Multi-isotope analysis and the reconstruction of prey species palaeomigrations and palaeoecology

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MULTI-ISOTOPE ANALYSIS AND THE RECONSTRUCTION OF PREY SPECIES PALAEOMIGRATIONS AND PALAEOECOLOGY

An investigation of the spatial and temporal aspects
of herbivore biogeography and dietary ecology
using stable isotope analysis and intra-tooth sampling,
with modern and archaeological case studies

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Abstract

This thesis explores the use of multi-element isotope analysis and intra-tooth sampling to reconstruct prey species ecology and biogeography. Modern caribou (*Rangifer tarandus* ssp.) and bison (*Bison bison*) from North America are used to assess the relationship between known lifetime movements and feeding habits, and those reconstructed through the stable isotope analysis of teeth and bone, including strontium ($^{87}Sr/^{86}Sr$), oxygen ($\delta^{18}O$), carbon($\delta^{13}C$), nitrogen ($\delta^{15}N$) and sulphur ($\delta^{34}S$). Teeth (enamel and dentine) were sequentially-sampled in order to reconstruct time-series isotopic profiles at an intra- and inter-individual scale, allowing an assessment of the applicability of these methods to archaeological materials. The $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ data indicate the clear potential for these methods to identify faunal movements, and to discern ranging behaviours from true migrations. $\delta^{34}S$ values of bone collagen complement enamel $^{87}Sr/^{86}Sr$ data in the same individuals, and suggest the use of this approach for the identification of geographical origin. $\delta^{13}C$ and $\delta^{15}N$ from sequentially-sampled dentinal collagen allows the identification of some seasonal foraging behaviours, most notably winter lichen consumption in the caribou.

The same stable isotope and sampling techniques are then applied to fauna from the late Pleistocene site of Jonzac (Chez-Pinaud), France, in order to investigate the biogeography and feeding ecology of Middle Palaeolithic prey-species. The elevated $\delta^{13}C$ values in reindeer bone collagen compared to the other species indicates lichen feeding and the prevalence of this niche feeding behaviour in this ancestral species. The sequential-sampling and strontium isotope analysis of herbivore enamel from the site clearly demonstrates seasonal migratory behaviour in reindeer (*Rangifer tarandus* sp.), and allows the identification of a non-migratory taxon, bison (*Bison* sp.) This is the first such evidence for migration in Pleistocene reindeer, allowing greater insight into the palaeoecology of this prey animal, and the palaeoenvironment in which Neanderthals lived and hunted.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

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CHAPTER ONE RECONSTRUCTING PREY SPECIES BEHAVIOURS: METHOD AND THEORY

1.1 Introduction

In order to understand the behaviours and subsistence choices of ancient hunter-gatherers it is essential to understand the behavioural ecology of their prey. Animal biogeography, seasonal movements, and feeding ecology shape landscapes and the reconstruction of these phenomena in the archaeological record shapes our understanding of the human past. Tracking animal movements and seasonal feeding behaviours is not only vital for appreciating the seasonal subsistence and hunting strategies employed by hominins, but also has implications for palaeoenvironmental or palaeoclimatic studies, and to understanding long-term biological processes such biological adaptation, speciation and extinction.

1.2 Animal biogeography, ecology and the total human landscape

Presumed or elucidated animal behaviour is commonly used to explain relationships between sites, landscape use, seasonal human movements and ranging, and hunting strategies in the Middle (Gaudzinski 1996; Gaudzinski and Roebroeks 2000) and Upper (Bahn 1977; Bratlund 1996; Gordon 1988) Palaeolithic. Understanding human movements and distribution decisions through the seasonal biogeography of their prey can be described as 'niche geography' (Binford 1987). 'Niche geography' is a form of landscape use whereby human mobility is primarily derived from resource availability and is determined by the feeding niche of humans and therefore also by the geographical niche of the animal species exploited. Therefore, an understanding of animal movement patterns is essential for the reconstruction of hominin behaviour. Although human movements in these cases would be defined by the movements of their prey, it must be noted that animal movements are not random and may be seasonally repetitive (Gaudzinski and Roebroeks 2000).

In the Upper Palaeolithic and late glacial period, 'cultural geography' (Binford 1987) tends to be the more favoured way of understanding human movements. This term describes a form of landscape use based around socially and culturally constructed centres, rather than occupying the environment and undertaking any movements through the satisfying of immediate physical and subsistence needs. 'Cultural geography' implies the addition of wider social parameters and more complex spatial contexts to human subsistence, aided by technology and centred around hunting camps and home-bases (see discussions in Gaudzinski and Roebroeks 2000; Kolen 1999). Where 'niche geography' determines human group mobility, an understanding of the seasonal movements and foraging habits of herbivorous prey species is essential for understanding the behaviours of contemporary hominins. However, this is also true of instances of 'cultural geography': Even where clear physical ordering of the landscape and more complex spatial and social organisation is apparent (i.e. 'cultural geographies'), resource availability often still provides the broader framework and is an ultimately restrictive influence: For example, with the technologically, socially and culturally complex landscape of south-west France during the late glacial period. Here, sites in the Périgord and the Pyrenees have been described as representing the different seasonal bases for the same groups of highly mobile Magdalenian 'reindeer followers' (Bahn 1977: 255). The theory of seasonally-moving populations, dependent on the migrations of reindeer, draws relationships between archaeological sites and material culture – tying human movements to animal migrations, inextricably knotting the 'cultural' and 'niche' landscapes. Such determinist theories have been developed further by some (e.g. Gordon 1988) but also contested by others (Burke and Pike-Tay 1997).

It is clear that throughout the Middle Palaeolithic, Upper Palaeolithic, and Mesolithic of Europe, understanding the seasonal availability and distribution of archaeologically-important prey species could be pivotal to interpreting human landscape movements and subsistence choices – whether we are considering

migratory interception/mass kill sites (such as the Middle Palaeolithic site of Salzgitter Lebenstedt, Germany, or the Late Glacial sites of Stellmoor, Germany, and Meiendorf, Germany), the total 'niche geography' of early hominid groups or the 'cultural geography' of a specialised techno-socio-cultural complex (such as the Magdalenian 'reindeer hunters').

1.3 Spatial aspects of animal ecology

The temporal and spatial distribution behaviours of a species are an important component of its physical fitness and reproductive success (MacArthur 1984). Genetic and, thus, morphological changes permit long-term adaptation to changing climatic and biotic conditions; however, changes in the distribution of a species are far more easily and immediately achievable than the development of new morphologies through genetic change. Physical movement through the tracking of habitat can therefore allow adjustments to environmental variations and help avoid species extinction (Pease et al. 1989). Other demands, such as inbreeding avoidance, mate selection, and predation avoidance can also influence the biogeography of a species. Therefore, animal movements and migrations have evolved in response to a combination of ecological and selective pressure (Dobson 1982, 1985).

Many animal species spend their lifetimes in a limited area or home range. However, other species undertake different types of movements outside the usual parameters of their home range boundaries. Animals may disperse permanently or periodically into new ranges; such dispersals are likely to be unpredictable in direction (Sinclair 1992) and are normally undertaken due to the selective pressures of inbreeding avoidance, mate competition or resource availability (Dobson 1982, 1985) and also to reduce the immediate risks of predation and disease (Waser 1985).

However, some animals move more deliberately (and even repeatedly) between different spatial units or ranges throughout life. Such movements are defined as migrations (Baker 1978). When these movements are irregular, or only loosely defined, they are referred to as nomadic migrations or seasonal ranging. Modern herbivores in mountainous regions often move seasonally, although this is rarely a true migration. Such behaviour is commonly seen in some modern populations of bison (*Bison bison*) in western North America. This altitudinal seasonal ranging is often driven by snow cover, temperature changes and seasonal food abundances – with higher altitude summer ranges and lower altitude winter ranges (Cannon 2007; e.g. van Vuren 1983; van Vuren and Bray 1986).

Other species may move in a more defined way, the same pattern recurring year after year – these are seasonal migrations. Such movements normally occur between two or more different environments (at an ecological, if not physical, distance) and truly migratory species are those adapted to several distinct habitat types that fluctuate in suitability – perhaps seasonally (Baker 1978). These movements can be described as calculated migration – that is, movements to a specific destination known to the animal at the time of migration, either through direct perception, previous acquaintance or social communication (Baker 1978). These migrations may be undertaken with annual or seasonal regularity, and the global occurrence of migratory behaviours in modern large herbivorous species suggests common underlying causes. These include the gaining of access to high quality forage, the avoidance of predation, thermal stress, insect harassment, and contact with disease or parasitic vectors (Coughenour 2008; Fryxell and Sinclair 1988). The fact that many migrations occur during transitional seasons (for example, during spring and autumn at mid- and high- latitudes) appears to confirm that movements may often be due to the changing availability of resources throughout the year. Furthermore, at latitudinal extremes such movements can also be driven by immediate climatic pressures and such thermostress migrations usually involve movements along

latitudinal or elevation gradients (which tend to be climatic gradients). A good example is the north-south migration of some modern barren-ground caribou herds (*Rangifer tarandus groenlandicus*) (Banfield 1954).

1.4 Reconstructing animal movements and seasonal diets in the past

The spatial and temporal aspects of prey-species ecology are commonly used as a reference point for understanding the choices and movements of human predators in the past. Where subsistence strategies are dominated by the acquisition of medium or large game, it is perhaps a logical assumption that the geography of human populations might be influenced by the 'niche geography' of the species exploited. Currently only a small number of techniques can be used to reconstruct the seasonal ranging and foraging behaviour of extinct and ancestral animal species directly from their physical remains.

1.4.1 Indirect methods

A number of methods are currently utilised to explore animal palaeobiogeography and palaeoecology. Although some direct methods exist, one of the most commonly utilised 'techniques' is the indirect method of using modern analogues to explain animal behaviour in the past. The use of modern analogues to explain the behaviours of ancient species is a common but problematic practice in archaeology and palaeoecology. The use of modern analogues to reconstruct seasonal migrations or to estimate ranging habits of extinct and ancestral species is especially problematic.

Perhaps the most immediate issue with this approach is that, for extinct species, there are no suitable modern analogues. This is especially relevant to Europe and North America in the Pleistocene, where cold-adapted proboscidians and other megafauna were common. These large mammals would not only have been game and raw material resources (meat, ivory, hide, etc) but also their physical presence,

dietary and range-size demands would have shaped the natural (and early human) world (e.g. Guthrie 1990). This would include the creation of trails, thus allowing access to useful resources such as water sources, fruit patches, mineral licks and optimal feeding tracts for other species including humans. The dietary and migratory movements of these animals would also serve to create grasslands, attracting non-migratory grazers and helping to maintain high biotic productivity through seed distribution (Haynes 2002). An understanding of the ranging habits of such animals – as well as other, now extinct species, or ancestral extant herbivore species – is therefore essential for accurate reconstructions of the landscape ecology of the past and understanding how this may have influenced human populations. It must also be noted that a number of modern migratory animal species also have sedentary ecotypes. For example, both wildebeest (*Connochaetes* sp.) (Serneels and Lambin 2001) and reindeer/caribou (*Rangifer tarandus* ssp.) (Banfield 1961) have migratory and non-migratory populations. There may, however, not be any significant morphological or genetic distinctions that can be made between the two forms in the archaeological or palaeontological record.

The use of modern analogues is also limited by the range of modern environments available for comparison. Given this, even in cases where there is species continuity, faunal behavioural analogues cannot be drawn. For example, there is no suitable modern analogue for the mammoth steppe ecosystem of the European, Siberian and North American Palaeolithic. This is also true of the continental arctic tundra environments of Eurasia during recent cold phases. Unlike modern day barren-land or arctic tundra, these were ecotones combining glacial tundra with fertile loess soils. Furthermore, unlike today's northern plains, these ancient habitats were at low latitudes, were fully-continental and fully-terrestrial – favouring high bioproductivity (Frost 2006; Goebel 1999; Guthrie 1990; Hoffecker 2002). These modern arctic environments are clearly not suitable analogues for the vast plains of Palaeolithic Central and Eastern Europe. Therefore, the migratory behaviour of the modern

caribou in the extreme North-West of Alaska, for example, is not analogous for the seasonal ranging habits of Palaeolithic reindeer in Europe.

In addition to the issue of a lack of similar environments, it is also important to note that many modern environments (from which analogies are drawn) are in some way directly or indirectly influenced by modern human actions. This includes the very direct influences of infrastructure, range restriction and land-partitioning, and the shrinking of available resources and habitable areas through competition. This has been demonstrated in studies of the influence of roads, high-voltage power lines, pipelines, and tourist resorts on the winter foraging habits of wild reindeer (*Rangifer tarandus tarandus*) in south central Norway (Dahle et al. 2008). Another such example is the relationship between the caribou winter territory and the incidence of anthropogenically-controlled wildland burning. Such burning practices serve to increase vegetative diversity and productivity but destroy the lichen mats that form the bulk of caribou winter forage. GPS radio-collar tracking of individuals from the Alaskan Nelchina caribou (*Rangifer tarandus granti*) herd demonstrate that caribou will avoid tracts of land for decades after burning (Joly et al. 2002). The impact of controlled vegetation fires on species substitution, extinction, distribution and migration has been observed elsewhere (Weber and Flannigan 1997) and may even have been relevant in the past, where anthropogenically-controlled forest/wildland burning may have occurred (Lewis and Ferguson 1988). In addition to these obvious anthropogenic influences, there are other, global, human induced changes which have the potential to alter mass herd behaviour. Examples include anthropogenically-derived atmospheric and environmental pollutants, or the global rise in temperatures and increasingly erratic weather patterns (known to be the result of the combustion of fossil fuels) (IPCC 2001). There is growing evidence that recent global climate change has altered species distribution patterns, extending growing seasons, and the phenology of animal breeding and migration (e.g. Cotton 2003; Jenni and Kery 2003; Klein et al. 2008; Levinsky et al. 2007; Pitelka et al. 1997;

Rivalan et al. 2007; Travis 2003). Therefore, behaviours drawn from modern species, at a time when human behaviour has invariably altered their physical, biological and chemical environment, are not likely applicable to Palaeolithic species.

Another factor which must be taken into account when applying models of modern animal behaviour to the species of the past is that – even in relatively recent history – significant variations have been observed in the migratory behaviour of the same species. For example, pre-nineteenth century documents and ethnographic accounts indicate that plains bison in North America undertook long-distance, seasonal migrations (e.g. Bamforth 1987; Hamilton et al. 2006). Today, many populations are sedentary or undertake seasonal altitudinal ranging (e.g. van Vuren 1983; van Vuren and Bray 1986). It is not known whether such changes result from natural distribution and behavioural fluctuations in these populations, or whether such differences are the product of the influence of modern humans. Bison were hunted to almost total extinction in the wild in the 19th Century and most modern herds are bred and managed within conservation areas. Therefore, perhaps in the case of bison, historical records can provide a better indication of the natural biogeographical behaviour of this species. However, the use of historical plains bison as an analogue for the migratory behaviour of European Palaeolithic bison populations remains inappropriate for reasons previously discussed (i.e. the stark differences between the environment of the recent North American mid-west and Europe during the last glaciation).

Changes in the distribution and movement habits of other species have also been observed in recent centuries, even where there is no clear human-derived cause. For example, the regular demographic fluctuations (or cycles) that have been observed in populations of Greenland caribou. These herds have been shown to expand and contract enormously, with range expansion and long-distance migratory behaviour correlating with large populations. These 'boom-bust' cycles may be triggered broad-

scale climatic variations, forage availability and reproductive behaviours. These cycles occur approximately every 50 years and have been documented over the last two hundred years (Meldgaard 1986). As well as such cycles of behaviour, climatic variations also account for large variations in the geographical spread of species in relatively recent history. For example, changes in the distribution of populations of woodland caribou (*Rangifer tarandus caribou*) in eastern North America have also been observed over the last few hundred years. In the early and mid-19th Century, woodland caribou resided in Maine, northern Vermont, New Hampshire and northern Minnesota, Wisconsin and Michigan and throughout Atlantic Canada – the southern extent of the geographical distribution of the species being much further south than today (Banfield 1961; Bergerud and Mercer 1989). This pattern coincides with the later phase of the last global cooling period or 'Little Ice Age' (Mann 2007). This variation is therefore likely to have been climatically-induced, with favoured climatic conditions extending northward during the following warming period, opening up the landscape for other competing species and pushing the caribou further north into their suitable biome. The relationship between decadal climatic shifts and range use/geographical distributions have also been noted more recently in Alaskan caribou herds (Joly et al. 2007). Such studies give us some indication of what to expect in the behaviour of ancient animal populations during periods of climatic change but also reiterate that modern behavioural analogues may not be appropriate when applied to climatically-different periods of time.

Given the issues outlined above, it appears that the use of modern analogues is not an ideal solution to understanding the behaviours of ancient animals. In some cases there are no available analogous species (e.g. woolly mammoths) and, even where the species is extant, the modern physical, environmental and climatic suites are unlikely to be comparable to those in the past. It must be noted that, even in relatively recent history, variations in the demography and distribution of populations can be observed: Whatever the causes of such shifts, these century-level changes are on

significantly smaller timescales than those that may occurred during the many millennia of the Middle and Upper Palaeolithic. Given the significant (and potentially unknown) local and global climatic and environmental fluctuations associated with such long periods of time, the migratory and seasonal feeding behaviours of past mammalian species (even those that are extant) cannot be sufficiently elucidated from present-day observations.

1.4.2 Direct approaches

It is clear that the use of modern analogous species is insufficient to explore the prevalence and periodicity of migration, ranging and seasonal foraging in prehistory. There are few approaches that can be used to reconstruct animal ecology, behaviour, diet and life history in the past directly from their archaeological remains. These will now be explored.

The size, shape and form of extinct and ancestral animal skeletal and dental components can offer general information about the range size and diet of a taxon. For example, the shape and size of teeth (e.g. crown height, cusp shape, occlusal surface size, and enamel thickness) can be used to determine the method of predation employed by an extinct species (e.g. herbivory, carnivory, omnivory, etc) (see reviews in Hershkovitz 1971 and Hillson 2005). The relationship between diet (in the broadest sense) and dental and facio-cranial morphology can be useful in revealing the general predation habits of extinct animals (e.g. *Dinosauria*). Dental differences can also give more specific indications, such as the indication of grazing or browsing in herbivores - high-crowns indicating grazing (hypsodonts, e.g. bovids and equids) and low-crowns indicating browsing (brachydonts, e.g. cervids). Methods such as geometric morphometrics can be useful tools in the investigation of size, shape and form, and the relationship between these physical characteristics and feeding behaviours such as the correlation between mandibular shape and diet type,

e.g. Raia 2004 (modern and extinct terrestrial carnivores) and Hautier et al. 2009 (extinct giant Pleistocene dormice, *Hypnomys* and *Eliomys*). New three-dimensional geometric morphometric approaches can further contribute to our understanding of the evolution of specialised feeding behaviours in particular animal families, for example, amongst corvids (Kulemeyer et al. 2009). Morphometric approaches can also be complemented by other methods, such as biomechanical analyses, which may not only reveal diet but also predation methods, such as the potential for advanced carnivory (as opposed to occasional scavenging) in fossil armadillos (*Macroeuphractus outesi*; Vizcaíno and De Iuliis 2003).

Morphometric traits can also be utilised to estimate the spatial ecology of a species, for example, the relationship between body size and that of the geographical range of a species (reviewed in Gaston and Blackburn 1996). This relationship shows that larger-bodied taxa will have a larger range size due to the requirement for more food resources (given their larger body and higher energy expenditure). Given this, populations with larger home ranges would also need to have larger total geographical ranges in order to maintain minimum viable population sizes (Lindsted et al. 1986; McNab 1963). Analysis of the body size, range size and biomic specialisation of African large mammals indicates a relationship between latitudinal extent and body size (Fernandez and Vrba 2005). This has also been observed in other species from other areas (e.g. Olifiers et al. 2004). Such models could therefore be applied to archaeological and palaeontological materials through morphometric analysis. However, it has also been suggested that much of the observed modern variation in the variables of specialization and geographical range size in large mammals cannot always be attributed immediately to body size but is also the product of local biome-specific factors (Fernandez and Vrba 2005). Furthermore, although general information about the size of a species' range can be estimated from body size, and computer models can be used to elucidate the range sizes of

archaeological animals from their physical remains, this approach cannot provide any information about the direction or phenology of ranging or migration habits.

