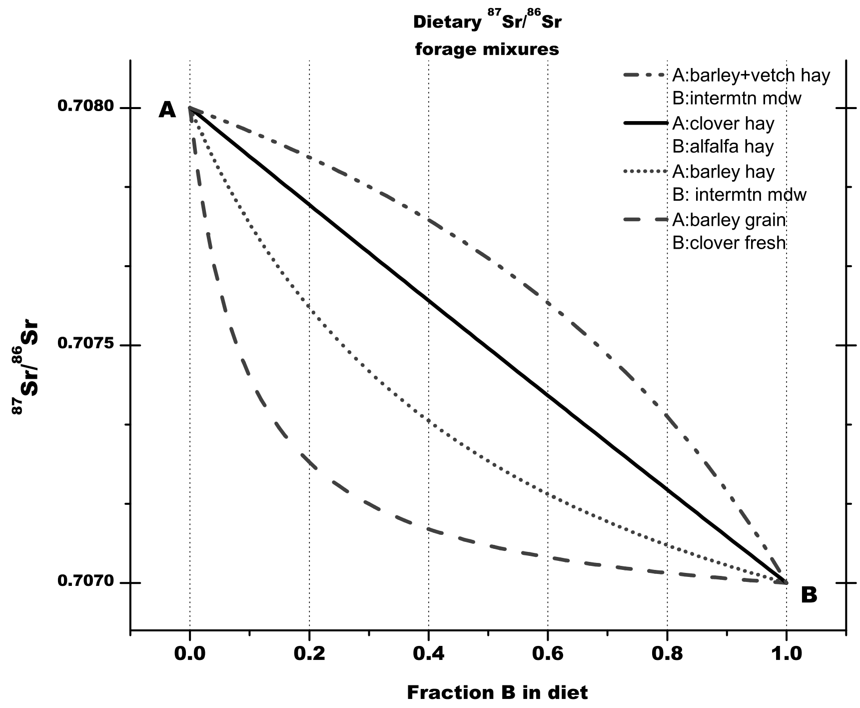

FIG. 7. – Change in $^{87}Sr/^{86}Sr$ isotope values between forage pairs as increasing proportion of Ca from region B in the diet.

them unaffected by biological processes (*i.e.* does not fractionate). Their geographic variability stems from the origins and geochemistry of particular rock formations. Briefly, ^{87}Sr is a stable, radiogenic product of the slow decay of rubidium-87, whereas ^{86}Sr is stable. So the $^{87}Sr/^{86}Sr$ ratio depends on the Rb/Sr ratio in a given rock and only varies over geological time scales. Generally, the geochemical behavior of Rb and Sr produces an uneven geographic distribution of rocks with potential for higher or lower $^{87}Sr/^{86}Sr$ (Faure 1986, Dickin 1995). Strontium isotopes have thus been used in archaeology and palaeoecology as a proxy for migration and mobility (Hoppe, Koch *et al.* 1999, Balasse, Ambrose *et al.* 2002, Hoppe 2004, Bentley 2006).

Since the numerical values of data from the Ca metabolism step of the model ranged from zero to one (*i.e.* from Ca from region B to that from region A), it was a simple matter in a spreadsheet to calculate the proportion of dietary Ca from each region and weight these based on each of the forage pairs chosen by Ca content (Table 2), specific Sr/Ca ratios (Elias, Hirao *et al.* 1982, Runia 1987) and strontium isotope value for each region using the same equation to produce Figure 6 iterated over each daily step. The equation generates composite $^{87}Sr/^{86}Sr$ ratios by summing the Ca-weighted contribution of each forage:

$$\left(^{87}Sr/^{86}Sr_{A}\right)\times\left[\frac{Ca.frac.\mathbf{A}\times\%Ca_{A}\times Sr/Ca_{A}}{(Ca.frac.\mathbf{A}\times\%Ca_{A}\times Sr/Ca_{A})+\left|(1-Ca.frac.\mathbf{A})\times\%Ca_{B}\times Sr/Ca_{B}\right|}\right]+$$
$$\left(^{87}Sr/^{86}Sr_{B}\right)\times\left[\frac{(1-frac.Ca.\mathbf{A})\times\%Ca_{B}\times Sr/Ca_{B}}{(Ca.frac.\mathbf{A}\times\%Ca_{A}\times Sr/Ca_{A})+\left|(1-Ca.frac.\mathbf{A})\times\%Ca_{B}\times Sr/Ca_{B}\right|}\right]$$

where $^{87}Sr/^{86}Sr_X$ is the strontium isotope ratio of the respective region, *Ca.frac.A* the fractional contribution to plasma Ca from region A (from metabolism model), (1-*Ca.frac.A*) the contribution of region B, $\%Ca_X$ is the percent as-fed content from Table 2, and Sr/Ca values for plant parts calculated using data from Elias *et al.* (1982).

The output of this equation represents the equilibrium plasma strontium isotope value for each step of the model. It carries with it all of the assumptions of the model made to this point, and the inability of the model to account for inter-individual variability. More specifically, the model so far has assumed: a steady-state metabolism (*i.e.* static Ca requirements); well-mixed body pools; that linear kinetics apply to the metabolic system; that nutritional and physiological factors other than those considered here have a minor influence on Ca flux; and that the retention of strontium is similar and related to the calcium composition of diet. This last assumption is consistent with the observations of Goldman *et al.* (1965) and Hogue *et al.* (1961).

No. 5. Amelogenesis

For the purposes of the study, maximum enamel height of the permanent M3 is set at 40 mm. Having obtained a day-by-day model of equilibrium serum $^{87}Sr/^{86}Sr$ values from the previous sections, these are then converted into a isotope profile along the growth axis of the tooth. First, an estimated rate of enamel growth in sheep is determined as a constant over the period of growth (length divided by formation time, see No.1 above). Mammalian enamel is laid down appositionally from the crown apex toward the cervical margin, and periodic structures exist in the enamel (Boyde 1989); but of particular interest are the striae of Retzius. These incremental structures are evenly spaced in imbricational enamel — such as that composing sheep enamel (Hillson 2005) — and at an oblique angle to the direction of the enamel prisms themselves so that they can be considered growth lines (Risnes 1998: 343; Smith 2006). The cervical direction of enamel growth is reflected in a gradient of cellular activity, and a model of this suggests these are isochronous surfaces in enamel formation (Moss-Salentijn *et al.* 1997: 20; Fig. 8). This allows a first approximation of tooth formation as appositional growth of a particular daily width. This provides an important process in the model to convert calculated daily isotope values into positions on a tooth. It is important to note this linear rate is the distance that the isochronous surface advances in a day, not the growth of enamel prisms themselves.

In addition to the appositional characteristics of enamel growth, the process of enamel formation

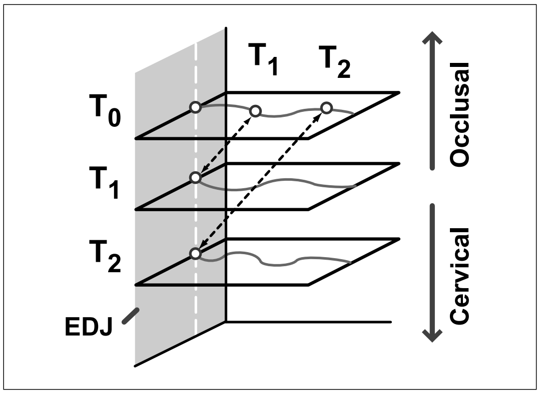

FIG. 8. – Ontogenetic model of enamel development (redrawn from Moss-Salentijn *et al.* [1997], fig. 6). Black rectangles indicate lateral planes from enamel surface to enamel-dentine junction (EDJ), and gray circles indicate position of ameloblasts at various times (T_0, T_1, and T_2). The dotted black arrows indicate isochronous planes in developing enamel.