Morphological analysis can be also used to provide information about the age at death and sex of animals in an assemblage. This can allow the reconstruction of mortality profiles, giving information about the way in which an assemblage was accumulated, including pre- and post-depositional history. For archaeological assemblages, age structures or mortality profiles are commonly compared to theoretical models that are based on wildlife observations and characterise typical, stable populations of large mammals – comparing the assemblage to the 'catastrophic' models (i.e. those resembling the 'living' structure of the population, the likely result of a broad-scale natural culling of an entire herd at one time e.g. by volcanic eruption or flash flood) or 'attritional' models (or 'U-shaped', the likely result of expected natural deaths in the population, i.e. the young and old) (Klein 1982a, 1982b; Stiner 1990). These two models are used as a baseline for comparison, allowing the likely pre-depositional accumulation processes and potentially the hunting choices of human populations to be discerned (Klein 1982a; e.g. Klein 1982b; Stiner 1990, 1991, 1994). Therefore, the morphological analysis of sex and age at death can indicate season of death and the choices and proficiency of human hunters. In domestic species, mortality profiles can also allow herd-use and animal husbandry practices to be inferred. However, differences in species, breed, domestication/semi-domestication, nutrition and age (as well as preservation and component representation) can skew the sexing and aging of bone assemblages. Such approaches are also potentially limited in terms of the detail and precision achievable and can reveal little about the living ecology and behaviour of an animal.

A small number of analytical techniques can also be employed to identify the types of food consumed by archaeological fauna. In some cases, associated preserved food (in the form of stomach or intestinal contents) or palaeofaecal material can be used to

directly reconstruct the diet of extinct animals. For example, the analysis of material from the lower intestine of a permafrost-preserved Siberian woolly mammoth (*Mammuthus primigenius*) not only revealed the dietary choices of the animal, but also permitted the reconstruction of local environmental conditions. Furthermore, the presence of dung-inhabiting fungi in the gut, indicated the behaviour of dung-eating (coprophagia) in this species (van Geel et al. 2008). In another recent study by Wood and colleagues (2008), macrofossil analysis of coprolites revealed a diverse diet of herbs and low shrubs in four species of New Zealand Late Holocene ratite moa – the extinct avian megaherbivore (*Aves* and *Dinornithiformes*) (Wood et al. 2008). This overturned previous hypotheses that moa were predominantly browsers of trees and shrubs. Although the study of ingested or palaeofaecal material can give direct insight into the dietary and behavioural ecology of a species (and also indirectly allow palaeoenvironmental reconstruction of a particular locale) the organic preservation conditions required for this type of analysis (e.g. frozen, arid or anaerobic) are extremely rare. Therefore, this technique cannot be applied routinely in archaeology and palaeoecology.

There are several other approaches that permit the reconstruction of the dietary niche and feeding ecology of animals in the past. One such method is the examination of pollen, phytoliths or diatoms trapped in the calculus of herbivore teeth. For example, analysis of opal phytoliths in the dental calculus of American mastodon (*Mammut americanum*) and phytoliths and diatoms in the dental calculus of Columbian mammoth (*Mammuthus columbi*) have been used to reconstruct the diet and palaeoecology of these extinct megafauna (Gobetz and Bozarth 2000; Gobetz and Bozarth 2001). Analysis of contemporary browsers, grazers and mixed feeders allows an assessment of the 'visibility' of these microscopic bodies in dental calculus. Comparison between the composition of the calculus and the known diet can account for differences in the preservation/representation of plant taxa, allowing provisions to be made for potential biases when studying archaeological materials.

However, methods for recovering microfossils from dental calculus are not yet firmly established and have not been agreed upon. Current methods have been demonstrated to be problematic and can cause surficial damage to teeth (Boyadjian et al. 2006). Furthermore, post-depositional damage has been shown to alter the viability of such methodologies – especially in the oldest or most taphonomically altered specimens (Henry and Piperno 2008).

The dietary habits and palaeoecology of herbivore species in archaeological deposits can also be reconstructed using dental wear analysis. The principles behind this approach are that the different dietary components will leave a distinct pattern of wear on dental enamel. Materials that cause wear include the macroscopic structures within the food itself (e.g. tough plant fibres), microscopic structures (e.g. silica phytoliths), along with any additional grit and dust. It must be noted that, in addition to abrasion (food-to-tooth contact), wear through attrition (tooth-to-tooth contact) can also be a factor. These dental wear approaches include both meso- and micro- wear. Mesowear is assessed visually using a scoring system and can be utilised to evaluate wear patterns in herbivore teeth and distinguish between browsers, grazers and mixed feeders – giving insight into the palaeodiet of a species (Fortelius and Solounias 2000). Microwear analysis can also be undertaken using stereomicroscopy or scanning electron microscopy (SEM). The study of microwear tracks in the teeth can provide further resolution to the identification of feeding regimes. Microwear features can include pits (circular or sub-circular microwear scars) and scratches (elongated microfeatures with straight, parallel sides). Pits are subcategorised by size, while scratches are defined by texture as fine or coarse and also by orientation (Semprebon et al. 2004; Solounias and Semprebon 2002). Dental wear has been used in a number of studies to reconstruct the biology of extinct species including Miocene/Pliocene three-toed horses (Franz-Odendaal et al. 2003), Pleistocene deer (Kaiser and Croitor 2004), Miocene pronghorn (Semprebon and Rivals 2007) as well as whole palaeoecosystems (Kaiser and Rössner 2007; Rivals et al.

2008; Stynder 2009). Such studies have the potential to reveal other features of palaeoecosystems such as intra-guild competition (Valli and Palombo 2008), seasonal dietary resource differences (Rivals and Athanassiou 2008), and have also demonstrated dietary differences between ancestral and extant examples of the same species through time (e.g. Palaeolithic and modern caribou; Rivals and Solounias 2007). However, some studies have demonstrated that exogenous grit and dust make the most significant contribution to wear on enamel (Sanson et al. 2007), which could complicate interpretation. Furthermore, experimental research has demonstrated that the turnover of wear can be rapid – in the order of days, hours or even minutes in primates (Teaford and Oyen 2005). A similar study on ruminants has demonstrated that even the largest microwear features can be obliterated within a very short time; a single day's grazing could result in the near total turnover of the texture of the enamel surface. This 'Last Supper Syndrome' is a clear issue with microwear analysis (Solounias et al. 1994: 226).

To summarise, there are a number of methods that can be used to reconstruct the diets of extinct and ancestral species, although a number of issues surround their application to archaeological materials. Significantly, even where the diet can be successfully estimated, the distribution of ancient animals (in terms of home range or localised habitat use/niche) is more complex. Furthermore, there are currently no non-isotopic approaches routinely used to directly establish zooarchaeological movements or migrations.

1.5 This study

1.5.1 Overview

This thesis examines the use of stable isotope analysis and the sequential-sampling of dental tissues to directly reconstruct the seasonal movements and dietary changes of archaeological animals. These methods are based on the principle that isotopes can

be used as tracers and that biological tissues will retain isotopic signatures of food and water consumed, and even an animal's geological and environmental surroundings during life. This study utilises multiple isotopic approaches, including carbon ($\delta^{13}C$), nitrogen ($\delta^{15}N$), oxygen ($\delta^{18}O$), sulphur ($\delta^{34}S$) and strontium ($^{87}Sr/^{86}Sr$) isotope analysis. A range of tissues (bone, dentine and enamel), and two different analytes (collagen and bioapatite), are analysed in order to demonstrate the potential of these methods to reveal seasonal herbivore behaviours. Modern caribou (*Rangifer tarandus* sp.) and bison (*Bison bison*) are used to assess the relationship between lifetime movements and feeding behaviours, and those reconstructed through the isotope analysis of their enamel, dentine and bone. Data from serially-sampled tissues is compared to patterns of tissues formation and the known occurrence of migrations and seasonal foraging behaviours. This innovative application of intra-tooth sampling and multi-element isotopic analysis results in a better understanding of the potential of these approaches to the reconstruction of the ecology of extinct and ancestral herbivore species. Through the use of modern materials, the success and effectiveness of these multi-isotope approaches is demonstrated. These techniques are then applied to archaeological fauna from the Middle Palaeolithic site of Jonzac (Chez Pinaud), Charente-Maritime, France, allowing the first demonstration of migratory behaviour in Pleistocene *Rangifer* and a greater understanding of Neanderthal hunting strategies and site use.

1.5.2 Aims

The specific aims of this study can be summarised as:

- to explore the potential of intra-tooth sampling and isotope analysis to reconstruct high-resolution patterns of faunal movements and migrations
- to assess whether or not seasonal variations in $^{87}Sr/^{86}Sr$ and $\delta^{18}O$ of sequentially-sampled enamel correspond with real-life seasonal movements in modern caribou and bison

- to determine if $\delta^{13}C$ and $\delta^{15}N$ of sequentially-sampled dentine correspond with known seasonal dietary variations in modern caribou and bison
- to determine if multiple isotope analysis of bulk dental tissues and bone can characterise individual herds, and to assess the potential of this method to identify the origin of archaeofaunal accumulations (single events, mass kill events or through-time multiple-event accumulations) in C_3 dominated environments.
- to determine, interpret and comment on isotope values obtained from sequentially-sampled dental tissues from Middle Palaeolithic reindeer and bison from Jonzac, France (with reference to the migratory and dietary behaviour of these species).

1.5.3 Objectives

The immediate objectives of this study are:

- to determine the isotope ratio composition (strontium; carbonate oxygen and carbon) of tooth enamel from modern caribou and bison from different herds in North America
- to determine the isotope ratio composition of dentinal collagen (carbon and nitrogen) and bone collagen (carbon, nitrogen and sulphur) from modern caribou and bison from different herds in North America
- to assess the relationship between the isotope ratios of intra-tissue samples from these modern wild fauna and their documented dietary and migratory histories
- to assess the relationship between the isotope ratios of bulk and intra-tissue samples of individuals within the same herd
- to determine the strontium isotope ratio composition of sequentially-sampled enamel from archaeological fauna remains (reindeer and bison) from late Mid- and early Upper Palaeolithic deposits at the site of Jonzac, Charente-Maritime, France.
- to determine nitrogen and carbon isotope composition of bone collagen from the Jonzac fauna
- to evaluate the use of intra-tooth sampling methods and isotope analysis in the reconstruction of prey-species behaviour and niche ecology in the Palaeolithic
- to comment on the seasonal, spatial and temporal aspects of herbivore ecology at Jonzac and the implications for our understanding of Neanderthal behaviour

CHAPTER TWO ISOTOPES OF STRONTIUM, OXYGEN, CARBON, NITROGEN AND SULPHUR IN THE NATURAL ENVIRONMENT AND IN BIOLOGICAL SYSTEMS

2.1 Introduction to stable isotope analysis

Stable isotope techniques are based around the principle that food and water ingested during life leave chemical 'signatures' in body tissues. Biogenic materials therefore have their own isotopic 'finger print' (Wada et al. 1995: 7), which depends on the isotopic composition of various reactants, pathway and reaction kinetics, as well as chemical and physical conditions (i.e. the isotopic inputs). Experimental data have confirmed that biological tissues reflect controlled diets (Ambrose and Norr 1993; Richards et al. 2003a; Sponheimer et al. 2003a; Sponheimer et al. 2003b; Tieszen and Fagre 1993). In the archaeological and palaeontological record the tissues most commonly represented are bone, enamel and dentine. The analysis the stable isotope composition of these tissues can indicate the types of foods and water consumed during life and place of residence. The application of stable isotope analysis to issues of animal palaeoecology is based upon the premise of a relationship between underlying geology (strontium and sulphur); the surrounding environment, soils and plants (carbon, nitrogen and sulphur); and ingested water (oxygen) to the body isotope chemistry of the individuals in question.

Stable isotopic structures within different ecosystems in different geographical areas can show regular features. For example, $\delta^{15}N$ values in an animal can be used to estimate trophic level and $\delta^{13}C$ values can be used to distinguish between diets consisting of plants of different photosynthetic pathways (e.g. C_3 and C_4 plants). However, it must be emphasised that patterns of stable isotopes observed at the individual level are the product of an interaction between ecological, physiological and biochemical processes.

2.1.1 Terminology

An element may have a number of isotopes (atoms of that element) that – although having the same number of protons - differ in the number of neutrons (Faure 1986). Different numbers of neutrons do not significantly affect an element's chemical properties, but affect the mass of atoms and molecules, resulting in so-called 'light' and 'heavy' isotopes. This can influence their behaviour and rates of movement and diffusion, altering their reaction rates and temperature of state transitions (Faure 1986). Unlike radioactive isotopes, stable isotopes (which can have radiogenic, primordial or cosmogenic origins) do not decay over time - ratios become fixed and preserved in media, reflecting the inorganic and biogenic processes and environments in which they were formed. Despite the fact that some strontium isotopes are formed by radioactive decay, there is negligible change in the $^{87}Sr/^{86}Sr$ over archaeological time scales and this system will be referred to as stable throughout this study (Bentley 2006).

2.1.2 Fractionation

Differences in reaction kinetics, as well as in equilibrium composition, can bring about discrimination or fractionation during biochemical and physical processes, as elements become incorporated into living systems or take part in inorganic chemical reactions (Schoeller 1999: 668). If the discrimination is against the heavier isotope of an element, its relative abundance will be lower, the product being 'lighter' and less enriched (Schoeller 1999: 668-669). During biogenic processes (i.e. assimilation and metabolic processes), fractionation usually comes about due to the preferential use or incorporation of one isotope over another by an organism. This means ratios of stable isotopes can become altered between diet and consumer's tissues. This can influence the isotopic values of different classes of compounds and different tissues to different degrees (DeNiro and Epstein 1981). Stable isotope ratios also vary between different species and individuals (due to their different biochemical

compositions) (McCutchan et al. 2003). Fractionation and dietary-body isotopic value shifts vary between elements of different isotopes and are not apparent at all in some systems (see individual sections below). Fractionation should not be confused with differential digestion and selective use of different ingested molecules, which can also influence the isotopic differences between ingested food and body tissues (also known as 'offsets'; discussed later). It must be noted that all isotopic outputs – including respired breath, urine, excrement and all other waste products, as well as the tissues developed – equal all isotopic inputs.

2.1.3 Notation

Differences in the natural abundance of different isotopes are usually very small – measured normally in parts per thousand (per mil or ‰) with reference to the ratios found within internationally-defined standards (the so-called δ-notation) (McKinney et al. 1950). Thus, isotope ratios can be defined as (after McKinney et al. 1950):

$$\delta\,(‰) = \left[\frac{R_{SAMPLE}}{R_{STANDARD}} - 1 \right] \times 1000$$

δ values denote a measured difference made relative to a standard (Fry 2006: 22). Standards, by definition, have a δ value of 0‰ though individual standards will contain appreciable amounts of heavy and light isotopes (Fry 2006: 24). It must be noted that for the 'heavy' isotope systems, this δ-notation is not commonly used (e.g. for strontium and lead). Information on the notations and internationally-defined standards for different materials and elements can be found in the individual sections below.

2.1.4 Analysis by Mass Spectrometry

Isotope measurements are normally made using mass spectrometers. Mass spectrometers are designed to separate ions (charged atoms and molecules) on the basis of their masses. This separation occurs because of their differential motions in magnetic fields. Most mass spectrometers consist of three basic parts – the source (producing the beam of ions); an electromagnetic analyzer; and an ion collector (Faure and Mensing 2005). Samples (e.g. plant, soil, bone) are normally pre-processed in the laboratory (e.g. ashing, collagen extracted, etc), may be ground or freeze-dried, and are sub-sampled prior to isotope analysis. Gaseous as well as solid samples can be analysed, depending on the type of ion source. During analysis, solid samples are first volatised (normally through the intense heat of a filament). This brings about the ionization of the atoms in the vapour. These ions are then accelerated under a high voltage and collimated into a beam. This beam of ions then enters an electromagnetic field whose direction is perpendicular to the passage of the travelling ions. This field deflects the ions into curved paths, the radii of which are determined by their mass, with lighter ones experiencing a greater degree of deflection than the heavier ones. The separated ion beams pass through the analyser into the collector, generating a positive charge. The collector includes a slit plate, behind which is a metal cup. Multiple collectors may be in use simultaneously in some instruments. The separated ion beams are focused into the collector/-s in succession, through varying either the magnetic field or the voltage (varying the acceleration). The resulting signal – in the form of a digital readout or passed to a recorder – consists of a sequence of peaks and valleys. This is the mass spectrum of an element, with each peak identifying each isotope in the mass spectrum of the element under analysis (Faure and Mensing 2005: 64-65). The main ion beams can be contaminated by a variety of minor ions. Calculations are normally made to routinely assess and correct for these problems (Fry 2006: 22).

2.2 Strontium

Strontium applications rely on the principle that radioactive decay produces isotope variations in different rock types and rocks of different ages. Given that these isotopic signatures undergo no further modification in the biosphere, strontium isotope ratios from the biological tissues of living and dead humans, plants and animals can be utilised to determine original geological provenance (and subsequently geographical origins). These methods, utilised by geologists to characterise rocks for over half a century, have also been used by ecologists and archaeologists for over two decades to map the geographical origins of modern and archaeological faunal species (e.g. Blum et al. 2000; Chamberlain et al. 1997; Evans et al. 2007; Hoppe et al. 1999; Koch et al. 1992; Pellegrini et al. 2008), environmental materials (e.g. Åberg 1995; Capo et al. 1998; Montgomery et al. 2006) and humans (e.g. Bentley et al. 2004; Budd et al. 2004; Ericson 1985; Evans et al. 2006; Ezzo et al. 1997; Montgomery et al. 2003; Montgomery et al. 2005; Montgomery et al. 2007; Schweissing and Grupe 2003).

2.2.1 Natural abundance, notation and standards

Strontium has four naturally-occurring stable isotopes; all with different natural abundances (see Table 2.1).

Table 2.1 Abundances of the naturally-occurring isotopes of strontium (taken from Capo et al. 1998: 199)

Isotope	Abundance
^{84}Sr	0.56
^{86}Sr	9.87
^{87}Sr	7.04
^{88}Sr	82.53

Strontium isotope compositions are most commonly expressed as the ratio, $^{87}Sr/^{86}Sr$. $^{87}Sr/^{86}Sr$ measurements are normalised using analysis of the international strontium

isotope standard NIST SRM987 (National Institute of Standards and Technology, Gaithersburg, USA). SRM987 is a highly pure and homogenised carbonate and has a published $^{87}Sr/^{86}Sr$ value of 0.710240 (e.g. Johnson et al. 1990; Terakado et al. 1988).

2.2.2 Strontium isotopes in the geosphere

Strontium (Sr), along with other Group II elements such as calcium (Ca) and barium (Ba), is a lithophilic ('silicate loving') alkali earth element. Strontium has a valency of +2 and an ionic radius of 1.32 Å – only slightly larger than that of calcium (Ca^{2+} = 1.18 Å). As a consequence of similar isotopic radii and the same valency, Sr^{2+} substitutes for Ca^{2+} in many minerals including plagioclase, feldspar, calcite and biological apatite (Capo et al. 1998).

The theories underlying the application of strontium isotope analysis to issues of faunal movement in the past rely on principles of radioactive decay and the formation of surficial lithology. The radioactive daughter-isotope ^{87}Sr is formed from the β-decay of ^{87}Rb (rubidium), with a half-life of approximately 4.88×10^{10} years and ^{87}Rb decreasing proportionately to the ^{87}Sr increase (Faure 1986: 119). If ^{87}Sr abundances are normalised to the non-radiogenic ^{86}Sr in the same sample, this 'cancels out' the effect of total Sr, allowing ^{87}Sr (resulting from the decay of ^{87}Rb) to be compared across different samples – the $^{87}Sr/^{86}Sr$ ratio being a function of the relative abundances of rubidium and strontium and therefore also of the age of the rock (Bentley 2006: 137). Comparison of ^{87}Sr to ^{86}Sr (as opposed to ^{84}Sr or ^{88}Sr) is done as these isotopes are most comparable in terms of abundance and atomic mass, therefore minimising measurement errors.

The strontium isotope composition of any rock will therefore derive from the Rb/Sr ratio at original crystallisation, the amount of ^{87}Sr evolved from the decay of ^{87}Rb (and therefore age), as well as any metamorphic action, mixing or isotopic exchange

that may have occurred. Chemical weathering is the primary mechanism by which strontium is released from rocks. Unlike that seen in lighter isotopes of elements (such as carbon, oxygen and nitrogen) strontium fractionation (i.e. alteration of the isotope ratio) has been demonstrated to be negligible during this and subsequent low-temperature geological, geochemical or biological processes (e.g. Blum et al. 2000: 95; Capo et al. 1998: 215; Graustein and Armstrong 1983). As a consequence, the isotope ratios that characterise a specific geology theoretically pass from the source rocks, into soil, groundwater and plants and eventually up the food chain into animal feeders.

2.2.3 Bioavailability

Despite the relationship between the surficial geology and the strontium isotope ratios of a local food chain, several secondary factors may influence the 'bioavailable' strontium of an area (i.e. the strontium which is transferred to soils, plants and further up the food chain). This is a very important consideration in strontium isotope studies, potentially resulting in the values measured in these substances not being the same as that of the underlying solid geology. One factor that must be considered is the nature of solid, heterogeneous, polymorphic rock. Minerals within a single rock can have a range of $^{87}Sr/^{86}Sr$ ratios and the proportion of these minerals within rocks also varies. Furthermore, some minerals can weather more rapidly than others, even within the same rock, greatly influencing the signature of the bioavailable strontium. Therefore, weathering may lead to values representative of bulk samples of the rock in question or perhaps only to values characteristic (but not wholly replicating that) of the lithology in question. Similarly, mixing systems of inputs (e.g. through the introduction of air or waterborne sediments) and outputs (e.g. through the weathering of local soils) in any given area must be considered. This results in the bioavailable strontium in a geographical area being the product of a number of contributing factors – both the local, geologically-driven inputs and other

non-local mixing factors. This may occur, for example, through the addition of river water; suspended (upstream) river load and aeolian deposits. A small amount of marine strontium is also transferred directly from the ocean to the atmosphere and the continents in the form of precipitation (e.g. Åberg 1995; Blum et al. 2000; Capo et al. 1998). Equations have been utilised in previous studies to evaluate the relative contribution of each input to the bioavailable reservoir (e.g. Graustein and Armstrong 1983; Kennedy et al. 2002), although these can be problematic given the variability of rock types; soil formation processes; water sourcing; and other contributions within any particular ecosystem. The relative contribution of Sr^{2+} derived from bedrock weathering as opposed to atmospheric sources (e.g. aeolian deposits, river load, precipitation, etc) can only be determined using a two-member mixing equation when these sources have distinct isotopic values. Given that both of these two sources themselves have multiple (and often poorly characterised) influences, and that these can vary through time, the determination of values using mixing equations is complicated by numerous uncertainties. Differential weathering, as discussed above, is another equally complex and difficult to characterise influence (Åberg et al. 1989; Graustein and Armstrong 1983; Kennedy et al. 1998; Kennedy et al. 2002).

2.2.4 Strontium isotopes in the biosphere

Calcium (Ca) is a major element and essential for plants and animals (Poszwa et al. 2000). Although considered a non-essential element, Sr is also found in living organisms, its biological uptake occurring as a substitution for the chemically-similar Ca. Other bivalent elements such as barium and lead can also substitute for Ca^{2+} during nutrient uptake, excretion and throughout internal biological tissues. However, given the similarities in atomic radii between Ca and Sr, Sr is substituted more readily than other elements (Kohn et al. 1999). Plants take up labile cations of strontium in soil solution and through the soil exchange complex, these terms

describe the uptake via water (soil water which contain ions held by capillary action) and from surficial-exchange at the roots (where ions in soils become attracted to the negatively charged surfaces of organic matter) respectively (Capo et al. 1998).

Bulk soil and soil waters will have the isotopic composition of the parent material, with some of the modifications described above. In turn, vegetation is dominated by the isotopic composition of labile strontium in the soil, although in very varied concentrations, from a few ppm in roots and leaves to 0.2% in wood and bark (Åberg et al. 1990; Capo et al. 1998; Graustein and Armstrong 1983). It must be noted that there can be significant contributions of strontium from atmospheric sources into the strontium of upper soil horizons (Åberg et al. 1990; Graustein and Armstrong 1983). Furthermore, biocycling (the addition of strontium in biomass) and the depth of root uptake/ground water depth can also influence bioavailable strontium concentration and $^{87}Sr/^{86}Sr$ ratios (Poszwa et al. 2004).

Given the relatively high-mass of strontium atoms, fractionation during biological processes is negligible compared to that in low-mass elements (e.g. H, C, O). Therefore, the measured $^{87}Sr/^{86}Sr$ ratio of a material reflects the amount of radiogenic ^{87}Sr, which is a function of its source and indicates the provenance of a sample. The strontium isotope ratio remains unmodified by local environmental conditions (i.e. temperature) or internal biological processes within the organism (Capo et al. 1998: 202). However, although the isotopic ratio of Sr remains unaltered up the food chain (i.e. there is no fractionation effect, see above), 'biopurification' does occur as plants and animals incorporate Sr. 'Biopurification' describes the discrimination that occurs during the uptake of Ca^{2+}, against substituting cations such as Sr^{2+}, ensuring the nutrient mineral Ca is obtained and leading to the suppression of Sr uptake in Ca-rich environments. 'Biopurification' may lead to varied concentrations of Sr in plants and also in their feeders (compared to soil Sr concentrations) but this does not affect the isotope ratios present (Burton et al. 1999; Elias et al. 1982). This mechanism

however does allow for Sr/Ca ratios to be utilised to identify trophic level, and therefore, the foods most likely consumed by different organisms in both marine and terrestrial foodchains (e.g. Blum et al. 2000; Burton and Price 1999).

As described above, Sr in soil and subsequently in plants and animals, is the product of a number of contributing factors. Although mineral weathering from local crustal geologies is normally the primary influence (e.g. Bacon and Bain 1995; Bern et al. 2005), other factors include ground waters (e.g. Graustein and Armstrong 1983); river/stream water, strontium cycling in soils (e.g. Dijkstra and Smits 2002; Morgan et al. 2001); atmospheric sources (e.g. Gosz and Moore 1989; Kennedy et al. 1998; Vitousek et al. 1999); aeolian deposition (e.g. Chadwick et al. 1999); surficial geological movement (e.g. Steele and Pushkar 1973: 338); precipitation, irrigation and sea-spray (e.g. Chadwick et al. 1999; Green et al. 2004; Xin and Hanson 1994); and, in some modern contexts, fertilisers (e.g. Németh et al. 2006). Outputs bringing about the removal of strontium from soils via weathering must also be considered. This leaching can of course result in the redistribution of strontium from other sites to different locales, with alluvial soils containing a mixture of sediments from sources weathered upstream (Bentley 2006: 149). Despite these varied influences, it has been observed that in most environments, the weathering of local lithology remains the most significant Sr contribution – especially in pre-modern times (Bentley 2006: 153). Furthermore, averaging effects observed in plant values (e.g. Blum et al. 2000; Sillen et al. 1998) and up the food chain to herbivore feeders, carnivores and humans (e.g. Burton et al. 1999; Price et al. 2002) have been demonstrated to widely eliminate local variation, demonstrating values in organisms more closely aligned to underlying geology and soil values.

2.2.5 Strontium isotopes in animals

The strontium isotope ratios of terrestrial herbivores reflect the isotopic composition of the strontium taken up by the plants they consume, therefore reflecting the environment they live in. Generally, herbivores living on older parent materials will have higher $^{87}Sr/^{86}Sr$ values; animals living on younger lithologies will have lower values.

Strontium is incorporated in significant concentrations during bioapatite formation (in bone, enamel and dentine), as a substitution for calcium. The amount of strontium in enamel is between 25 and 600ppm (parts per million), but can be greater, with concentrations dependent on the local environmental concentrations, dietary choices (herbivory, carnivory, etc) and extent of mineralisation in the tissue (Iyengar et al. 1978; Steadman et al. 1958).

Early applications of strontium isotope analysis within archaeology made use of bone apatite, taking advantage of the differential rates of turnover and formation in different tissues (bone, enamel and dentine) to identify non-local individuals at a site. This was commonly done through the comparison of enamel (which is unaltered throughout adulthood, therefore reflecting early-life geography) to bone (remodelled throughout life and therefore reflecting later life geography) to identify broad life-time movement trends. Many of these approaches incorporated steps to chemically leach diagenetic strontium from bone in order to separate original, intact bioapatite crystals (Sillen 1986; Sillen et al. 1998). However, such chemical leaching has been demonstrated to be insufficient to remove all contaminating strontium (e.g. Hoppe et al. 2003; Koch et al. 1992; Nelson et al. 1986; Trickett et al. 2003). Enamel is considered far less susceptible to such alteration or contamination and is now the preferred analyte in archaeological, palaeontological and palaeoecological studies. Furthermore, the analysis of intra-tooth samples of enamel (formed sequentially over

number of months) can be utilised to reconstruct time-series isotopic profiles and therefore annual and potentially seasonal geographical histories (Hoppe et al. 1999; Pellegrini et al. 2008). Diagenetic issues, chemical pre-treatments and tissue-specific analytical issues are explored in greater detail in later sections (see Chapter 3.2 and 3.3).

2.2.6 Analysis

Analysis of strontium isotope ratios from bioapatites normally first involves the dissolution of tooth or bone in acid, through one or multiple-steps. Solutions are then purified using cation exchange columns (containing Sr exchange resin) or other methods to chemically isolate the strontium (e.g. Deniel and Pin 2001). This is then normally followed by measurement using thermal ionization mass spectrometry (TIMS) or multicollector inductively coupled plasma mass spectrometry (MC-ICP-MS), the latter of which is accurate, precise and produces replicable results but it is also fairly destructive with 5-20mg of bone/enamel needed per analysis.

Strontium isotope ratios in biogenic and geological materials can also be measured directly *in situ* using laser ablation MC-ICP-MS (e.g. Richards et al. 2008a). There is no need for chemical preparation or sample destruction, with a laser path typically around 250 x 750μm (Copeland et al. 2008a). However, this method is also less precise and may be susceptible to isobaric molecular interference. This comes about due to the inadvertent creation (and subsequent measurement) of Ca-P-O molecules during the laser ablation process. With a total mass of ~87, these molecules will artificially increase the measured $^{87}Sr/^{86}Sr$ ratios, producing what may or may not be a consistent offset from measured solution strontium values (Copeland et al. 2008a; Horstwood et al. 2008; Nowell and Horstwood 2009; Simonetti et al. 2007).

2.3 Oxygen

Oxygen isotope studies of skeletal materials are based on the correlation between the oxygen isotope composition of mineralised animal tissues and that of ingested water (Longinelli 1965, 1966; Longinelli and Nuti 1968, 1973; Longinelli 1984). Mammals have a metabolically-controlled, relatively constant body temperature (they are endothermic homeotherms) and biogenic phosphate precipitates in isotopic equilibrium with body water (Longinelli 1984; Luz et al. 1984). Fractionation does occur between ingested water and body water and this varies interspecifically. However, fractionation factors have been established for a number of extant species of mammal and, although showing some interspecific variation, the body water-drinking water relationship appears to be linear (Ayliffe et al. 1992; Bryant and Froelich 1995; Kohn 1996; Kohn et al. 1996; Longinelli 1984; Luz et al. 1984). This (and the premise that ingested water is the same or very similar to the oxygen isotope composition of precipitation) has allowed the application of oxygen isotope analysis to archaeological and fossil bone and teeth in order to reconstruct palaeoclimate, palaeotemperatures and seasonality (e.g. Balasse et al. 2003; Bryant et al. 1994; Bryant et al. 1996a; Fricke et al. 1998a; Hoppe et al. 2004a; Koch et al. 1989).

2.3.1 Natural abundance, standards and notation

There are three naturally-occurring isotopes of oxygen (Table 2.2)

Table 2.2 Abundances of the naturally-occurring isotopes of oxygen (taken from Schoeller 1999: 668)

Isotope	Fractional Abundance
^{16}O	0.99755
^{17}O	0.00039
^{18}O	0.00206

The standard initially used in some of the first applications of oxygen isotope analysis to palaeoclimatology was PDB (Pee Dee Belemnite) – a fossil belemnite from the Pee Dee Formation of South Carolina, USA (e.g. Urey et al. 1951). The supply of this material is now exhausted. The IAEA then recommended that oxygen isotopes of carbonates be expressed relative to V-PDB (Vienna Pee Dee Belemnite) by adopting a consensus oxygen isotope value for the standard NBS19 carbonate, relative to V-PDB. For oxygen isotope analysis, this solution, although satisfactory, has only limited distribution and is not commonly used. Another, more widely accepted, standard material for oxygen isotope analysis is the mean composition of ocean water or SMOW (Standard Mean Ocean Water) – a reference value established in terms of an actual water standard (Craig 1961). However, nowadays V-SMOW (Vienna Standard Mean Ocean Water) – a recalibration of the original SMOW definition by the International Atomic Energy Association (IAEA) – is the recommended international standard (Coplen 1995).

2.3.2 Oxygen isotopes in the hydrosphere

The ratios of ^{18}O to ^{16}O in water are altered by natural environmental process through fractionation (where there is a separation of the heavier and lighter isotopes). This occurs at various points in the hydrocycle, giving precipitation in a particular area its local oxygen isotopic signature.

The average annual worldwide isotope composition of rainfall and other types of precipitation is depleted in the heavier isotope (^{18}O) compared to the ocean and other surface water. Evaporation from these water bodies serves to initially deplete the evaporating water, making it isotopically lighter than the source. Global and local meteoric processes then continue to bring about further depletions (Dansgaard 1964). These are the result of thermal and geographical parameters, related to local and regional climate, such as:

- **Temperature variations.** Given that the rate of fractionation processes is energy dependant, this is the biggest influence on the depletion of ^{18}O of precipitation (Yurtsever 1975). A strong relationship between temperature and the $\delta^{18}O$ of precipitation, a product of the greater fractionation taking place at low temperatures than at higher ones, has been demonstrated (Dansgaard 1964).
- **Coastal proximity** (the 'rainout' and 'continental' effects). As water vapour moves inland, condenses and falls, the resultant precipitation is isotopically enriched relative to the water vapour. However, as water moves inland there is a progressive depletion of ^{18}O. This is known as the 'continental effect', as the heavier isotope is 'rained out' (Clark and Fritz 1997; Cuntz et al. 2002; Dansgaard 1964).
- **Latitude.** Given the relationship between temperature and fractionation in precipitation, there is also a latitudinal effect. This is also true of altitude and season. The latitude effect shows an increased depletion of ^{18}O with latitude, e.g. 0.5‰ $\delta^{18}O$ per degree latitude over North America (Dansgaard 1964; Yurtsever 1975).
- **Altitude.** As there is a temperature decrease with altitude there is also an effect on oxygen isotope ratios of precipitation, resulting in more negative $\delta^{18}O$ values with higher altitudes (Clark and Fritz 1997; Dansgaard 1964; Gat 1980). The altitude effect is also influenced by climate as well as topography and gradients of 0.15-0.5‰ $\delta^{18}O$ per 100m are typical (Gat 1980).
- **Season.** Given the relationship between temperature and the oxygen isotope chemistry of waters, at mid- and high-latitudes precipitation will demonstrate seasonal variations with precipitation depleted in the heavier isotope (^{18}O) in winter months relative to the warmer seasons (Dansgaard 1964). This effect is amplified at higher latitudes, where seasonal temperature differences are exaggerated.

After rain has fallen, there are additional processes that can occur to further alter the isotopic composition, such as evaporation processes that occur in surface water bodies causing ^{18}O enrichment. Lakes, rivers and other bodies may have a lower degree of seasonal isotopic variability than meteoric water. The drinking water from these, as well as any plants growing nearby or animals consuming such water will reflect this reduced seasonal variability. There may be other local processes such as water mixing, water movement and groundwater recharge which can influence the oxygen isotope composition of drinking water.

The isotopic composition of snow cover is primarily derived from the isotope content of local snowfalls (i.e. precipitation) – as well as wind-blown snow from other areas and local frozen water vapour in the form of frost (Moser and Stichler 1980: 142). As with rain and other forms of precipitation, the amount of ^{18}O in snowfall is governed by the origin of the water and the temperature at which condensation occurs – with the addition of a small isotopic fractionation factor between the ice-liquid-vapour phases of water. As with rainfall, both large-scale weather patterns and local seasonal variations can be detected in the oxygen isotope ratios of snowfall. Furthermore, where snow settles and remains, seasonal isotopic variations can remain detectable for considerable periods (Moser and Stichler 1980: 145).

2.3.3 Oxygen isotopes in animals

Initial investigations utilising oxygen isotope systematics in bioapatite were first applied to carbonate shells and marine organisms – demonstrating a clear relationship between isotopic composition and temperature (Longinelli 1965). Work on thermoregulating terrestrial vertebrates that followed indicated that isotope composition varies systematically with local water composition (Longinelli 1984; Luz et al. 1984). The isotopic composition of oxygen in bioapatite (both phosphate and

carbonate fractions) depends on the isotopic composition of body water and the temperature at which it is precipitated. The isotopic composition of body water is directly related to that of drinking water, although there are contributions from other types of ingested water (i.e. through food), from molecular O_2 in the body and other sources (Bryant and Froelich 1995; Kohn 1996; Podlesak et al. 2008) Of course, responses in body water and tissue values within an organism are not instantaneous. Where the daily turn-over of total oxygen is 5-10% then a time-lag of 10-20 days can be predicted (Kohn and Cerling 2002). The rate of body water turnover has been evaluated using tracers and through experimental studies using dietary switches (from depleted to enriched drinking waters). Although there are intra- and inter-specific variations, this period of time is universally small. For example, body water turnover in rats has been established to be between 1.4 – 3.3 days, reaching full isotopic equilibrium with drinking water in two weeks (Luz et al. 1984; Podlesak et al. 2008). Subsequent isotopic variations were also observed in continually-growing enamel of the same animals, which reached full isotopic equilibrium with the new dietary water after approximately 25 days (Podlesak et al. 2008). The rate of turnover and equilibrium can be expected to vary between different species depending on their degree of water-dependence or drought resistance – with more water-dependent species having a shorter time-lag and recording isotopic input variations with a greater fidelity.

Oxygen isotope analytical methods have utilised both the CO_3 (carbonate) and PO_4 (phosphate) components of mammalian mineralised tissues. Tooth and bone mineral (biogenic phosphates) contains several carbonate (CO_3) components. This includes structural CO_3 which substitutes for PO_4 and OH as well as other non-structural, mobile CO_3 components. A linear correlation appears to exist between $\delta^{18}O$ from phosphate and that of carbonate in the same modern mammal tooth samples, indicating that PO_4 and structural CO_3 are cogenetic oxygen-bearing phases

in isotopic equilibrium with the same oxygen reservoir at the same temperature (Iacumin et al. 1996).

Mammals have a metabolically-controlled, relatively constant body temperature and biogenic phosphate precipitates in equilibrium with body water (Longinelli 1984; Luz et al. 1984). Fractionation does occur between ingested water and body water and this appears to be broadly linear and predictable (Ayliffe et al. 1992; Bryant and Froelich 1995; Kohn 1996; Longinelli 1984; Luz et al. 1984), with a consistent offset between the $\delta^{18}O$ of body water and PO_4 in mineralised tissues (~18‰) (cited in Kohn and Cerling 2002: 464). There is a further offset between PO_4 and CO_3 of ~9‰, although values have been reported ranging from ~8 to ~12‰ (e.g. Bryant et al. 1996b; Iacumin et al. 1996; Longinelli and Nuti 1973; Martin et al. 2008).

Recent research has identified interspecific differences and other variables that produce differences in the relationship between the oxygen isotopic composition of ingested water and that of animal tissues. Oxygen isotopic differences have been demonstrated in animals in the same environments. These have been attributed to food source, water source (e.g. surficial, plant, river water), leaf feeding, C_3 vs. C_4, humidity, species-specific metabolic activity and volume of water ingested. A number of studies on modern skeletal material from extant species (see Table 2.3) have investigated the relationship between local water $\delta^{18}O$ and that of mammalian biogenic PO_4/biogenic carbonates. These have not only allowed the production of species-specific calibrations but have also led to a better understanding of the influences of varied diets and physiologies (Kohn 1996). Furthermore, these experimental studies are essential for predicting the expected isotope composition for extinct taxa where there will be limited prior knowledge of physiology.