proceeds in steps, with the initial secretion of enamel matrix by ameloblasts only containing 20-30% mineral. This is followed by a phase of maturation in which the enamel mineral (inorganic) content is dramatically increased to approximately 96-98% by weight (Boyde 1989, Smith 1998). It also appears that the maturation phase takes longer than the secretion phase (Suga 1982, Smith 1998). Passey and Cerling (2002) present a mathematical model of this process of enamel formation, based on observations of ungulate teeth. Because their model mimics the phased nature of enamel mineralization, it forms the final piece of the model. Each daily isotope value is assumed to be one unit of width, as calculated above, of appositional enamel with a mineral content of 25% (in this case, the daily $^{87}Sr/^{86}Sr$ value). The remaining mineral content of the layer is calculated as an average of a specified number of preceding layers. This number was determined by a calculated estimate of the maturation length of a sheep tooth (Suga 1982). The maturation length of sheep teeth has not been determined empirically, and measurements from microradiographs presented by Suga (1982) can only be indicative. Two values were examined in the experiment, ca. 3 mm and ca. 9 mm. The sum of these values becomes the full mineral content of each layer. The resulting profiles show variation in strontium isotope values for both the movement pattern and forage combination investigated between regions A and B. Comparison of dietary input and the generated enamel profiles for the shorter maturation length (Fig. 9, left) shows that the input dietary signal is not significantly shifted along the tooth, indicating good correspondence between distance and period in the animal's life. A longer maturation length significantly affects observed enamel isotope signal, largely obscuring patterning in the 3-stop meander movement.

RESULTS AND DISCUSSION: MODELED ISOTOPE PROFILES

The model isotope profiles are presented in Figures 10A-C. The results for each possible forage combination are shown for three different movement schedules. The difference between individual curves in a particular schedule (*e.g.* Fig. 10A) is only due to changes in calcium content of forage. The solid black profile indicates forage with equivalent Ca content between region A and B. From bottom to top, the profiles represent a trend of increasing Ca content in region A forage with attendant decrease in forage from region B (see Table 1).
Several observations are possible from these results:
a. — Relatively fast turnover of plasma Ca permits high sensitivity to changes in dietary Sr/Ca and thus changes in $^{87}Sr/^{86}Sr$. This is consistent with a relatively small serum Ca concentration and thus proportionally high daily Ca flux through the system. A reasonable estimate of serum Ca concentration is 6.5 mg/kg of body weight (MacFarlane 1975, Moodie 1975, Yokus *et al.* 2004). From the metabolic parameters used here, this is approximately 10-16% of the total quickly exchangeable Ca pool (P), and only a about a third of the daily Ca *loss* through the intestine (Braithwaite, Glascock *et al.* 1969, Braithwaite & Riazuddin 1971).