Table 2.3 Selected references to species-specific studies of the correlation between local environmental water, ingested water and mammal body water (*Latin names given where specified in the literature)

Reference	Species*	Analyte
(Longinelli and Peretti Padalino 1980)	Laboratory rat (*Rattus norvegicus*)	Blood
(Longinelli 1984)	Domestic pig (*Sus scrofa*), Human (*Homo sapiens sapiens*)	Blood, bone phosphate
(Luz et al. 1984)	Human (*Homo sapiens sapiens*), dog (*Canis* familiaris), muskox (*Ovibos moschatus*), laboratory rat (*Rattus norvegicus*)	Bone phosphate Blood
(Levison et al. 1987)	Human (*Homo sapiens sapiens*)	Tooth phosphate, urinary stone phosphate
(Ayliffe and Chivas 1990)	Australia Macropoda (kangaroos and wallabies)	Bone phosphate
(D'Angela and Longinelli 1990)	Woodmice (*Apodemus sylvaticus, A. flavicollis*), deer (*Cervus elephus*), cattle (*Bos taurus*), sheep (*Ovis aries*)	Bone phosphate
(Yoshida and Miyazaki 1991)	Various cetacean taxa (whales, dolphins and porpoises)	Bone phosphate
(Ayliffe et al. 1992)	African elephant (Loxodonta africana), Asian elephant (Elephas maximus)	Bone and tooth phosphate
(Sánchez Chillón et al. 1994)	Fossil horses (*Equus stenonis*)	Bone and tooth phosphate
(Delgado Huertas et al. 1995)	Goat (*Capra* sp.), Ibex (*Capra ibex*), mouflon (*Ovis ammon musimon*), roe-deer (*Capreolus capreolus*), horse (*Equus caballus*), rabbits (*Oryctolagus sp.*), hares (*Lepus sp.*)	Bone phosphate
(Stuart-Williams and Schwarcz 1997)	Canadian beaver (*Castor canadensis*)	Bone, enamel and dentine phosphate
(Iacumin and Longinelli 2002)	Reindeer (*Rangifer tarandus*), fox (*Vulpes vulpes, Alopex lagopus, Vulpes zerda*), golden jackal (*Canis aureus*)	Bone and tooth phosphate
(Longinelli et al. 2003)	Reindeer (*Rangifer tarandus*), mice (*Pitymus* sp., *Microtus arvalis, Arvicola terrestris*)	Bone/tooth phosphate
(Hoppe et al. 2004a)	North American plains bison (*Bison bison*)	Enamel carbonate
(Hoppe 2006a)	North American feral horse (*Equus caballus*)	Enamel carbonate
(Daux et al. 2008)	Human (*Homo sapiens sapiens*)	Enamel phosphate
(Podlesak et al. 2008)	Woodrats (*Neotoma cinera, N. stephensi*)	Blood, breath, hair, enamel phosphate, enamel carbonate

2.3.4 Analysing bioapatites

In order to analyse the phosphate component, the PO_4 must first be separated from other O-containing structures. This is normally done through dissolution in an acid such as nitric (HNO_3) or hydrofluoric (HF), separating the PO_4 from other O-bearing components. This is followed by purification on ion exchange columns or direct chemical processing to bismuth phosphate ($BiPO_4$) (e.g. Kolodny et al. 1983; Longinelli and Nuti 1973) or silver phosphate (Ag_3PO_4) (e.g. Crowson et al. 1991; Dettman et al. 2001). Being significantly less hydroscopic than $BiPO_4$, Ag_3PO_4 is now favoured. The $BiPO_4$ or Ag_3PO_4 is then fluorinated, brominated or thermally decomposed in the presence of carbon using furnaces and lasers. This produces carbon monoxide (CO) or carbon dioxide (CO_2) – which is measured for its isotope composition using a mass spectrometer. The carbonate (CO_3) component of bioapatite (in bone and teeth) is normally analysed by dissolution in phosphoric acid (H_3PO_4), similar to the analysis of rock carbonates.

Methods have also been utilised to measure bulk or combined bioapatite components. Although methods such as ion probe and laser-ablation can accommodate *in situ* analysis, bulk analysis has clear disadvantages including the need for accuracy corrections, biased compositions brought about by pre-treatment requirements, and a potential difficulty in determining the influences of diagenesis or contamination (see below). This is especially important when considering archaeological or fossil bioapatite as bulk analysis incorporates all oxygen components (PO_4, CO_3, OH, diagenetic oxides and silicates, etc).

2.4 Carbon

The relative abundance of the stable isotopes of carbon, ^{13}C and ^{12}C, varies characteristically between different biomes and ecosystems e.g. between plants and different photosynthetic pathways (DeNiro and Epstein 1978; Smith and Epstein

1971) or between terrestrial and marine environments (Schoeninger and DeNiro 1984). The carbon isotope composition of both bioapatites (the mineral fraction of skeletal tissues) and collagen (the bone protein) are directly related to the dietary isotopic inputs. Therefore, the analysis of these tissues can provide information about an animal's diet and therefore about the feeding ecology of a species, locally-available plant species and the local environment (Balasse and Ambrose 2005; Balasse et al. 2005; Hedges et al. 2004; Hoppe et al. 2006; Richards and Hedges 2003).

2.4.1 Abundance, standards and notation

The abundances of the naturally-occurring stable isotopes of carbon are shown below (Table 2.4).

Table 2.4 Abundances of the naturally-occurring isotopes of carbon (taken from Schoeller 1999: 668).

Isotope	Fractional Abundance
^{12}C	0.98889
^{13}C	0.01111

As with many other isotope systems, the carbon isotopic content of a material is commonly expressed as a delta (δ) value, $\delta^{13}C$, in parts per thousand or per mil. The international standard for carbon isotope analysis is based upon the carbon dioxide composition of limestone from the Pee Dee Belemnite formation in South Carolina, USA or PDB (Craig 1957). Although this standard is now exhausted, the $\delta^{13}C$ content 0.011237‰ has been correlated with another standard (V-PDB) and this notation is now commonly used.

2.4.2 Carbon isotopes in the natural environment

The carbon isotope composition of terrestrial ecosystems reflects the photosynthetic pathways and environmental responses of primary producers (plants) at the base of

food webs. The contemporary $\delta^{13}C$ value of atmospheric CO_2 is around -8‰ (Keeling et al. 2005). This value is becoming increasingly negative (~0.03‰ per annum) through the introduction of extremely negative $\delta^{13}C$ values to the atmosphere from the combustion of fossil fuels and deforestation (Keeling et al. 1979). During diffusion into plant leaves the lighter isotope (^{12}C) is positively discriminated for. Therefore, plants are depleted in ^{13}C relative to the atmosphere (O'Leary 1995). During the processes of photosynthesis (including CO_2 diffusion into leaves, dissolution and carboxylation), the discrimination against ^{13}C continues. This discrimination is principally brought about during the chemical uptake of CO_2 (carboxylation) and the physical transport of CO_2 (diffusion). The degree of this discrimination varies depending on the photosynthetic pathway in question. C_3 and C_4 plants display different degrees of carbon isotope fractionation during the process of photosynthesis; these differences come about due to the differential discrimination against ^{13}C in C_3 (Calvin-Benson) and C_4 (Hatch-Slack) pathways (O'Leary 1981: 554), resulting in more negative $\delta^{13}C$ plant tissue values in C_3 plants. This is because – in addition to discrimination due to leaf (stomatal) diffusion and carboxylation – there is also CO_2 hydration. $\delta^{13}C$ values for most C_3 plants lie between -24 and -34‰, and -6 and -19‰ for C_4 plants (Smith and Epstein 1971), allowing the relative contributions of each type of plant to the diet to be assessed from the $\delta^{13}C$ values of body tissues (DeNiro and Epstein 1978: 505). C_3 plants include trees, herbaceous plants and grasses in temperate and cold areas and at latitudinal extremes. C_4 plants are native to tropical and savannah areas and include many grasses. There is a third group of plants which undertake a different pathway, crassulacean acid metabolism (CAM). CAM plants are classically adapted to arid conditions and include some mosses, ferns and flowering plants, as well as orchids, bromeliads and cacti. These plants have the same enzymes as C_4 plants but utilise them differently during the day and night, fixing CO_2 during the night and then releasing and refixing the carbon during the day. Some species are facultative CAM plants and switch to daytime C_3 photosynthesis during the day. Obligate CAM plants have values of around -11‰

(Lajtha and Michener 1994: 2-3). Facultative CAM plants have shown $\delta^{13}C$ values intermediate between those of obligate CAM plants and fully-C_3 plants, and carbon isotope analysis can be used to estimate the proportion of CAM vs. C_3 photosynthesis in these facultative ecotypes (Kluge et al. 1991; Mooney et al. 1989). However, carbon isotope analysis cannot effectively differentiate between C4 and CAM plants and therefore C4- and CAM-based diets. However, comparatively few plant species are CAM plants.

In addition to the influences of photosynthetic pathway and other minor physiological influences (respiration, carbon exportation, etc) (see Farquhar et al. 1989), there are other environmental, temporal and spatial effects that can lead to varying carbon isotopic ratios in plants – including water availability (Ehleringer and Cooper 1988), water-use efficiency (e.g. Farquhar and Richards 1984; Farquhar et al. 1989), relative humidity (Madhavan et al. 1991), temperature and altitude (Korner et al. 1988; Korner et al. 1991; Morecroft and Woodward 1990), light intensity, nutrient availability, salinity (Downton et al. 1985; Flanagan and Jefferies 1989) and soil quality. These can come about due to regional and global scale changes in climate and atmospheric CO_2, in addition to smaller-scale influences affecting individual plants and ecosystems such as fruiting, seasonal growth (more positive in growing season) and dormancy (Smedley et al. 1991) and foliage cover (or 'canopy effect') (Heaton 1999; Medina and Minchin 1980; Medina et al. 1986). The combined influences of biochemical pathways and variations in light intensity, nutrient and water availability, temperature and CO_2 source lead to inter- and intraspecies variations in plant $\delta^{13}C$ values (Lajtha and Marshall 1994). For example, lower temperatures (Michelsen et al. 1996) and water stress (Lajtha and Marshall 1994) have been demonstrated to increase $\delta^{13}C$ values in plants of the same species. In addition, certain species within ecosystems systematically demonstrate idiosyncratic $\delta^{13}C$ such as the higher values often observed in lichens (Maguas and Brugnoli 1996;

Park and Epstein 1960) and mushrooms (Ben-David et al. 2001: 424) compared to other terrestrial plants.

Furthermore, individual plants can have significantly varied $\delta^{13}C$ values between their different biochemical and anatomical fractions (Ambrose and Norr 1993: 3; O'Leary 1981). Generally, photosynthetic tissues such as leaves have more negative values, whereas seeds, roots, tubers and stems of the same organism may be more positive (O'Leary 1981).

2.4.3 Carbon isotopes in animal tissues

Dietary carbon isotope inputs from all foods consumed are recorded in the body tissues of animal feeders, with the average carbon isotopic composition of an animal's tissues reflecting the average carbon isotopic composition of its diet. Fractionation occurs throughout an organism's metabolic pathways, giving consistently different isotope compositions for its various biochemical fractions (i.e. lipids, proteins and carbohydrates), with the visible 'shift' between dietary and body values largely dependent on the choice of tissue under analysis (DeNiro and Epstein 1978).

The 'shift' between carbon isotopic composition of the diet and that of bone collagen has been investigated through various laboratory experiments (e.g. DeNiro and Epstein 1978). Experimental studies on small mammals (e.g. Tieszen and Fagre 1993) and large mammals indicate diet-collagen $\delta^{13}C$ offsets between 3.7 and 6.0 ‰ for herbivores and omnivores (Bocherens and Mariotti 2002). In carnivores, resulting offsets between prey collagen and predator collagen are ~1‰ (Bocherens and Drucker 2003: 49). Although signals from other major food components explain some variations, dietary protein is the best predictor of the isotopic composition of collagen. This can be related specifically to the amino acid composition of collagen.

Glycine comprises 33% of the amino acids found in collagen and is 8‰ more positive than bulk diets in controlled feeding experiments (Tieszen and Fagre 1993: 151-152).

Food consumed either contributes to growth through the organism's anabolic pathways or is lost through excretion or respiration. Respired carbon has been demonstrated to be depleted in ^{13}C relative to body tissues (i.e. assimilated carbon), balancing this relationship between isotopic input (diet) and outputs (tissues, excretion and respiration) (DeNiro and Epstein 1978). However variation between different biochemical components/fractions (and, therefore, tissues), different individuals/species and the influence of different diets can lead to larger offsets (DeNiro and Epstein 1978). For example, offsets between plant producers and animal consumers may be due to differential digestion of different components of plants, which vary in carbon isotope composition (McCutchan et al. 2003).

Bone and tooth (dentine and enamel) bioapatite are also potential recorders of mammalian carbon dietary inputs. As with other biological tissues, there is an offset between the $\delta^{13}C$ of the diet and the bioapatite. This offset has been reported to be between 9 and 14‰ and appears to vary with predation (e.g. herbivore, carnivore, etc), and has also been demonstrated to vary between laboratory and field studies (Koch et al. 1998; Krueger and Sullivan 1984; Lee-Thorp et al. 1989).

2.5 Nitrogen

The study of two of the naturally occurring isotopes of nitrogen (^{15}N and ^{14}N) is also a useful tool in physiological and biochemical investigations. The principle reservoir for all nitrogen cycles is atmospheric nitrogen, largely in the form of N_2 as well as nitrogen oxides (NO_X) and ammonia (NH_3). In soils and aqueous environments, nitrogen usually occurs as NH_4^+, NO_3^-, NO_2^- and amino acids. Nitrogen is

incorporated into biological systems by bacteria and soil micro-organisms, with plants and primary producers exhibiting a range of values, largely depending on local environmental conditions. $\delta^{15}N$ data from different biological compounds indicate a state of isotopic disequilibrium or fractionation between different materials (e.g. atmospheric nitrogen and synthesised organic matter). Therefore, in contradistinction to carbon isotopes, significant enrichment in ^{15}N occurs between the diet and the body tissues of between around +2.6 and +3.4‰ (DeNiro and Epstein 1981; Minagawa and Wada 1984). However, trophic level shifts of between +1.7 and +6.9‰ have been observed (Bocherens and Mariotti 2002). The nitrogen in the body and diet is present almost entirely as proteins and their component amino acids (Schoeller 1999: 671).

2.5.1 Natural abundance, notation and standards

There are two naturally-occurring isotopes of nitrogen (Table 2.5).

Table 2.5 Abundances of the naturally-occurring isotopes of nitrogen (taken from Schoeller 1999: 668).

Isotope	Fractional Abundance
^{14}N	0.99634
^{15}N	0.00366

The accepted standard for nitrogen isotope analysis is AIR – the natural abundance of ^{15}N in air being constant within analytical precision (0.3663‰) (Sweeney et al. 1976 cited in Létolle 1980). Therefore, concentrations of ^{15}N are usually given as permil (‰) differences from the atmospheric N_2 written in the usual δ notation.

2.5.2 Nitrogen isotopes in the natural environment

The $\delta^{15}N$ values of soil N are largely positive and generally range between +2 and +10‰, although there are far greater (and also negative) measured values. The $\delta^{15}N$

values of soil nitrogen absorbed by the plants can be affected by a number of factors including temperature and water availability (Schwarcz et al. 1999), nitrogen transformation in soils and the addition of fertilisers (Choi et al. 2003; Kohl et al. 1973; Schwertl et al. 2005; Yoneyama 1990), stocking rate of animals (Schwertl et al. 2005), salinity (Britton et al. 2008; Heaton 1987; van Groenigen and van Kessel 2002), and the input of marine nitrogen through marine biomass (Hicks et al. 2005) and sea-spray (Heaton 1987; Virginia and Delwiche 1982). In typical soil profiles, $\delta^{15}N$ values increase with depth and despite varying surface values may approach a common value of between +5 and +7‰ (Létolle 1980: 418).

The pool size of nitrate in soil is large compared to nitrite and ammonium. Nitrate, nitrite and ammonia are assimilated into amino acids in the same way as one another after sequential reduction of nitrate to nitrite and then nitrite to ammonia. Higher rhizobial (leguminous) plants also gain nitrogen from atmospheric dinitrogen (N_2). This is reduced to ammonia and assimilated in amino acids (Yoneyama 1995).

Isotopic discrimination occurs during the uptake of these enriched ^{15}N substrates. This occurs to different degrees, and the mechanisms and effects in many species are not currently understood. The influence during the uptake of nitrate, nitrite and ammonia results in universal positive enrichment in ^{15}N from substrate to plant. Dinitrogen (N_2) fixers such as legumes also gain nitrogen during N_2 fixation by symbiotic systems, resulting in a small, slightly negative offset.

2.5.3 Nitrogen in animal tissues

Herbivore tissues are normally enriched in ^{15}N compared to the plant matter they consume (DeNiro and Epstein 1981), the ^{15}N content of animal tissues appearing to be magnified step-wise up the food chain. This can provide information about the trophic level of an organism (Minagawa and Wada 1984). The shift in $\delta^{15}N$ between

diet and consumer is normally between +2.6 and +3.4‰ (DeNiro and Epstein 1981; Minagawa and Wada 1984). However, higher and lower offsets have been reported (Bocherens and Mariotti 2002). Differences have been reported between high and low protein diets (Post 2002); with an increase or decrease of dietary C:N ratio (Adams and Sterner 2000; Webb et al. 1998) and during periods of fasting or starvation (i.e. a low quality diet with very low protein content) (Mekota et al. 2006). It is probable that these different observed effects are all induced by a common cause - that when dietary nitrogen is well below (or even well in excess of) the requirement for optimal growth, body tissue $\delta^{15}N$ values become high (McCutchan et al. 2003). During periods of dietary fasting (i.e. total starvation or very low protein intake), protein is lost in animal tissues by the action of proteases and is broken down into the constituent amino acids. These amino acids are then either locally deaminated *in situ* or exported to other organs. This has been demonstrated to lead to lower $\delta^{15}N$ values in excreted by-products and a remaining pool of ^{15}N enriched amino acids. These are then incorporated into proteins, leading to high $\delta^{15}N$ values in contemporary-forming tissues (i.e. those that maintain significant synthesis during the period of starvation) (Caloin 2004; Macko et al. 1986; Macko et al. 1987).

This trophic effect is also evident during mammalian suckling – where maternal milk places the offspring at a trophic level above the mother (Balasse and Tresset 2002; Fogel et al. 1989; Mays et al. 2002; Richards et al. 2002; Wright and Schwarcz 1998, 1999). In marine systems, ^{14}N is preferentially fixed but also substantially favoured during denitrification ultimately resulting in significant ^{15}N enrichment. Marine food chains also tend to be longer than terrestrial ones, incorporating a greater number of piscivorous trophic levels (Sealy 2001: 272).

Although this principle of bioamplification (i.e. that $\delta^{15}N$ values of consumers are predictably higher than their diets) is commonly used to infer trophic relationships and to understand intra-ecosystem relationships between different organisms, the

reasons behind this pattern are poorly understood (Vanderklift and Ponsard 2003). This bioamplification up the food chain can be unpredictable, is rarely linear, and ^{15}N enrichment or depletion at the base of a food chain can lead to very different nitrogen isotope values in animals normally at the same trophic level (see influences on nitrogen isotope composition of primary producers, plants and soils described above).

The cause of this enrichment is likely to be the fact that catabolic pathways in living organisms discriminate against small nitrogen-bearing molecules depleted in the heavier isotope, ^{15}N. However, whether this fractionation occurs during protein synthesis, or, conversely, during the process of nitrogen elimination is debated. Excreted nitrogen has been demonstrated to be depleted in ^{15}N compared to an animal's tissues or diet (DeNiro and Epstein 1981) although this has been recently questioned (Sponheimer et al. 2003a). The study by Sponheimer and colleagues indicated that $\delta^{15}N$ values of excreta were equal to that of food. However, tissue values were not measured. It could therefore still be possible that excreta depleted in ^{15}N can be a sufficient explanation for the more positive $\delta^{15}N$ values observed in tissues (compared to diet) but it is not a prerequisite. Ultimately, the current understanding of the mechanisms that regulate $\delta^{15}N$ are insufficient to resolve this issue.

In summary, different tissues within an individual can vary greatly in $\delta^{15}N$ value. These differences can be explained by their amino acid contents and by the nitrogen isotope composition of the individual amino acids themselves. This variation in $\delta^{15}N$ values of amino acids is seen in primary producers at the base of an ecosystem and appears to be amplified up the food chain.

2.6 Sulphur

Unlike carbon and nitrogen, the analysis of the stable isotopes of sulphur in bone (and dentine) collagen is far from routine in archaeological science. However, a small number of case studies have indicated the potential of this type of analysis for archaeological materials (Craig et al. 2006; Fornander et al. 2008; Linderholm et al. 2008; Privat et al. 2007; Richards et al. 2001). Furthermore, the recent publication of quality control criteria (along with a large body of modern reference data) and a review of the method will encourage more research (Nehlich and Richards 2009), ensure data reliability, and permit cross-comparisons to be made between studies.

2.6.1 Natural abundance, notation and standards

There are four naturally occurring isotopes of sulphur – ^{32}S, ^{33}S, ^{34}S and ^{36}S, the most abundant of which is the lightest isotope (see Table 2.6) (Faure 1986).

Table 2.6 Abundances of the naturally-occurring isotopes of sulphur (taken from Faure 1986).

Isotope	Abundance (%)
^{32}S	95.02
^{33}S	0.75
^{34}S	4.21
^{36}S	0.02

The agreed standard material is Arizona Canyon Diablo Troilite (CDT) (Krouse 1980). Results are expressed as $\delta^{34}S$ in parts per mil (‰). Sulphur isotopes in animal collagen are analysed using mass spectrometry. The extracted and freeze-dried protein is combusted, and isotopes of sulphur in the resulting SO_2 (and SO) are measured. It is necessary to correct for the heavier oxygen isotopes which can skew the data and mask the detection of the sulphur isotopes (Coleman 1980, 2004).