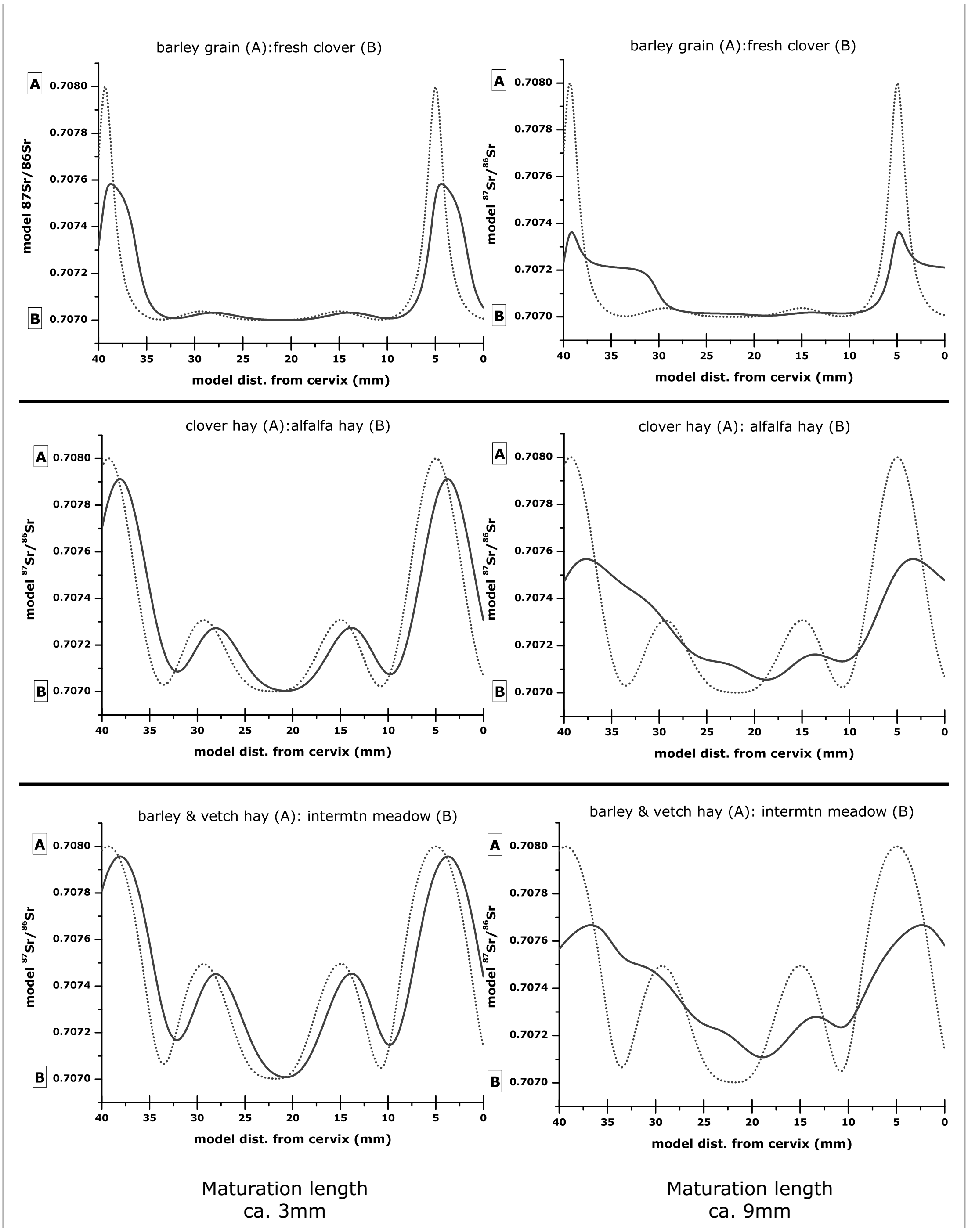

FIG. 9. – Overlay of dietary input (dotted) with modeled enamel $^{87}Sr/^{86}Sr$ profiles for cyclical movement of 16 mo. old wether for three forage pairs. Attenuation increases with increasing difference in Ca content in mixed diets. Left column, ca. 3 mm maturation length; right column, ca. 9mm maturation length.