2.6.2 Sulphur isotopes in the natural environment

The main global reserves of sulphur are oceanic soluble sulphate, sulphate in ancient evaporites and sulphides (predominantly in the form of reduced pyrites FeS_2); with lesser reserves in soils, fossil fuels and the atmosphere. Environmental sulphur in the atmosphere and biosphere ultimately originates from oceanic and soil sulphur and cycles through the water cycle, weathering and tectonic movements (Bottrell and Newton 2006; Newton and Bottrell 2007). There is a large natural variation in environmental $\delta^{34}S$, although most values lie between -20‰ and +30‰ (Krouse 1980).

Contemporary oceanic sulphate (SO_4^{2-}) has a mean sulphur isotope value of around +20‰ and is fairly uniform across the globe (Rees et al. 1978). However, studies have demonstrated that oceanic sulphur isotope values have changed over geological time (Claypool et al. 1980; Paytan et al. 1998; Paytan et al. 2004). Marine sulphate can be carried inland through sea-spray, coastal precipitation and aerosols, and can influence terrestrial $\delta^{34}S$ values many kilometres from the coast (O'Dowd et al. 1997; Wadleigh et al. 1996). Freshwater (precipitation and groundwater) sulphate isotopic values are highly variable, although most values fall between 0‰ and +10‰ but can be considerably higher or lower (Krouse 1980; Nriagu and Coker 1978) and depend on local terrestrial environmental and geological conditions (soils, rocks, minerals) and marine input at the mouths of rivers and estuaries.

Values of crustal rocks vary with rock type and composition. As with strontium isotope analysis, an understanding of the geological complexity of the study area is the first step in a sulphur study. However, as with strontium isotopes, underlying geological $\delta^{34}S$ values are not necessarily the same as those that are bioavailable (i.e. in soils and plants) and likely to get into the food-chain to higher organisms and eventually to humans. Bioavailable sulphur (i.e. that which is incorporated into

biomolecules) derives from precipitation/ground water and atmospheric sources. The influence of geological sources (rocks and minerals) to the $\delta^{34}S$ of an ecosystem can be variable.

Sources of plant sulphur are predominately groundwater and the atmosphere. Plants incorporate inorganic sulphur from these sources into biological organic compounds. Cysteine is the end product of the reductive pathway that binds inorganic sulphur into amino acids in the plant, and this is then the starting material for the production of methionine, glutathione and other metabolites (Leustek and Saito 1999: 638). Plants are typically depleted in ^{34}S by 1.5‰ compared to their sulphate sources but the relationship between environment, assimilated sulphur and tissue sulphur can be very varied and complex (Trust and Fry 1992). Furthermore, sulphur isotope ratios may vary seasonally within the same plant, between different plants in the same area, and even between different parts of the same plant (Mekhtiyeva et al. 1976; Trust and Fry 1992). This variability can result in a broad range of baseline sulphur isotope values at a given locale or within a food-web.

2.6.3 Sulphur isotopes in animal tissues

The total sulphur pool in an organism, the organic sulphur in animal tissues and their isotope ratio is derived from organic sulphur in the diet (i.e. plants in herbivores), with contributions from environmental inorganic sulphur. Depending on the contribution of inorganic sulphur to the body pool, and given natural variations between inorganic and organic sulphur within the environment and even within the same plant, consumers may have tissue sulphur isotope ratios slightly different from their diets (McCutchan et al. 2003; Mekhtiyeva et al. 1976). There is little or no fractionation (<1‰) associated with the incorporation of sulphur-containing amino acids (cysteine and methionine) into tissues. These are brought into the body as proteins in the diet (especially methionine, which is essential for

mammals and cannot be synthesised) are absorbed, catalysed and incorporated into the amino acid pool of the body. For the purposes of archaeological and palaeoecological research – where type I collagen is the most common analyte – results should only reflect dietary methionine as cysteine is not found on this protein (Eastoe 1955).

Unlike carbon or nitrogen, there is no clear evidence for fractionation/step-wise enrichment up the food chain or 'trophic level effect' (Gonzalez-Martin et al. 2001; Richards et al. 2003a). Therefore, sulphur isotope values of herbivore tissues reflect their food sources and are directly related to the plant and environmental values (predominantly local geology and hydrology). Importantly, bone and dentine can now be analysed for sulphur isotopes in relatively small amounts, from extracted bone collagen (with no additional pre-treatment) and using established quality criteria (Nehlich and Richards 2009; Richards et al. 2001).

CHAPTER THREE ANIMAL TISSUES AS ANALYTICAL MATERIALS

3.1 Introduction

Given the relationships between chemical inputs and animal tissue composition described in the previous chapter, the isotopic composition of biological materials can be used as a record of biogenic processes and contemporary environmental parameters – with surrounding environmental conditions providing the total range of isotopic inputs then altered via the organism's dietary preferences, physiology, behaviour and metabolic processes. This allows the reconstruction of both the environmental and climatic conditions in which the animal lived (i.e. where and when the relevant tissues were forming) and also the nature of the subject-specific biological processes which were in place (e.g. dietary choices, species-specific physiologies, etc).

Some skeletal tissues such as bone remodel during life, providing life time average isotopic inputs for diets, climate and environment. Other tissues, such as teeth, form and mineralise progressively (or 'incrementally') and remain unaltered chemically and structurally *in vivo* (aside from wear and physical alterations due to dental pathologies). Given this, dental tissues have the potential to reveal variations in isotopic input within a temporal context (e.g. seasonally). Depending on the species a single herbivore tooth can take anything from a few months to a year or more to fully form. These tissues often survive intact in the archaeological record and their structural and chemical integrity permits stable isotope analysis - allowing the reconstruction of changes in diet, climate and locality into the archaeological and even geological past. In mammals, bioapatite is found and commonly sampled from three materials: bone, dentine and enamel. Strontium, oxygen and carbon isotope signatures from these tissues can be utilised to explore unknown aspects of the palaeoecology of extinct or archaic species such as geographical origin, lifetime movements, diet, local palaeoclimatic conditions, and seasonality. Carbon, nitrogen

and sulphur isotopic values can also be obtained from the organic phase of bone and dentine (collagen) and can potentially be used to explore the migratory and dietary behaviours of palaeofauna.

However, it is necessary to consider the nature of animal tissues as analytes. In doing this, aspects of their synthesis, chemistry, structure and histology must be considered. Furthermore, an understanding of tissue integrity – both pre- and post-mortem, as well as during burial – is necessary.

3.2 Tissue synthesis, isotopic variations and time-series information

3.2.1 Bone

There are two types of bone found throughout the mammalian skeleton – compact (or cortical) bone and trabecular bone. Compact bone is the dense, hard, outer layer found on the outside of bones. The porous trabecular bone (also called cancellous or spongy bone) forms the interior of bones. Bone constitutes several types of living cells, including bone-forming osteoblasts, matrix-trapped osteocytes and osteoclasts (responsible for bone resorption). Bone is first deposited as woven bone, with a disorganised structure and a high proportion of osteocytes (Bronner and Farach-Carson 2004). Woven bone is soon replaced by lamellar bone, which is stronger and has a more organised structure (Rho et al. 1998; Weiner and Wagner 1998).

The majority of bone is made up of the bone matrix – this comprises approximately 80% mineral and 20% protein (collagen) by dry weight. The mineral phase includes bioapatites, based on calcium ions (Ca^{2+}) (and any substituting strontium ions, Sr^{2+}) and phosphate (PO_4^{2-}) (and any substituting carbonates and other compounds). Collagen is the major insoluble fibrous protein in connective tissue and in the extracellular matrix, with a characteristic spectrum of different amino acids including glycine, proline and hydroxyproline. These amino acids form three spiral

chains, the triple helix, which twist together forming a larger macromolecule. These macromolecules form the fibrils of collagen, a long, thin protein. There are at least 16 types of collagen but 80-90% of collagen in the body is Type I, II or III collagen (Lodish et al. 2000). Apatite crystals become closely associated with collagen in mineralised tissues, although pretreatments of bone (and dentine) can remove mineral components and heat can break collagen down into gelatine (Longin 1971). Collagen is very stable, resistant to bacteria or fungal attack and insoluble in water. It can survive readily in the burial environment where conditions are constant and favourable, i.e. where soil pH is low and conditions are anoxic through water-logging, aridity or low temperature (Schwarcz and Schoeninger 1991; van Klinken 1999).

Bone is remodelled or renewed throughout life, a process often referred to as 'turnover', and different skeletal components (such as rib) can have higher turnover rates than others (Hedges et al. 2007; Richards et al. 2002: 205). This turnover involves the incorporation of new mineral and organic material, replacing the old, and leading to the introduction of new isotopic inputs. As a result, bone strontium, oxygen and carbon (mineral phase) and carbon, nitrogen and sulphur (collagen) will alter gradually throughout life. For bone collagen, a tissue turnover rate of approximately 10 years has been calculated using ^{14}C analyses, although this may vary with age (e.g. Geyh 2001; Hedges et al. 2007). Shifts in diet during this period will be reflected in the tissues. Isotopes of elements in body proteins (e.g. carbon, nitrogen and sulphur in bone collagen) will change gradually in response to isotopic compositional changes in diet. This rate of turnover can be slower for certain tissues and tissue values may be influenced by initial diet for a considerable period after the dietary switch. Given that different skeletal components can have different turnover rates it is possible that different parts of the skeleton can record dietary history at specific points in an individual's life. However, bone collagen will represent the

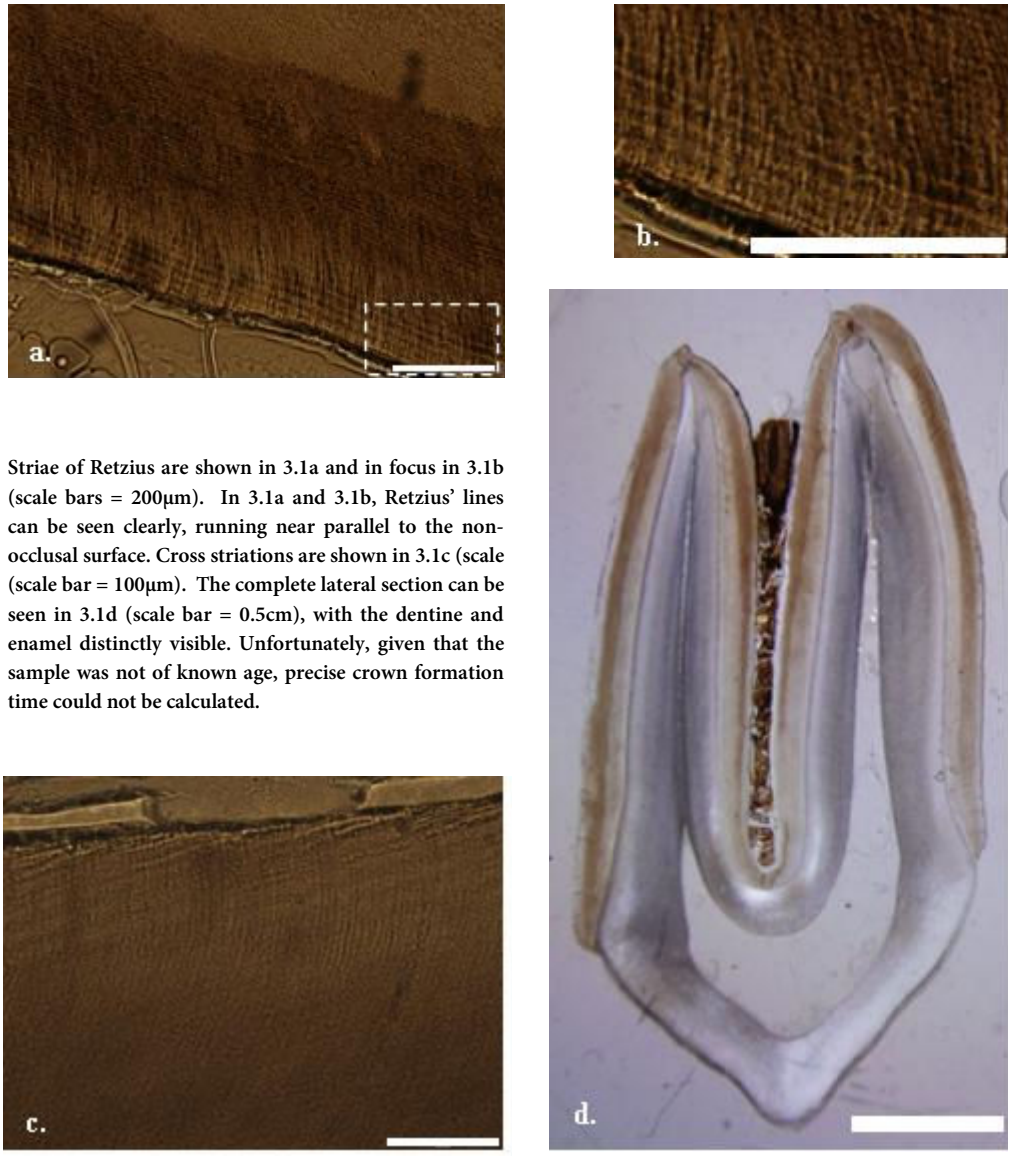
average isotopic composition of diet ingested over these periods, giving mid- to long-term isotopic averages.

3.2.2 Enamel

A complex series of growth stages are involved in tooth formation and mineralisation, many of which are only rudimentarily understood. Mature dental enamel is acellular and almost entirely inorganic – with approximately 96% inorganic material (by dry weight), less than 1% organic material and ~3% water (Williams and Elliott 1989). Enamel demonstrates no remodelling or renewal after initial formation and mineralisation (Hillson 2005: 152-153), therefore preserving the isotopic signatures during formation throughout life.

However, tooth enamel is not fully mineralised when it is first formed. Initially deposited enamel has a mineral content of approximately 25% (Passey and Cerling 2002) or less and is approximately 30% protein, the remainder being water. Enamel is formed by ameloblasts, a sheet of cells on the internal enamel epithelium (Hillson 2005: 155). Amelogenesis occurs in two phases, the production of the original protein-rich matrix (formation) and then maturation (a prolonged phase of mineral accumulation). The majority of initial proteins are amelogenins which are rich in proline, histidine, leucine and glutamine. The structural features of enamel are laid-down during the initial phase but the majority of mineralisation occurs in the later phase of maturation – where proteins and water are broken down and removed, crystals grow in size, producing the densely mineralised mature enamel (Robinson et al. 1997). Different areas of enamel in the crown undertake this process at different times. Ameloblasts at the crown start first and those at the cervix start last, this rhythm is preserved in patterns observed in the prism structure of mature enamel – in the dark and light bands of prism cross striations (Hillson 2005: 156; see Figure 3.1c). These may be caused by variation in the rate and extent of mineralisation,

perhaps due to the ratio of phosphates to carbonates in the crystals. There are also larger structures marking out the matrix-forming front in most mammals, the brown striae of Retzius (Figure 3.1a & 3.1b). These are parallel to the cross striations and also record the history of initial crown formation (see Figure 3.1a, b, c, d).



Striae of Retzius are shown in 3.1a and in focus in 3.1b (scale bars = 200μm). In 3.1a and 3.1b, Retzius' lines can be seen clearly, running near parallel to the non-occlusal surface. Cross striations are shown in 3.1c (scale (scale bar = 100μm). The complete lateral section can be seen in 3.1d (scale bar = 0.5cm), with the dentine and enamel distinctly visible. Unfortunately, given that the sample was not of known age, precise crown formation time could not be calculated.

Figure 3.1 Enamel structure in a domestic reindeer molar thin section (*Rangifer tarandus*).

Counts of cross striations during thin-section histological studies correspond well to estimates of crown formation times using other methods (e.g. radiograph or dissection-based studies), although samples from multiple unworn teeth of known age at death are required to complete such studies. Furthermore, chemical markers have been administered to captive animals to investigate the timing on these cross striations and have identified clear correlations between marker lines and periods of chemical injections (e.g. Smith 2006). However, although cross striations may be able to help establish a reliable chronology of enamel formation (e.g. Dean 2000), there is currently a large amount of uncertainty concerning the assumed pattern and timing of post-accretional mineral uptake (i.e. when the remaining 75% of mineralised material will be incorporated, including strontium, the oxygen in structural phosphates and the carbon and oxygen in structural carbonates). The Retzius' striae only record the orientation of mineralisation during the formation of the protein-rich matrix, which only displays <15% of the density of fully mineralised enamel (Hoppe et al. 2004b). Multiple mineralisation fronts have been identified during the maturation phase, moving in various directions (Suga 1982).

However, an understanding of the phasing, timing and directional progress of subsequent mineralisation is critical for undertaking stable isotope research, designing sampling strategies and understanding and modelling data (Balasse 2002, 2003; Passey and Cerling 2002; Zazzo et al. 2005). Given that no visible structures of mineralisation (as opposed to formation) are preserved, other techniques have been employed to reconstruct the timing and geometry of enamel mineralisation and maturation – including radiographs taken of developing teeth (e.g. Hoppe et al. 2004b), MicroCT imaging (Podlesak et al. 2008) and isotopic labelling (Balasse 2002; Zazzo et al. 2005).

Radiographic analyses have indicated that the mineralisation front during maturation may run almost parallel to the Retzius' striae and that this process lags

behind formation, extending time to crown completion by weeks or months (Hoppe et al. 2004b). However, MicroCT images of developing teeth demonstrate that the mineral uptake during enamel maturation is not always linear and can also be sigmoidal through time (Podlesak et al. 2008).

Experimental isotopic studies have demonstrated that the isotopic input ('dietary signal') is attenuated over weeks and months in herbivore teeth (Balasse 2002, 2003; Hoppe et al. 2004b; Kohn et al. 1996; Passey and Cerling 2002). This confirms that each portion of the enamel is subject to a significant period of development (and therefore to potentially varying isotopic inputs) – including phases of original secretion or deposition of the organic rich matrix, to the series of mineralisation phases in enamel.

After the bulk of mineralisation has occurred during the enamel maturation phase, any particular volume of enamel will include multiple layers of enamel accreted at different times – both on the appositional front during enamel matrix accretion and during the later phases of mineralisation. Given that conventional sampling procedures normally involve the removing of material perpendicular to the tooth length axis or cemento-enamel junction, this leads to a mixing of isotopic inputs and influences the results of isotopic analyses (Kohn et al. 1998; Passey and Cerling 2002; Passey et al. 2005; Podlesak et al. 2008; Zazzo et al. 2005). Furthermore, the location and direction (and size) of subsamples from enamel and dentine have been demonstrated to influence the values obtained using stable isotope analysis and the resolution achievable (Zazzo et al. 2005, 2006). It can be noted that even where the most refined sampling tools are in use (e.g. microdrilling or laser ablation) and samples are collected only along well defined growth lines, enamel may represent material that mineralised over several weeks or more (Hoppe et al. 2004b: 364). Despite this, seasonal isotopic changes have been identified in oxygen isotope analysis in both enamel and dentine using a range of serial-sampling procedures

(Cerling and Sharp 1996; Fricke and O'Neil 1996; Fricke et al. 1998b; Fricke et al. 1998a; Gadbury et al. 2000; Koch et al. 1989; Kohn et al. 1998; Sharp and Cerling 1998). In the case of oxygen, in experimental and observation studies, it is clear that seasonal climatic variations are the primary influence on isotope compositional variations in dental enamel (e.g. Fricke et al. 1998b; Kohn et al. 1998). Dietary switches in controlled feeding experiments (e.g. C_3 to C_4 diet) have also confirmed that – in spite of some time-lagging and attenuation (or 'dampening') of isotopic signal – changes in diet can be reconstructed from the isotopic analysis of enamel and dentine (Balasse et al. 2001; Balasse 2002; Zazzo et al. 2005, 2006). This approach has also identified seasonal dietary shifts in modern and archaeological domestic animals – such as seasonal foddering of brown kelp in modern and Neolithic sheep (Balasse et al. 2005; Balasse et al. 2006) and the seasonal foddering of sheep and goats by modern Mongolian pastoralists (Makarewicz and Tuross 2005). These studies confirm the potential for this type of analysis to reveal time-series patterns of mobility, diet and seasonality in zooarchaeological and palaeoecological samples.