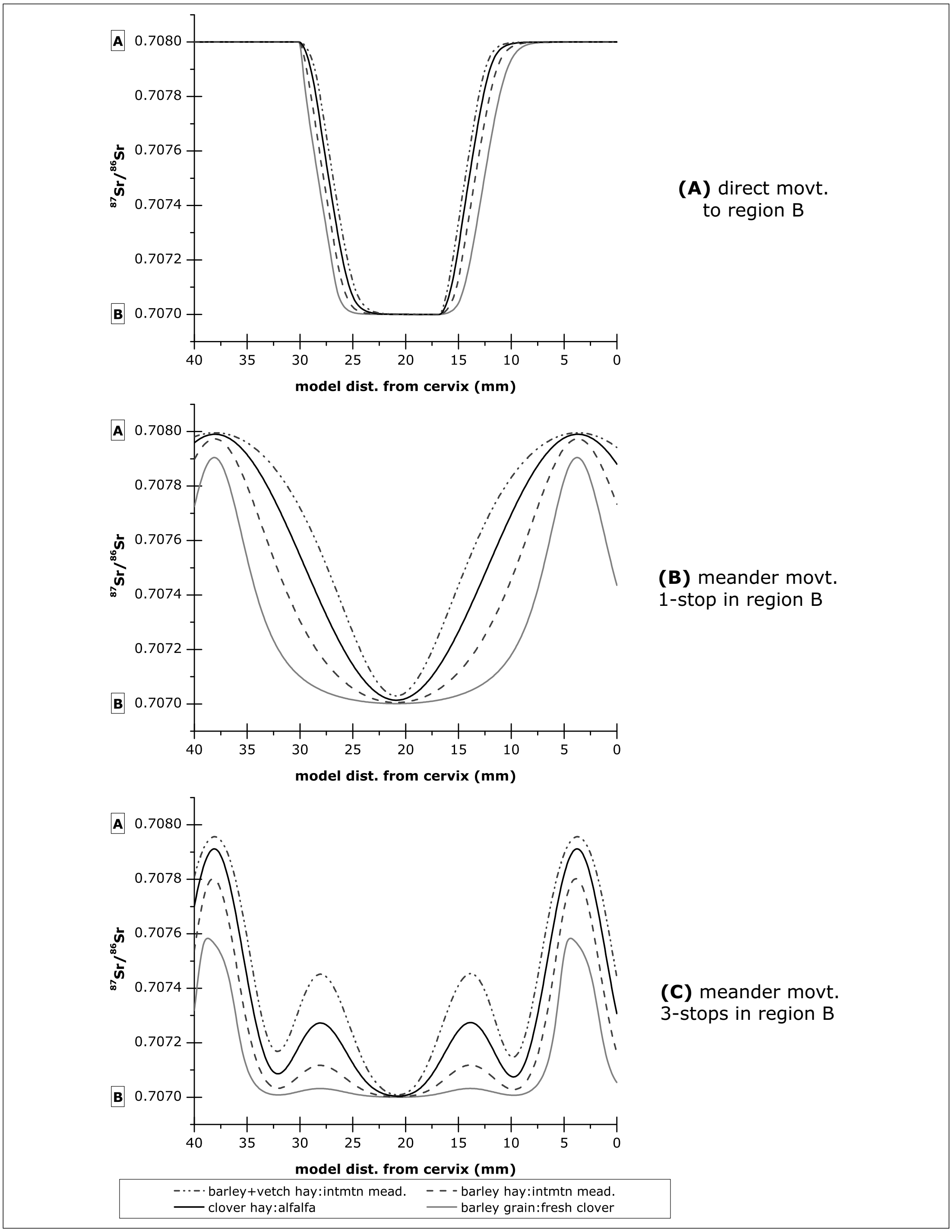

FIG. 10. – Results. Model $^{87}Sr/^{86}Sr$ enamel profiles for all forage pairs in 16 mo old wether (using ca. 3mm maturation length). (A) 'direct' movement; (B) 3-period 'meander' movement; and (C) 1-period 'meander' movement.

b. — Although metabolism itself does not mask dietary fluctuations, changes in dietary Ca concentration with similar Sr/Ca as used here have a marked effect on the nature and shape of the transitions (Fig. 9, dotted lines, and Fig. 10). That is, foods higher in Sr — resulting either from increased soil availability in Sr (Menzel & Heald 1959) or dietary Ca — will mask the contribution of foods with lower mineral content, as observed by Ericson (1989). Comparing forage pairs results in both meander and direct movement patterns (Fig. 10 and *cf.* Table 2) shows broadening of the dietary isotope curves can attenuate the values represented in geographic movement (*cf.* Burton & Wright 1995), and thus not mirror geological ('pure' biologically available) $^{87}Sr/^{86}Sr$ values. In particular, note differences between profiles with large differences in Ca content between region A and B (*e.g.* uppermost and lowermost curves in Fig. 10C). This carries the implication that linear mixing of strontium isotopes must reflect equal dietary weight from component isotope sources (*cf.* Montgomery *et al. 2007).*

c. — The observed enamel values are also strongly affected by the maturation length of the tooth, potentially masking all structure of movement, as in the right column of Fig. 9 or the lower panel of Fig. 12. Interestingly, it is the periodicity and amplitude of changes in dietary isotope values that is the critical variable. Figure 11 shows a simulated seasonal change in isotope values (*e.g.* oxygen) and its predicted enamel profile for a ca. 9 mm maturation length. As observed by Kohn (2004), the shape of this type of change is preserved regardless of how much it is attenuated by physiology. This may not be the case, however, for strontium isotopes (Figs 9 and 12). Because strontium isotopes ultimately vary biologically based on mobility (*i.e.* geology/geography), patterns in isotope shifts that interest archaeologists result from anthropogenic — and potentially irregular — mobility patterns in herded animals. Herding strategies similar to the direct pattern used here (if only in isotope shift) may be more clearly observable in sheep teeth than one in which isotope values,