3.2.3 Dentine

Dentine is composed of approximately 72% mineral, 18% collagen and 2% other organic material (Williams and Elliott 1989). Like enamel, the formation of dentine takes place in two phases – secretion of the organic matrix (pre-dentine) and the subsequent addition of apatite crystals. During this process the original organic matrix remains in the tissue and is not removed or replaced by the incoming apatite. As with bone collagen, dentinal collagen isotope composition reflects the dietary protein isotope composition. Unlike bone, dentine demonstrates little or no renewal after formation (Hillson 2005: 185), therefore preserving the isotopic signatures during formation throughout life. Whereas enamel is effectively a 'dead' tissue within the body, dentine has living cells (odontoblasts). These long, narrow cells line the

pulp chamber, backing onto the developing dentine. Odontoblast processes pass through the full thickness of the dentine via the dentinal tubules (Hillson 2005: 186). As with enamel, dentine first begins to form at the dentine-enamel junction at the crown of the tooth, a short while before enamel. Predentine is first laid down under the centre of the cusps, followed by the first immature enamel (Hillson 2005). Dentine grows as a succession of stacked cones – primary dentine in the crown forming first, with successive growth occurring in sloping sleeves.

The structure of dentine is normally visible in dentine sections using light microscopy. As with enamel, labelling experiments have indicate that the smallest laminar structures grow on a circadian rhythm. There are also longer-period lines, similar to Retzius lines (Dean 1995). Given the dental formation and tooth eruption patterns in mammalian teeth, studies have demonstrated that it is possible to reconstruct time-series dietary information from the longitudinal sequential sampling of dentine and the subsequent analysis of the extracted collagen (e.g. Balasse et al. 2001; Drucker et al. 2001; Fuller et al. 2003; Zazzo et al. 2006).

It must be noted that, whatever the abruptness of a dietary change, the reflection of this in the carbon, nitrogen and sulphur isotopic composition of newly-synthesised tissues (even those that are not subject to remodelling or renewal) will rarely exhibit itself suddenly or rapidly. An equilibrium period in which the turnover of the metabolic pool occurs will precede any isotopic shift (related to the new diet) evident in the tissues. The breakdown of old tissues and stored metabolites, along with the new dietary input, results in a mixture of pre- and post-dietary 'signals' until an equilibrium point is reached (Balasse et al. 2001: 238). Bi-weekly hair sampling in experimental studies has established that the diet-hair nitrogen isotope equilibrium is established in less than 24 weeks after a dietary change, varying little after only 8 weeks (Sponheimer et al. 2003b: 82). This study by Sponheimer and colleagues involved a number of different animal species including llamas (*Lama glama*),

alpacas (*Lama pacos*), goats (*Capra hircus*), cattle (*Bos Taurus*), horses (*Equus caballus*) and rabbits (*Oryctolagus cuniculus*). In addition, experimental studies have indicated that the diet-hair carbon isotope equilibrium period is approximately 8 to 12 weeks in cattle (Jones et al. 1981 cited in Balasse et al. 2001).

3.3 Diagenesis, degradation and collagen loss

3.3.1 Diagenetic alteration in bioapatites

Post-depositional alteration must be considered closely in any application of stable isotope analysis to archaeological and palaeontological materials. Diagenesis refers to the post-mortem chemical alterations of both the protein and mineral fractions of bone and teeth that may occur in the burial environment.

A large amount of recent research has demonstrated that, despite a number of 'successful' earlier studies, archaeological bone bioapatite is often contaminated or chemically-altered during burial. Therefore, although bone is extremely common in the archaeological record, its small crystal size, high porosity and organic content render it highly susceptible to recrystallisation and diagenesis (the alteration of the isotopic composition through chemical substitution, replacement or contamination within the burial environment). During this process of diagenetic alteration, exogenous strontium, carbon and oxygen in the burial environment can affect and even replace original strontium, carbon and oxygen in the mineral phase of bone (Jans et al. 2004; Nielsen-Marsh and Hedges 2000a; Nielsen-Marsh et al. 2000; Price et al. 1992; Tuross et al. 1989). This can occur in a number of different ways – through the pore-filling by secondary minerals; through the recrystallisation or remineralisation of hydroxyapatite; by the direct exchange of environmental Sr or Ca with original Sr and Ca in hydroxyapatite crystals (Hoppe et al. 2003: 26) as well as through surficial absorption or via microcracks on hydroxyapatite crystals (Nelson et al. 1986).

Although less likely to be affected than bone, dentinal bioapatite is also highly susceptible to diagenetic alteration. Although being significantly more dense, dentine has a comparable crystal size to bone and, although enamel may afford the internal dentine some protection, it has been demonstrated that dentine is likely to be affected by diagenetic alteration and is not a reliable reservoir of original *in vivo* isotope composition (Budd et al. 2000; Hoppe et al. 2003; Montgomery 2002; Trickett et al. 2003).

Many methods have been published arguing that the effects of such diagenetic contamination or exogenous isotopic inputs into bone and dentine apatite can be removed using pre-treatments – most commonly involving the application of weak acids to leach the bone (Garvie-Lok et al. 2004; Koch et al. 1997; Nielsen-Marsh and Hedges 2000b; Price et al. 1992). Whilst initial and successive stages of acid leaching may remove some diagenetic strontium or carbonates from bone and dentine, it has been demonstrated that the application of such methods is limited and ineffective if significant re-crystallisation or direct exchange has occurred (Beard and Johnson 2000; Budd et al. 2000; Collins et al. 2002; Hoppe et al. 2003; e.g. Nelson et al. 1986; Trickett et al. 2003; Tuross et al. 1989). A recent study by Hoppe et al. (2003) has demonstrated that, in spite of acid pretreatments, as much as 80% of diagenetic strontium remains in Holocene and Miocene bone (Hoppe et al. 2003: 26). It must be noted of course that acid treatments do not isolate diagenetic strontium, and *in situ* biogenic strontium may also be leached out and lost (Hoppe et al. 2003: 26).

However, given its density, compact structure (with large, densely packed crystals and smaller pore spaces) and inert nature, enamel appears to be more resistant to post-mortem diagenesis and chemical/isotopic alteration in the depositional environment than either bone or dentine (Budd et al. 2000; Hoppe et al. 2003; Koch et al. 1997; Kohn et al. 1999; Trickett et al. 2003). Furthermore, it has been suggested that enamel can be utilised to assess the extent of contamination in bone and dentine

from the same individuals/at the same site (Montgomery 2002: 331). Within the highly-packed, dense structure of enamel, the PO_4- and OH-substituting structural CO_3 have a degree of diagenetic resistance. It is necessary to remove the labile non-structural CO_3 with an acid pre-treatment, which may also remove calcitic compounds, dolomites and other contaminants. Due to the strength of the P-O bonds within the PO_4 component of bioapatite, it has been suggested that phosphate has a greater resistance to diagenetic alteration than carbonate components from the same samples (Kohn et al. 1999; Kolodny et al. 1983; Luz et al. 1984; Nelson et al. 1986). It has also been demonstrated that, although carbonate components are often diagenetically altered through frequently occurring chemical contamination in the burial environment, less common biological and enzymatic attack is more likely to affect the phosphate component. However, bacterial action on teeth and bones can normally be determined visibly or using light microscopy and samples can be avoided as necessary.

3.3.2 Collagen loss, alteration and quality indicators

Post-depositional alterations can also occur in the organic fractions of archaeological and palaeontological skeletal materials. Diagenesis can occur as a result of microbial attack as well as gradual chemical degradation in the burial environment (Nielson-Marsh et al. 2000). Biological degradation increases the porosity of bone or tooth, exposing the organic components to microbial attack (Collins et al. 2002; Jans et al. 2004). As well as biological enzymatic degradation, the organic components of bones and teeth also undergo chemical degradation involving the hydrolysis of the peptide bonds of collagen (Hare and Hoering 1977 cited in Nielson-Marsh et al. 2000: 442). This leads to a weakening of the structure, fragmentation and leaching (Collins et al. 2002: 387). It has also been demonstrated that microbial action can accelerate rates of diagenesis (Collins et al. 2002), which has also been demonstrated to occur at extremes of pH or at elevated temperatures (Collins et al. 2002: 26). Given the

presence of a protective tooth crown and denser mineralised structure, archaeological dentinal collagen is afforded more structural protection in the burial environment than bone collagen. However, crown damage or loss can lead to exposure and weakening of the dentine through collagen loss (Beeley and Lunt 1980). The collagen component of bones and teeth can also be susceptible to contamination – referring to the process with which exogenous substances can enter the matrix, with the potential to alter collagen isotopic ratios (van Klinken 1999: 688). The rate of this contamination can be accelerated by microbial degradation, porosity and diagenetic alteration (Jans et al. 2004).

Unlike with bioapatites, there are several well-established quality control indicators used by laboratories to indentify the extent to which extracted 'collagen' has been degraded or contaminated (see van Klinken 1999). These include assessments of 'collagen' yields and the amounts and ratios of carbon and nitrogen in the 'collagen'. 'Collagen' yields are expressed as weight percentages or as weight ratios (mg/g). Modern fresh bone contains about 22 wt % collagen, but this drops progressively during burial. Low-'collagen' bones (i.e. less than 1%) are commonly considered unsuitable for analysis and should be considered as 'indications of breakdown of sample integrity' (van Klinken 1999: 689). Intact collagen should have a characteristic carbon content of around 35 wt % and nitrogen content of between 11-16 wt %. It has been suggested that these parameters are reliable indications of the integrity of extracted 'collagen' (Ambrose 1990). Furthermore, it is also suggested that the measured atomic C:N ratio of extracted 'collagen' is an indication of sample integrity. It has been suggested that contamination is likely when C:N ratios fall outside of the range determined by modern humans and animals – between 2.9-3.6 (DeNiro 1985). However, this range has been criticised as being too broad and, as a result a 'more sensitive' C:N ratio of 3.1-3.5 is often used (van Klinken 1999: 691).

Quality criteria have also been established for the sulphur isotope analysis of bone collagen (Nehlich and Richards 2009). The extensive study of Nehlich and Richards (2009) indicates that the amount of sulphur in modern mammalian bone collagen is 0.28 ±0.07%. They also defined the ranges for atomic C:S ratio (600 ±300) and N:S ratio (200 ±100) for the same material (*n*=140) (Nehlich and Richards 2009).

CHAPTER FOUR STABLE ISOTOPE ANALYSIS AND THE RECONSTRUCTION OF ANIMAL LIFE-HISTORIES

4.1 Introduction

This chapter shall focus the previous applications of stable isotope analysis to the investigation of the animal movements and dietary behaviour in the past and assess the contributions made to the field over the last several decades. The stable isotope analyses of biological materials can be used to investigate an organism's place within a food web and within the broader landscape (see Chapter 2). Determining provenance of an organism may include connecting it to a specific geographical area through relating its tissue chemistry to a particular geology or associating it more generally with an environment, ecosystem or climatic zone. Investigating an animal's place within a particular food web may include assessing dietary components, its foraging/feeding behaviours, potential movements across vegetative communities and its trophic level. In domesticated animals, dietary analysis can also help to elucidate animal management strategies in human populations. Stable isotope analysis can allow the determination of the fate of assimilated nutrients and allow assessment of physiological condition, food quality and even certain pathological conditions.

Isotopic methods have numerous applications across many fields including food provenancing and authentication, forensic science, law enforcement, ecology, anthropology and archaeology (e.g. Aggarwal et al. 2008; Beard and Johnson 2000; Ericson 1985; Hobson 1999; Hoppe et al. 1999; Koch et al. 1998). These techniques are increasingly utilised in modern animal ecological investigations and are used to address issues of ecosystem, physiology, population, nutritional and migratory ecology (Hobson 1999; Hobson and Wassenaar 1999; Rubenstein and Hobson 2004). Many recent archaeological studies have utilised isotopic analysis to determine the life histories of wild and domestic fauna. These approaches have been used to infer

patterns of animal husbandry, herd-use and herding practices in domestic species and the migration, diets and behavioural ecology of wild species.

Bulk sampling of tissues such as bone can provide averaged isotopic inputs allowing the reconstructing of lifetime foraging habits and range. However, the serial sampling of enamel or dentine (or hair/wool, horn, hoof and other keratinous tissues in modern samples) can provide higher resolution information about dietary changes and seasonal movements. These approaches have the potential to reveal the temporal and spatial aspects of feeding, migratory and reproductive behaviour in wild animals on a population as well as individual level. Such techniques could be used to define the interaction between wild animals and their environments and reveal the fundamentals of their ecology. This has implications for our understanding of their evolutionary history, their behaviours and the behaviours of their dependent predator species, including humans. In the case of domesticates, this can allow the reconstruction of interaction between humans and their managed animal stock, with isotopic profiles offering insight into herding and animal husbandry practices and the human control and manipulation of diet, movement and reproductive behaviours. This in turn can be significant for inferring information about past human diets, subsistence economies and societies.

4.2 A review of modern and archaeological applications of isotope analysis to wild and domestic animal dietary and migratory behaviour

Over the past 15 years, the frequency of the use of stable isotope analysis in animal ecology has grown significantly (Wolf et al. 2009). Stable isotope analysis has been applied to many aspects of animal ecology including palaeoecology, although it is arguably still an underutilised technique (Sponheimer et al. 2003c). Isotope methods can be applied across different taxa and the most commonly-used analytes are found across different species. This can allow the analysis of multiple species within

different ecosystems, allowing the assessment of behavioural and feeding ecology at many levels of the food chain. The standardisation of sampling and measurement procedures on similar analytes allows the comparison of multiple species and across multiple geographical areas (Hobson and Wassenaar 2008). Furthermore, stable isotope methods can permit a temporally integrated approach to the reconstructing of foraging behaviour and animal ecology. Compared to other methods, stable isotope methods do not rely on the re-capture or re-sighting of previously sampled individuals (Rubenstein and Hobson 2004). When a large-enough survey is conducted, data is meaningful on a population level, with archiving allowing the assessment of temporal trends.

Although isotope analysis can offer lower resolution results than other methods of reconstructing foraging and ranging behaviour in modern animals (e.g. tagging, satellite collaring, etc), the use of multiple isotopes in combination can increase this resolution (Hobson and Wassenaar 2008). The field of isotope ecology has been aided by numerous experimental and observational studies which have generated a large volume of data from modern wild and domesticated species. These approaches have allowed a greater understanding of how quickly and how faithfully animals assimilate the stable isotopes in their food into their tissues – allowing the development of models of the dynamics of isotopic incorporation, mixing, routing and discrimination/fractionation (Gannes et al. 1997; Gannes et al. 1998; Wolf et al. 2009). Such theoretical models can aid the application of isotope analysis to palaeoecology. An understanding of the time-scale of ingestion to incorporation and the relationship between the isotopic inputs to the tissue outputs is essential to reconstructing dietary, locational and seasonal input changes.

There are a number of important and widely-cited controlled feeding experiments using mammals which provide the background required to interpret isotope data from unknown populations (whether modern or archaeological). A summary of

major controlled feeding experiments are shown in Table 4.1. These have included both laboratory (e.g. Ambrose and Norr 1993; Ambrose 2000) and domestic (e.g. Balasse et al. 2001; Sponheimer et al. 2003b) animals and have involved a range of analytes such as:

- **blood** (De Smet et al. 2004; Norman et al. 2009)
- **muscle** (Bahar et al. 2009; Yi et al. 2004)
- **hair** (Sponheimer et al. 2003b; Zazzo et al. 2007)
- **wool** (Norman et al. 2009; Zazzo et al. 2008)
- **hoof** (Harrison et al. 2007a; Harrison et al. 2007b; Zazzo et al. 2007)
- **bone** (Ambrose 2000)
- **tooth** (Balasse et al. 2001; Zazzo et al. 2005, 2006)

Table 4.1 Summary of major controlled feeding studies on laboratory, domesticated or captive wild mammals.

Reference	Species	Analyte	Isotope	Detail
(Ambrose and Norr 1993)	Rat (*Rattus* sp.)	Bone collagen, bone carbonate	$\delta^{13}C$	C_3 vs C_4, diet-tissue relationship
(Tieszen and Fagre 1993)	Mice (*Mus* sp.)	Respiratory CO_2, bone collagen, bioapatite, soft tissues	$\delta^{13}C$, $\delta^{15}N$	C_3 vs C_4, diet-tissue relationship
(Ambrose 2000)	Rat (*Rattus* sp.)	Bone collagen	$\delta^{15}N$	Dietary protein content, climate influences
(Balasse et al. 2001)	Cattle (*Bos taurus*)	Dentinal collagen	$\delta^{13}C$, $\delta^{15}N$	C_3 vs C_4, dietary switch, diet-tissue relationship
(Howland et al. 2003)	Pig (*Sus scrofa*)	Bone apatite, collagen and lipids; bone fatty acids and cholesterol; amino acids from collagen	$\delta^{13}C$	C_3 vs C_4, marine protein
(Sponheimer et al. 2003b)	Llamas (*Lama glama*), alpacas (*Lama pacos*), goats (*Capra hircus*), cattle (*Bos taurus*), horses (*Equus caballus*), rabbits (*Oryctolagus cuniculus*)	Hair	$\delta^{15}N$	Dietary protein content, isotope metabolism
(Sponheimer et al. 2003a)	Llamas (*Lama glama*)	Urine, faeces	$\delta^{15}N$	Dietary protein content
(Richards et al. 2003a)	Horse (*Equus caballus*)	Hair	$\delta^{34}S$	Diet-tissue fractionation
(De Smet et al. 2004)	Cattle (*Bos taurus*)	Blood, plasma, liver, kidney fat, hair, muscle, ruminal contents	$\delta^{13}C$	C_3 vs C_4, dietary switch, tissue turnover, isotope metabolism
(Jim et al. 2004)	Rat (*Rattus* sp.)	Bone cholesterol, bone	$\delta^{13}C$	C_3 vs C_4, marine protein

		collagen, bone apatite		
(Yi et al. 2004)	Pikas (*Ochotona curzoniae*)	Muscle	$\delta^{13}C$, $\delta^{15}N$	C_3 vs C_4, dietary switch, tissue turnover, isotope metabolism
(Zazzo et al. 2005)	Cattle (*Bos taurus*)	Enamel bioapatite	$\delta^{13}C$	C_3 vs C_4, dietary switch, tissue turnover, tissue mineralisation
(Zazzo et al. 2006)	Cattle (*Bos taurus*)	Dentinal collagen	$\delta^{13}C$	C_3 vs C_4, dietary switch, tissue turnover, tissue formation
(Harrison et al. 2007b)	Cattle (*Bos taurus*)	Hoof	$\delta^{13}C$	C_3 vs C_4, dietary switch, tissue turnover, tissue formation
(Harrison et al. 2007a)	Cattle (*Bos taurus*)	Hoof	$\delta^{13}C$	C_3 vs C_4, dietary switch, tissue turnover, tissue formation
(Zazzo et al. 2007)	Cattle (*Bos taurus*)	Hoof, hair	$\delta^{13}C$, $\delta^{15}N$	C_3 vs C_4, dietary switch, tissue turnover
(Zazzo et al. 2008)	Sheep (*Ovis aries*)	Wool	$\delta^{13}C$	C_3 vs C_4, dietary switch, tissue turnover
(Bahar et al. 2009)	Cattle (*Bos taurus*)	Muscle	$\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$	C_3 vs C_4, marine protein, isotopic authentication
(Norman et al. 2009)	Sheep (*Ovis aries*)	Blood plasma, faeces, urine, wool	$\delta^{13}C$	C_3 vs C_4, tissue turnover

These controlled experiments are a very important component of modern stable isotope studies and help establish an understanding of basic aspects of stable isotope metabolism in organisms and the relationship between dietary values and those exhibited in the tissues of the feeder. These include issues such as tissue turnover rates, fractionation effects and bioavailability. For example, controlled feeding experiments have been used to demonstrate the potential for isotope analysis to differentiate between the consumption of C_3 and C_4 plants in herbivores. As previously discussed (see Chapter 2), these plants have different photosynthetic pathways giving them characteristic $\delta^{13}C$ values. The consumption of different quantities of C_3 and C_4 plants will therefore alter the carbon isotope ratios of consumers' biological tissues. This has been demonstrated by recent studies of modern bovine tooth enamel (Balasse 2002) and dentine (Balasse et al. 2001; Zazzo et al. 2006). Dentine and enamel were sequentially-sampled from five modern steers raised in controlled environments – initially fed on a C_3-dominated and then switched to a C_4-dominated diet. Both studies generated high-resolution carbon isotope profiles with large intra-tooth variations in bioapatite (enamel) and collagen (dentine) $\delta^{13}C$ values. These corresponded with the enforced diet-switch experienced by the five animals during tooth growth (Zazzo et al. 2006). Not only do such studies replicate dietary shifts that could be seen in archaeological populations but also the measurement of isotope ratios in supposed incrementally-developing tissues can allow a greater understanding of the formation of the tissues themselves (e.g. Zazzo et al. 2005, 2006).