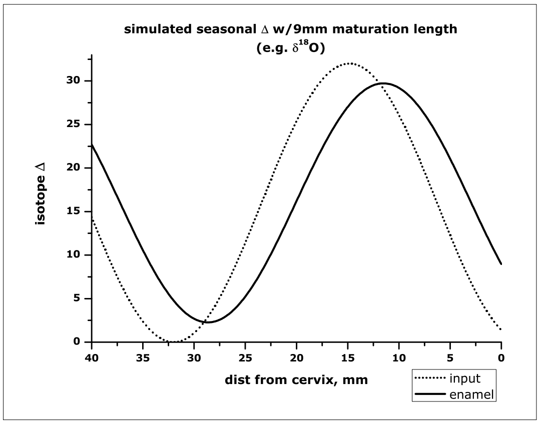

FIG. 11. – Comparison of simulated seasonally periodic dietary isotope signal (*e.g.* $\delta^{18}O$, dotted) and predicted enamel profile (solid) using ca. 9 mm maturation length. Shift in enamel signal is less pronounced for ca. 3 mm length (not shown).

weighted by diet, shift in varying amplitudes and frequencies within the period of enamel formation. A shorter maturation length in sheep teeth will more closely track such irregular isotope shifts.

Strontium isotopes can serve as a useful proxy for prehistoric animal mobility, as archaeological studies have suggested (Hoppe, Koch *et al.* 1999, Balasse, Ambrose *et al.* 2002, Bentley & Knipper 2005b). But its sensitivity will be conditioned by biological processes — amelogenesis and changing Sr/Ca in the whole diet — as well as the particular herding strategies employed by ancient herders. Close temporal correspondence between diet and plasma $^{87}Sr/^{86}Sr$ isotope values suggests that more precise understanding of sheep amelogenesis (*i.e.* maturation length) may allow more precise reconstruction of geographic mobility (*cf.* Passey *et al.* 2005). And the effect of dietary Sr/Ca flux presents both a problem and an opportunity. From an interpretive point of view, the possibility that an isotope profile has undergone significant attenuation, not reflecting the full range of geographic values, may obscure and confound placing animal mobility in a geographic context. The two uppermost curves in Figure 12, taken individually, might well be interpreted as two different patterns of

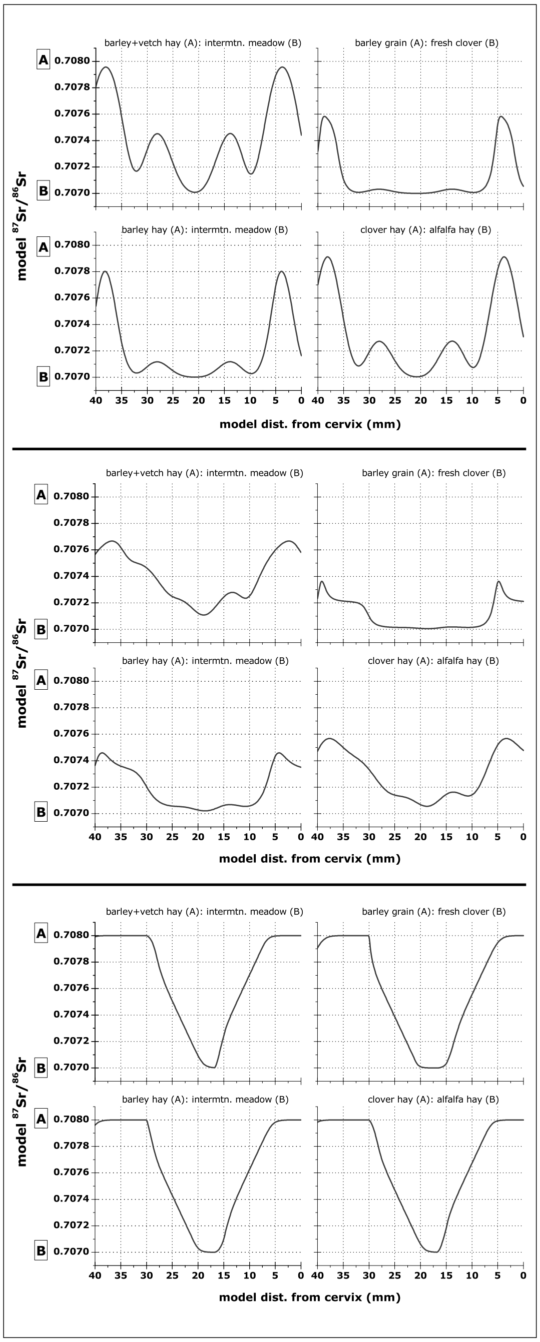

FIG. 12. – Similar profiles as in Figure 10, but separated and arranged to show difference between forage pairs with greatest difference in Ca content (top pair in each section). Top: 3-stop meander pattern using shorter maturation length; middle: same as above except longer maturation length; bottom: direct pattern using longer maturation length.