Experimental studies help to promote a fundamental understanding of trophic relationships, geographical variations and intra- and inter-individual variations that underlie the use of these methods in ecology, archaeology and anthropology. There is a clear need for a greater number of such studies given that factors such as tissue turnover rates, fractionation effects and the influences of animal physiology are only rudimentarily understood for many species (Hobson and Wassenaar 2008: 10).

However, one clear limitation of controlled feeding experiments is that in each instance, by design, the diets (and behaviours) of the animals are humanly manipulated. This means that such studies cannot account for the inclusion of natural foraging and feeding behaviours, physiologies and pathologies. Furthermore, in some instances, diets are manipulated to such an unnatural degree that this could, in itself, cause additional stable isotope metabolic effects. For example, Sponheimer and colleagues (2003b) determined that interspecific physiological differences can account for varied diet-tissue offset in herbivorous animals otherwise at the same trophic level. However, their study also demonstrated that the fractionation effect between the diet and the measured analyte (in this case hair) varied depending on the protein content of the diet (low vs. high) (Sponheimer et al. 2003b). This in itself demonstrates how models formed on the basis of experimental data could be potentially flawed, being both subject and condition specific and, most importantly, perhaps not replicating 'real life' situations. Such data may then be used to develop models which can facilitate the understanding and interpretation of archaeological isotope data (e.g. Kellner and Schoeninger 2007). However, these – along with theoretical models – can be misleading, especially since biological processes such as amino acid and protein synthesis are complicated by many variables (Hedges and van Klinken 2000).

Observational experimental approaches involving the survey and dietary assessment of wild animals and the subsequent isotope of their tissues are therefore a necessary component of stable isotope ecology and archaeology. A number of such 'field studies' have been conducted over the last 20 years using isotope analysis to explore the dietary, spatial and behavioural ecology of wild and domesticated animals (see Table 4.2). A significant number of studies have also been conducted on avian species and butterflies. However, only mammalian taxa have been included in this summary. A number of studies have been conducted on modern wild mammalian fauna and have included the reconstruction of diets (Copeland et al. 2009), resource

partioning (Feranec 2007), trophic relationships (Ambrose 1991), foraging habits (Ben-David et al. 2001; Kielland 2001) and movement patterns (van der Merwe et al. 1990). These studies provide useful data for comparison to archaeological and palaeontological case studies. These are an important addition to the field of isotope archaeology and are complementary to the controlled feeding experiments discussed above and to the data obtained from domesticated or captive animals. They are particularly important because they provide data from the natural behaviour of species, giving an indication of the influence of factors such natural physiological variability, feeding and ranging behaviour. Studies on extant archaeologically-analogous wild species such as reindeer and bison are especially pertinent to European Palaeolithic archaeology. Many studies on wild animals have involved soft tissue analytes such as blood or used keratinous tissues such as hair/wool and hoof. For example, Ben-David and colleagues identified differences in seasonal foraging behaviours in caribou (*R. tarandus*) and moose (*Alces alces*) in the Denali National Park and Reserve, Alaska, using stable isotope analysis of blood (Ben-David et al. 2001). Similarly, another study by Kielland (2001) demonstrated the potential to trace seasonal foraging and dietary changes in moose from different areas of north-central Alaska through the sequential isotope analysis of incrementally-developed keratinous hoof tissue (Kielland 2001). However, as both these studies incorporated the analysis of tissues not commonly preserved in the archaeological record, the practical application of these methods to identify seasonal dietary change in ancient *Alces* or *Rangifer* (using archaeologically-available analytes such as tooth or bone) remains unknown.

Table 4.2 Summary of major studies investigating nutritional or migratory ecology of mammals (including archaeological and domestic species) using stable isotope analysis (after Hobson 1999).

Reference	Species	Analyte	Isotope	Detail
(Ambrose and DeNiro 1986)	East African mammals (multiple species)	Bone collagen	$\delta^{13}C$, $\delta^{15}N$	Trophic relationships, C_3 vs C_4, canopy effect, moist vs arid
(Schell et al. 1989)	Bowhead whale (*Balaena mysticetus*)	Muscle and visceral fat	$\delta^{13}C$, $\delta^{15}N$	Marine isotopic gradients
(van der Merwe et al. 1990)	African elephant (*Loxodonta africana*)	Ivory	$\delta^{13}C$, $\delta^{15}N$, $^{87}Sr/^{86}Sr$	C_3 vs C_4, drought stress, geology
(Vogel et al. 1990)	African elephant (*Loxodonta africana*)	Bone, ivory	$\delta^{13}C$, $\delta^{15}N$, $^{87}Sr/^{86}Sr$, Pb	C_3 vs C_4, drought stress, geology
(Fleming et al. 1993)	Bats (*Leptonycteris curosoae, Glossophaga soricina*)		$\delta^{13}C$	C_3 vs CAM
(Koch et al. 1995)	African elephant (*Loxodonta africana*)	Ivory	$\delta^{13}C$, $\delta^{15}N$, $^{87}Sr/^{86}Sr$	C_3 vs C_4, drought stress, geology
(Best and Schell 1996)	Southern right whale (*Eubalaena australis*)	Baleen	$\delta^{13}C$, $\delta^{15}N$	Marine isotopic gradients
(Ben-David et al. 1997)	Mink (*Mustela vison*)	Blood	$\delta^{13}C$, $\delta^{15}N$	Marine vs freshwater vs uplands
(Hobson et al. 1999)	Norway rats (*Rattus norvegicus*)	Muscle, liver	$\delta^{13}C$, $\delta^{15}N$, $\delta^{34}S$	Marine vs terrestrial
(Hoppe et al. 1999)	Mammoth (*Mammuthus sp.*), Mastodont (*Mammut americanum*)	Tooth enamel	$^{87}Sr/^{86}Sr$	Geology
(Burton and Koch 1999)	Pinnipeds (multiple species)	Bone collagen	$\delta^{13}C$, $\delta^{15}N$	Marine isotopic gradients, nearshore vs offshore foraging/migration
(Cerling et al. 1999)	Modern and fossil elephants (*Loxdonta*	Tooth enamel	$\delta^{13}C$	C_3 vs C_4

	and *Elephus*)			
(Ben-David et al. 2001)	Moose (*Alces alces*), caribou (*Rangifer tarandus*)	Blood	$\delta^{13}C$, $\delta^{15}N$	C_3 foraging habits, species differentiation
(Clementz and Koch 2001)	Various marine/coastal mammal species including seals (Pinnipedia), whale/dolphins (Cetacea), otters and other Carnivora and deer (Artiodactyla)	Tooth enamel	$\delta^{13}C$, $\delta^{18}O$	Nearshore vs offshore, marine foraging ecology
(Drucker et al. 2001)	Caribou (*Rangifer tarandus*)	Dentinal collagen	$\delta^{13}C$, $\delta^{15}N$	C_3 foraging habits
(Herrera et al. 2001)	Bats (*Artibeus jamaicensis* and *Glossophaga soricina)*	Blood	$\delta^{13}C$, $\delta^{15}N$	C_3 vs CAM, trophic level
(Kielland 2001)	Moose (*Alces alces*)	Hoof	$\delta^{13}C$, $\delta^{15}N$	C_3 foraging habits
(Darimont and Reimchen 2002)	Gray wolf (*Canis lupus*)	Hair	$\delta^{13}C$, $\delta^{15}N$	Seasonal diet change, marine vs terrestrial
(Balasse and Tresset 2002)	Archaeological domestic cattle (*Bos taurus*)	Dentinal collagen	$\delta^{15}N$	Early weaning
(Balasse et al. 2002)	Archaeological domestic sheep (*Ovis aries*)	Tooth enamel	$\delta^{13}C$, $\delta^{18}O$, $^{87}Sr/^{86}Sr$	C_3 vs C_4, geology, birth seasonality
(Kurle and Worthy 2002)	Northern fur seal (*Callorhinus ursinus*)	Multiple tissues (fur, muscle, blubber, brain, liver, and kidney tissues)	$\delta^{13}C$, $\delta^{15}N$	Nearshore vs offshore, trophic level
(Roth 2002)	Arctic fox (*Alopex lagopus*)	Hair	$\delta^{13}C$	Marine vs terrestrial, trophic level
(Schulting and Richards 2002)	Domestic dog (*Canis familiaris*)	Bone collagen	$\delta^{13}C$, $\delta^{15}N$	Marine vs terrestrial
(Bocherens 2003)	Palaeolithic mammoth steppe fauna (herbivores and carnivores)	Bone collagen	$\delta^{13}C$, $\delta^{15}N$	Feeding/niche ecology, trophic level
(Boner and Forstel 2004)	Domestic cattle (*Bos taurus*)	Commercial meat (muscle)	$\delta^{13}C$, $\delta^{15}N$, $\delta^{18}O$, $\delta^{34}S$	Production system, provenancing

(Das et al. 2004)	Harbour porpoise (*Phocoena phocoena relicta*)	Liver, kidney, muscle, brain	$\delta^{13}C$, $\delta^{15}N$	Nearshore vs offshore, trophic level
(Cerling et al. 2004)	African elephant (*Loxodonta africana*)	Hair	$\delta^{13}C$, $\delta^{15}N$	C_3 vs C_4
(Balasse et al. 2005)	Sheep (*Ovis aries*)	Tooth enamel	$\delta^{13}C$, $\delta^{18}O$	Seasonal foddering, marine vs terrestrial (seaweed)
(Balasse and Ambrose 2005)	Sheep (*Ovis aries*), goat (*Capra hircus*)	Tooth enamel	$\delta^{13}C$	C_3 vs C_4, species differentiation
(Makarewicz and Tuross 2005)	Domestic sheep (*Ovis aries*)	Dentinal collagen	$\delta^{13}C$, $\delta^{15}N$	C_3 vs C_4, seasonal foddering
(Schwertl et al. 2005)	Domestic cattle (*Bos taurus*)	Hair	$\delta^{13}C$, $\delta^{15}N$	C_3 vs C_4, fertilisers, agricultural production systems
(Balasse et al. 2006)	Archaeological domestic sheep (*Ovis aries*)	Tooth enamel	$\delta^{13}C$, $\delta^{18}O$	Seasonal foddering, marine vs terrestrial (seaweed)
(Cerling et al. 2006)	African elephant (*Loxodonta africana*)	Hair	$\delta^{13}C$, $\delta^{15}N$	C_3 vs C_4
(Evans et al. 2007)	Domestic cattle (*Bos taurus*)	Tooth enamel	$^{87}Sr/^{86}Sr$	Geology, animal husbandry
(Feranec 2007)	Modern bison (*Bison bison*), red deer (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis Canadensis*)	Faeces, bone collagen, tooth enamel	$\delta^{13}C$	Resource portioning, niche ecology
(Feranec et al. 2007)	North American Holocene mammals (multiple species)	Bone, tooth enamel, tooth dentine	$^{87}Sr/^{86}Sr$	Geology, niche geography
(Britton et al. 2008)	Archaeological domestic sheep (*Ovis aries*), goats (*Capra hircus*) and cattle (*Bos sp.*)	Bone collagen	$\delta^{13}C$, $\delta^{15}N$	Terrestrial vs salt-marsh environments

(Pellegrini et al. 2008)	Horse (*Equus hydruntinus*), red deer (*Cervus elaphus*)	Tooth enamel	$\delta^{13}C$, $\delta^{18}O$, $^{87}Sr/^{86}Sr$	Geology
(Copeland et al. 2008b)	Waterbuck (*Kobus ellipsiprymnus*)	Tooth enamel	$\delta^{13}C$	C_3 vs C_4
(Richards et al. 2008b)	Palaeolithic cave bear (*Ursus spelaeus*)	Bone collagen	$\delta^{13}C$, $\delta^{15}N$	Dietary specialisation, predation type
(Guo et al. 2009)	Cattle (*Bos taurus*)	Meat, fat, hair	$\delta^{13}C$, $\delta^{15}N$	Environment, production system
(Copeland et al. 2009)	Impala (*Aepyceros melampus*)	Tooth enamel	$\delta^{13}C$	C_3 vs C_4
(Garcia et al. 2009)	Pleistocene faunal suite at Sierra De Atapuerca (multiple species)	Tooth enamel	$\delta^{13}C$, $\delta^{18}O$	Dietary specialisation, predation type
(Feranec et al. 2009)	Pleistocene bison (*Bison* sp.) and horse (*Equus* sp.)	Tooth enamel	$\delta^{13}C$, $\delta^{18}O$	Dietary specialisation, niche partioning
(Newsome et al. 2009)	California sea otters (*Enhydra lutris nereis*)	Vibrissae (whiskers)	$\delta^{13}C$, $\delta^{15}N$	Dietary specialisation, trophic level

A small number of observational experimental studies on modern wild animals have incorporated the analysis of archaeologically-relevant analytes. Such case studies are important as they allow the testing of isotope methods against known behaviours or situations using materials that occur in archaeological and palaeoecological contexts. For example, the stable isotope analysis of dentinal collagen was recently utilised to identify seasonal foraging habits in the modern Kaminuriak barren-ground caribou population of central Canada (*Rangifer tarandus groenlandicus*) (Drucker et al. 2001). Carbon isotope analysis of tooth enamel (bulk and intra-tooth sampling) has been used to explore the different feeding behaviours of African impala and waterbuck (Copeland et al. 2008b; Copeland et al. 2009). $\delta^{13}C$ values of bone collagen have also been used to reveal resource partitioning among different modern ungulate species in C_3-dominated environments (Feranec 2007). Such studies are often designed by archaeological scientists or physical anthropologists and have included the subsequent analysis of archaeological materials. A recent study of intra-herd isotopic variation for the identification of single and mass kill events in North American archaeological bone beds utilised both modern (Fenner 2008) and archaeological pronghorn (*Antilocapra americana*) (Fenner 2009). Fenner used bulk multiple isotope analysis of tooth enamel (carbon, oxygen and strontium) to evaluate the origins of faunal deposits (single events, mass kill events or through-time multiple-event accumulations). Analysis of modern materials demonstrated that three isotope ratio distance measurements best determine the origins of bone deposits. Such an approach has a clear applications to the identification of archaeological 'herds' and for the provenancing of archaeological accumulations (Fenner 2009).

The development of sampling and analytical protocols on modern materials allows a testing of these methods prior to their application to archaeological materials. Given that preparation techniques for isotopic analysis are often destructive and archaeological/palaeontological materials are limited resources, this is of critical

importance. To date, only a small number of modern studies have developed and evaluated isotope methods in advance of applications on archaeological faunal samples in order to explore their ecology. The number of published studies using stable isotope analysis to explore feeding and migratory behaviour in wild archaeological faunal populations is also small. A larger number of studies have been conducted on archaeological domestic fauna, perhaps as a result of the greater body of modern comparative isotope data from contemporary domesticates or due to the research interests of individuals and their work groups. These have included isotope studies of bulk samples and serially-sampled incrementally-developed tissues. Isotope analysis of domestic animals allows the reconstruction of animal husbandry, herding and foddering practices in the past (Balasse and Tresset 2002; Balasse et al. 2002; Balasse et al. 2006; Bentley and Knipper 2005a, 2005b). Such studies also provide insight into ancient production systems and human palaeoeconomies. Where large-scale foddering is practised, it also follows that provisioning for this must be an integral aspect of the wider subsistence economy. This could include the cultivation of foddering crops or the coordinated gathering of wild foods. For example, a study by Pechenkina and colleagues (2005) has explored the relationship between animal foddering and the large scale production of Millet (a C_4 cereal) in Neolithic China. This study confirmed that millet was both directly consumed by the humans themselves and used as a fodder crop for pigs - identifying a 'tight mutualism' between millet agriculture and animal husbandry, which may have developed in tandem (Pechenkina et al. 2005: 1186). Recent work by Balasse and colleagues (2005, 2006) has demonstrated the potential of using isotope analysis to identify very specific foddering practices in the past involving wild foods. The study focused on North Ronaldsay, Orkney, using the carbon and oxygen isotope ratio analysis of enamel bioapatite to identify the practice of seaweed foddering in modern and Neolithic sheep. Here the preliminary analysis of modern teeth confirmed a definite 'seaweed signature' (Balasse et al. 2005), testing the method before applying the techniques to the Neolithic sheep (Balasse et al. 2006). This is significant because,

although there are only limited modern examples of seaweed foddering, this practice could have been far more extensive in the past and this study is representative of the current range of ongoing research in coastal exploitation and animal husbandry in the past (e.g. Britton et al. 2008).

Archaeofaunal dietary data also provides an important baseline for human data at archaeological sites, and the analysis of contemporary animal bones (especially those that may have formed a component of the diet) is a necessary aspect of archaeodietary studies (see discussion in Britton et al. 2008). The application of stable isotope techniques also has enormous potential in the field of Palaeolithic archaeology and palaeoecology. In order to understand the behaviours and the hunting strategies and landscape use of prehistoric hunter-gatherers, it is vital to understand the behavioural, feeding and migratory ecology of the prey species. However, relatively few studies have been conducted – either on modern wild analogous species to explore methodologies or on Palaeolithic materials. Numerous studies have incorporated bulk bone collagen carbon and nitrogen isotope analysis of fauna to accompany human Mesolithic (e.g. Richards and Hedges 1999; Richards et al. 2003b; Schulting and Richards 2002; Schulting et al. 2008) and Palaeolithic dietary studies (e.g. Richards et al. 2000; Richards et al. 2005; Richards et al. 2008c). Such data have also been reviewed diachronically and geographically in order to investigate the relationship between carbon and nitrogen values in animals and changing climatic/environmental conditions (Richards and Hedges 2003; van Klinken et al. 2000). Intra-tooth sampling methods, combined with isotope analysis, have also been used to establish climatic variations and palaeoseasonality (e.g. Fricke et al. 1998b; Nelson 2005).

A small number of studies have used these methods to look specifically at issues of ancient animal ecology, with or without reference to human behaviours. Richards and colleagues (2008b) utilised carbon and nitrogen isotope analysis of bone collagen

to investigate the predation habits of Palaeolithic cave bears. Other Palaeolithic steppe fauna have also been analysed using bulk bone collagen isotope analysis, offering insight into foraging and predation habits and trophic relationships (Bocherens 2003). Carbon isotope analysis of bulk bone collagen in prehistoric plains bison in North America has been used to provide insight into the palaeogeography and foraging ecology of this species in the past through an estimation of the relative contribution of C_3 and C_4 plants to their diets (Chisholm et al. 1986).

As well as bulk bone sampling, studies have also utilised intra-tooth sampling and isotope analysis to establish time-series dietary reconstructions in pre-domestication archaeological faunal samples. This has the potential to reveal seasonal dietary changes. Gadbury et al. (2000) used sequential sampling of early Holocene bison enamel from Nebraska to establish palaeclimatic seasonal variations and the amount of C_4 grasses in the annual diet of the bison (Gadbury et al. 2000). The same analytical approach revealed niche specialisation and potential seasonal competition for C_3 and C_4 resources in bison and horse in Late Pleistocene California (Feranec et al. 2009). Intra-tooth sampling and carbonate analysis of bison enamel has also been used to establish Pleistocene seasonal temperature variations in south-western France (Bernard et al. 2009). Modern studies of horse (Hoppe et al. 2004a) and bison (Hoppe 2006a) have correlated enamel carbonate oxygen isotope values and local water oxygen values. Knowledge of this relationship in each species under consideration is essential for its application to archaeological materials.

In addition to the reconstruction of diet, ecosystem resource partitioning, trophic relationships and climate, the isotope analysis of faunal remains can also be used to reconstruct the geographical and migratory ecology of a species. However, to date, very few studies have incorporated the use of strontium isotopes to explore ranging and movement habits of extinct and ancestral animals. In one such study, bulk strontium isotope analysis of calcified tissues in 3000 year old mammals from

Yellowstone National Park have been used to investigate their landscape use (Feranec et al. 2007). Feranec and colleagues determined that strontium isotope ratios in small and mid-sized mammals correlated with the values of local substrates. Large-body-sized individuals demonstrated $^{87}Sr/^{86}Sr$ ratios indicative of foraging behaviours that incorporated variable geologies. When compared to modern mammals, the data suggests continuity in the behaviour and foraging radii of different animal species at Yellowstone and, therefore, that the niches of species can be conserved over considerable periods of time (Feranac et al 2007). Isotope analysis and intra-tooth sampling can be used in combination to address landscape use in archaeo- and palaeo- faunal samples (e.g. Pellegrini et al. 2008). In a study by Hoppe (1999) $^{87}Sr/^{86}Sr$ analysis of bulk enamel samples from mastodon (*Mammut americanum*) and mammoth (*Mammuthus* sp.) from late Pleistocene Florida were used to assess differences in their movement and (potentially) migratory behaviour. Analysis of the bulk samples revealed that $^{87}Sr/^{86}Sr$ values in mastodons were universally higher than mammoths, indicating that mastodons spent considerable periods of time in Georgia as well as Florida (Hoppe et al. 1999). Intra-tooth strontium data from a mastodon molar revealed a cyclical pattern, indicating this species made regular seasonal migrations between Florida and the Georgian foothills (Hoppe et al. 1999).