movement. This effect is less pronounced in all cases arising from diet or amelogenesis in the direct movement pattern (compare Fig. 10A and lowermost quartet in Fig. 12), indicating that broadly seasonal transhumance between summer and winter pastures is faithfully reflected in ^{87}Sr/^{86}Sr enamel profiles Given the procedure generally used to obtain intra-tooth samples — in which an individual sample is 1-2 mm wide (Passey & Cerling 2002, Balasse 2003) — it is unlikely that the patterns observed here would be obscured by sampling itself.

Such results underscore the need for a clear understanding of regional variation in ^{87}Sr/^{86}Sr, calcium content and Sr/Ca in plant communities. A variety of processes (fluvial, eolian, and weathering) all may effect the pattern of ^{87}Sr/^{86}Sr with a given geological region, and empirical observation of regional values is necessary (Price, Burton *et al.* 2002, Bentley 2006). Thus, animals may not necessarily encounter sharp ^{87}Sr/^{86}Sr boundaries in their peregrinations, and the biologically available strontium may display a different value than that predicted by geology alone (Price & Gestsdóttir 2006). Measurement of strontium concentrations in enamel profiles in addition to ^{87}Sr/^{86}Sr presents an opportunity implicit in Ericson's (1989: 255) identification of potential masking of isotope values by high Sr foods. The results of this study suggest that analysis of Sr concentrations and ^{87}Sr/^{86}Sr from enamel profiles could be used in concert as ecological and dietary proxies, given consideration of regional edaphic conditions and trace element characteristics of possible plant communities.

CONCLUSION

Specific mobility strategies utilized by prehistoric people form an important aspect of understanding past social and economic dynamics. Intra-tooth isotope analysis shows increasing potential to elucidate and reconstruct these strategies at the level of the individual animal. Strontium isotope analysis is exceptionally suited to consideration of lifetime geographic movement, as its environmental variability stems from the geochemistry of regional bedrock. Unlike light isotopes, however, there has been little consideration of potential physiologically-based influences on isotope values in tooth enamel. As a initial foray to consider this topic, this paper presents an *a priori* physiological model of strontium isotopes in ovicaprine tooth enamel as a theoretical experiment considering plausible interactions between an animal's diet, metabolism, and ultimately enamel formation.

The results show, as first approximations, that there can be a close and sensitive relationship between calcium metabolism, dietary Sr/Ca ratios, and modeled enamel isotope values. Both diet and amelogenesis strongly influence the nature of the profiles which depend on the periodicity and magnitude of any isotope gradient, the magnitude of shifts in dietary Ca, and the maturation length along a tooth. Although this may present some interpretive difficulties, a better understanding of these factors opens the possibility of using enamel Sr concentrations jointly with $^{87}Sr/^{86}Sr$ in enamel profiles as ecological and dietary proxies. To pursue these aims, further research should consider geographic, environmental distribution and variability in biologically available strontium, both from a trace element and isotope perspective. Refinement of the metabolic model can be made with further consideration of the effect of periods of high Ca demand (pregnancy, lactation) when bone resorption may be at its highest, and physiological studies for empirical comparison to model parameters. Finally, clarification of specific parameters of amelogenesis in ovicaprines presents the opportunity to reconstruct seasonal geographic mobility, even if the patterns are not immediately visible from measured isotope values.

Acknowledgements

The genesis of this paper was presented as part of the session "Herding Practices and Techniques: Models and Methodological Tools for Archaeozoological Analysis" at the 2006 ICAZ meeting in Mexico City. I wish to thank the organizers, M. Balasse, H. Yaccobaccio, J.-D. Vigne, D. Helmer, and N. Goepfert for including it, and the session participants for feedback on the ideas herein. An anonymous reviewer and M. Balasse provided constructive comments which improved the text, and particularly the figures. And I appreciate support, discussion, comments, and insight from Dr. J. H. Burton and Prof. T. D. Price.

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Submitted on 12 January 2007;
accepted on 28 October 2007.