There are relatively few studies that incorporate strontium isotope analysis and intra-tooth sampling to address the issue of animal movement and ecology, potentially due to the relatively high costs of traditional strontium isotope analysis compared to other methods (e.g. carbon/nitrogen isotope analysis of bone collagen, carbon/oxygen isotope analysis of tooth enamel, etc). This could also be due to the more complex sampling techniques and preparation methods involved in strontium isotope analysis. These factors may also explain why very little modern observational experimental work incorporating strontium isotope analysis and archaeologically-relevant analytes has been undertaken. Therefore, as with other, more established

areas of isotope archaeology, it is essential that more modern experimental work be undertaken using strontium isotope analysis and intra-tooth sampling.

4.3 Summary

Stable isotope analysis is a well-established and routine method in archaeology and ecology. Commonly used in domestic zooarchaeological studies, the multi-isotope stable isotope analysis of dental tissues also represents a potentially-powerful tool in the reconstruction of faunal palaeobiogeography and palaeoecology. However, in spite of many significant experimental and observational studies, there are areas of the field that require exploration using modern materials before they can be applied to archaeological and palaeoecological materials.

One important issue that must be addressed before these methods can be used to explore mass herd movements and feeding behaviours in the past is that of intra-herd variability. The sequential sampling of incrementally-developed tissues has been demonstrated to permit reconstruction of individual life histories. However, the potential of this to indentify and characterise broad-scale (population level) movements and feeding behaviours in wild populations is not known. Prior to the application of these techniques in archaeological or palaeoecological contexts it is therefore necessary to assess the expected level of variation between individuals of the same herd. The use of multiple modern herds (and different species) from a range of geological and ecological communities would permit an assessment of this. This could also allow the establishment of local factors which could influence intra-herd variability such as local geological complexity, herd size and daily foraging radii.

Through the use of modern materials it will be possible to assess how faithfully multi- isotope signatures are preserved in incrementally-developed dental tissues and whether seasonal migrations and ranging habits can really be detected using this

approach. Only through the use of modern samples would it be possible to establish the resolution achievable using intra-tooth sampling and multi-isotope analysis and also to gain insight into the influences of migratory and seasonal feeding behaviours on tissue chemistry. Modern case studies on wild animals allow the evaluation of isotope methods, both compared to known behaviours within familiar environmental contexts and also to other methods for the reconstruction of migratory and feeding behaviours.

CHAPTER FIVE MODERN MATERIALS

5.1 Rangifer

5.1.1 Definition

Caribou and reindeer are members of the *cervidae* family (sub-family: *odocoilinae*). Within this sub-family, they all belong to the genus *Rangifer* and the species *Rangifer tarandus*. Members of this species are known as both caribou and reideer, with caribou being the wild North American counterpart of the European reindeer (which includes modern semi-domesticated groups and ancestral wild groups). Notably, Eurasian semi-domesticated reindeer were also introduced to North American in the 19th Century. There are a number of sub-species (e.g. *R.t.granti*, *R.t.groenlandicus*), which can be distinguished phenotypically, genetically and (in some instances) behaviourally. Further distinctions are made on the basis of ecotype, population and herd.

5.1.2 Ecology, diet and behaviour

Modern caribou and reindeer are distributed at northern circumpolar latitudinal extremes. They include both semi-domesticated and wild herds. Wild herds include both sedentary and migratory ecotypes, with some herds occupying enormous herd ranges and undertaking extensive seasonal movements over thousands of kilometres (Bergman et al. 2000). These can be long-distance 'thermostress' migrations (normally on a north-south trajectory), or smaller-distance movements. Such movements are thought to be triggered by a range of factors including forage abundance, predation avoidance and insect pestilence (Bergerud and Luttich 2003). Despite the strong seasonality and high latitudes, the Canadian and Alaskan arctic and sub-arctic supports a large insect biomass. Mosquitoes are estimated to take up to 2kg of blood from individual caribou in a single season (Toupin 1994).

In migrating herds, the spring migration takes place between March and May for most herds, with pregnant females leading the way. Yearlings, non-maternal cows and males lag behind. Caribou, like many other herding mammals, display birth synchronicity and caribou herds show a high degree of fidelity to calving areas (Schaefer et al. 2000). In fact, a caribou or reindeer herd is conventionally defined on the basis of its repeated use of a discrete calving area (Skoog 1968). It is believed that traditional calving areas may have been selected on the basis of their topography, as well as geography, believed to help to reduce risk of predation for new born calves (Bergerud and Luttich 2003). Cows, normally aged two years and over, give birth between late May and early June, depending on the herd (Dauphiné 1976; Prichard et al. 1999; Reimers 1997). Calves are weaned at the age of two or three months (Skoog 1968).

After calving, it is common for females and neonates to disperse over the wider summer range, which normally incorporates the areas surrounding the calving grounds. These areas can be extremely vast, and herds may fracture into smaller aggregations. Individuals of the same 'herd' can be hundreds of kilometres apart during summer grazing and the extent and locations of summer range can vary inter-annually as well as inter-individually. However, some animals display a high degree of philopatry during the time of calving and breeding, utilising similar portions of the range year to year (Brown and Theberge 1985; Gunn and Miller 1986; Schaefer et al. 2000).

Larger aggregations will form during the rut in late summer/early autumn when the animals breed. The term 'fall (or autumn) migration' refers to the period when a population moves from the area of the rut (in the wider summer range) to the winter area. Although individual migrations can be very rapid, the autumn migration can last several months (normally between mid-September and mid-November, depending on the herd). Normally this movement is in a southerly direction, the

migration ceasing when the animals cease this southerly movement (Parker 1972: 47). Winter ranges can be varied and a low degree of fidelity to particular areas is displayed between individuals and different years (Schaefer et al. 2000).

In addition to undertaking seasonal movements, caribou also have a seasonally-varied diet. Modern caribou and reindeer are intermediate feeders (Hofmann 2000). Their preferred browse includes fresh shoots, forbs and grasses. The summer diet is primarily composed of grasses and deciduous shrub leaves (such as *Salix* sp.), with forbs, mushrooms and lichens comprising a much smaller proportion of the summer diet (Bergerud 1972; Boertje 1984; Palmer 1926; Skoog 1968; White et al. 1975). Winter forage consists primarily of lichens when other food is scarce (Boertje 1984) and adult animals can consume up to 2.6kg of lichen per day (dry mass) (Kumpula 2001). This feeding behaviour is unique among *Rangifer*. Lichens have a particularly high acid content, which the more sensitive gut flora of most artiodacyls are unable to chemically digest. However, the rumen microbiology of caribou and reindeer is unusual. Modern *Rangifer* are able to digest lichens, through hosting slightly different substrate-specific bacteria for lichen degradation (Nieminen et al. 1980; Nilsson et al. 2006). These bacteria (*Eubacterium rangiferina*) are able to tolerate and grow in the presence of acids found in lichens, a clearly adaptive mechanism (Sundset et al. 2008).

Although lichens have a low protein content, there is high representation of lichens in the modern caribou diet. This is most likely due to these species being the most available and accessible in the field (Crête et al. 1990; Lundberg and Palo 1993). Given their ability to digest lichen and other ground-cover, caribou and reindeer are able to inhabit environments in which other ungulates are unable to thrive including climax boreal forest (taiga) and arctic tundra (Spiess 1979: 63). Lichens are therefore a critical component in the supporting of migratory behaviour and the size of herds found in North America (Klein 1991). Sedges, mosses and shrubs also supplement

the winter diet (Boertje 1984; Gaare and Skogland 1975; Scotter 1967; Skoog 1968). The abundances of seasonal forage can influence population sizes and range selection, and migratory habits have to balance with climate (influencing vegetative communities and wildlife frequency), caribou population, range size and biomass productivity and predation.

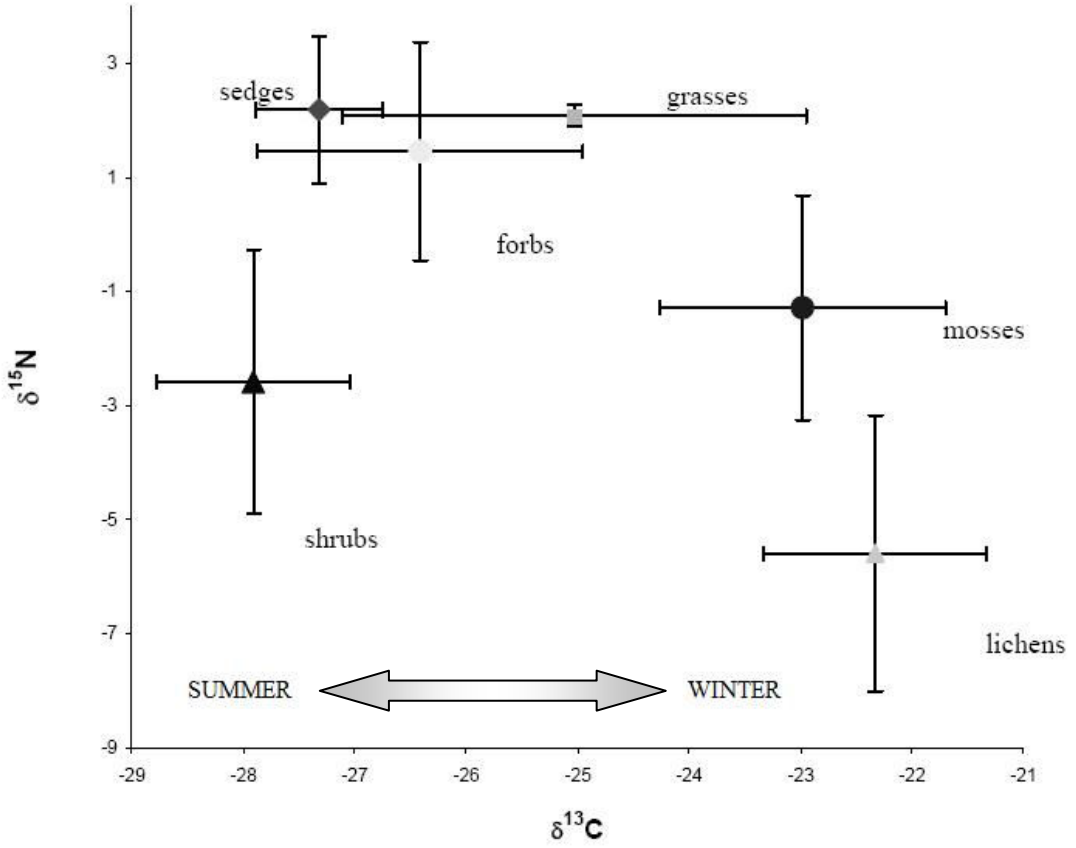


Figure 5.1 Mean $\delta^{15}N$ and $\delta^{13}C$ values (1σ) for plant samples from Southampton Island, Nunavut (adapted from McLeman 2006: 46, Figure 3.2).

The different plant foods that form the mixed seasonal diet of caribou have distinct isotopic signatures (see Figure 5.1). Lichens, along with mosses, are enriched in $\delta^{13}C$ compared to other terrestrial plants (Ben-David et al. 2001). These plants are also 'low-quality' in terms of their protein content and exhibit a depletion of ^{15}N. ^{13}C-enrichment and ^{15}N-depletion has been demonstrated in the stable isotope analysis of rumen samples of Nunavut barren ground caribou (*Rangifer tarandus groenlandicus*), where mosses and lichens contributed to up to 70% of the winter diet

(McLeman 2006). High quantities of lichen (≤70%) have been noted in the winter diet of other caribou herds, with mosses making up between 20-49% of the winter/late-winter diet (Russell et al. 1993). This low-quality forage may induce ^{15}N enrichment in the contemporary-formed tissues – a result of seasonal nutritional stress. These seasonal dietary shifts (and, in the case of nitrogen, their associated physiological influences) have been demonstrated to produce changes in stable nitrogen and carbon isotope ratio of blood, hoof and dentinal collagen (Ben-David et al. 2001; Drucker et al. 2001). Sequentially-sampled dentine from the base of the tooth root of Kaminuriak caribou (*Rangifer tarandus groenlandicus*) has revealed evidence for these seasonal changes (see Figure 5.2).

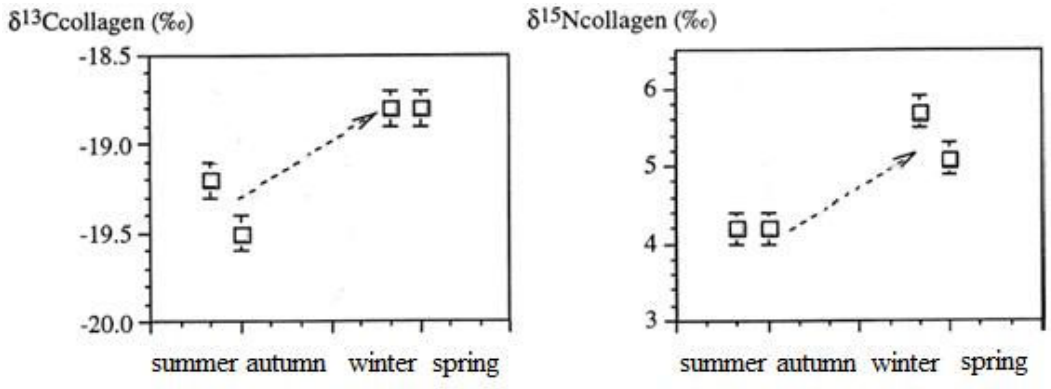


Figure 5.2 $\delta^{13}C$ and $\delta^{15}N$ values from dentinal collagen taken from the first incisor and third premolar of two Kaminuriak caribou. Season of growth of the sections are shown on the x-axes (adapted from Drucker et al. 2001: 308, Figure 3).

Stable isotope analysis could offer a relatively simple and cost effective method for assessing caribou/reindeer ecology. Agreement in sampling and preparation procedures could allow inter- as well as intra-population assessments. Given that isotope methods do not require the re-sampling or re-capture of the same individuals, repeated studies can allow the development of a data archive and the identification of long-term temporal trends.

However, the interaction between ecological, physiological and biochemical processes on the individual level (and the relationship between these factors and

tissue isotope chemistry) is complex. Furthermore, baseline environmental variations – in spite of season – across the large ranges occupied by the caribou may add further complication to the interpretation of faunal carbon and nitrogen stable isotope data (e.g. Britton et al. 2008; van Klinken et al. 2000). It is hoped that ongoing investigations involving bone and dentinal collagen on this herd may further contribute to this discussion. Such approaches could allow the identification of bulk seasonal diets and any seasonal dietary changes in individuals and herds and also allow the assessment of long-term dietary trends, seasonal variations and broader-scale climatic or vegetation changes.

5.1.3 Dental development

Rangifer calves are born with eight (incisiform) deciduous teeth in place and with six deciduous premolars erupting. The M1 erupts at 3-5 months. By the age of 10-12 months, the M2 has also risen above the gum. By 15 months, all eight permanent incisiform teeth, and the M1 and M2 are erupted. At this time the M3 has also risen above the gum and begun to erupt. By the age of 22 months, the permanent premolars begin to erupt and by the age of 27-29 months, the premolars and M3 are all fully-erupted and all dentition is permanent (Banfield 1954; Bergerud 1970; Miller 1972; Skoog 1968).

However, given that the isotope chemistry of dental tissues is fixed during matrix formation and/or mineralisation, it is important to understand the process and periodicity of enamel and dentine formation. Although there is a small amount of published information on caribou/reindeer tooth eruption and attrition (Bergerud 1970; Miller 1972), there is currently no published material on the timing and process of crown (enamel and primary dentine) formation or enamel mineralisation. Therefore, the timing of crown formation and the period of time expected to be represented in an unworn tooth is based on the results of mandibular radiography

studies of other deer species (Brown and Chapman 1991a, 1991b). Brown and Chapman (1991a: 373) determined that formation of the M2 and M3 crowns of fallow deer (*Dama dama*) commence at <3.5 and 9 months of age and complete at 9 and <18 months respectively. As fellow low-crowned herbivores, it is predicted that a full, unworn *Rangifer* molariform tooth represents between 6 and 9 months of enamel growth (Brown and Chapman 1991a, 1991b). However, given that samples are unlikely to be very young or all of the same age, a varying degree of post-eruptive wear is expected. It is therefore likely that the enamel of each molar will therefore reflect a shorter period of time.

Dentinal collagen is also a suitable archaeologically-available analyte for the reconstruction of time series dietary, environmental and physiological information. As a tooth develops and grows into occlusion, dentine incorporates collagen produced at different times in the animal's life (Drucker et al. 2001). Tissue near the crown is considered to be to be the first formed, with collagen at the bottom of the root being the last formed. Dentine formation starts a short time before enamel formation in the same tooth. Predentine is first laid down under the cusps, closely followed by the first layer of enamel. Dentine builds up as a series of stacked cones, leaving a space in the centre of the tooth for the pulp chamber and root canal (Hillson 2005: 185-186). Primary dentine spans the length of the tooth, developing with the enamel portion of the crown in question. However, dentine formation continues after that of the enamel, as the root is laid down and eventually closed. In low crowned herbivores, root formation is complete soon after the initial eruption of the tooth (Hillson 2005: 188-189). Data from fallow deer indicate late root formation in molars takes place around the age of 18 months (M2) and 26 months (M3), but not closing until considerably later at ~27 and 38 months respectively (Brown and Chapman 1991b). We can therefore infer that the total volume of dentine in a tooth available for isotope analysis should represent a longer period of formation (and therefore more months of isotopic inputs) than enamel of the same tooth. The

sampling of early and late forming dentine, including the root, could allow the reconstruction of an isotope history spanning 15 or 20 months (see Table 5.1).

The methods of continuously serial sampling dental tissues assume that *Rangifer* tooth enamel and dentine form sequentially from cusp to cervix or root tip. These methods also assume that tooth enamel mineralises sequentially (from cusp to cervix) and also at a continuous rate. These assumptions are only partially correct and must be kept in mind, along with the attenuating or dampening effect brought about through the successive phases of mineralisation and the homogenizing influence of this type of transverse sampling, when interpreting the data.

Wild caribou calves are weaned within the first two months of life (Dauphiné 1976; Skoog 1968). Dentine formed before this would be expected to be enriched in ^{15}N compared to later forming tissue due to the suckling calves being a trophic level above their lactating mothers. After this period is complete (and the full period of amino acid turnover is complete), the isotope chemistry of resultant tissues should then reflect only the plant foods consumed, with influences from the broader environment, climate and physiological effects within the organism itself. Both the M2 and M3 enamel and dentine should be formed after weaning and therefore little isotopic influence of nursing or weaning is expected in the oxygen or carbon values of enamel or the nitrogen values of dentinal collagen.

Table 5.1 Predicted crown and root formation times for second and third molars of *Rangifer*, based on data from other cervids (Brown and Chapman 1991a, 1991b).

Development	Second molar (months)	Third molar (months)
Crown formation begins	3.5	9
Crown formation completed	9	18
Root formation completed	18(closed: ~27)	26 (closed: 38)

5.2 Rangifer: Herds

5.2.1 Western Arctic, Alaska, USA[1]

The Western Arctic herd is one of the largest caribou herds in the world. The herd are members of the sub-species *Rangifer tarandus granti*, commonly known as Porcupine caribou or Grant's caribou. The herd has been undergoing continual growth since 1976, the herd having now reached 490,000 individuals (Dau 2003) Its annual range covers more than 363,000km^2 of north-west Alaska, from 63 to 71^{o}N and from 148 to 166^{o}W (Dau 2003; Davis et al. 1982). This area encompasses about one quarter of the total area of Alaska (Joly et al. 2007: 199) and includes complex and varied geologies (Figure 5.3a). The northern extent of the range includes the calving grounds and summer range in the northern foothills of the Brooks Range. Its southern extent includes their winter range in the Buckland River Drainage, Nulato Hills and the Seward Peninsula (Dau 2003) (see Figure 5.3b). Over the last 30 years, traditional aerial and terrestrial survey (alongside targeted radio and satellite collaring) has allowed the reconstruction of detailed annual migrations of the herd (Figure 5.3b).

The spring migration begins in April. Pregnant cows move first, followed by non-natal cows, bulls and yearlings, arriving at the Utukok Upland calving grounds by late May (Dau 2003). The geology here is predominantly lower and upper Cretaceous sedimentary continental rocks and conglomerates (Figure 5.3a.). These deposits are largely non-marine, with some marine and marginally marine sandstones (Mull et al. 2006).

[1] This case study was published in the recent paper: BRITTON, K., GRIMES, V., DAU, J. & RICHARDS, M. P. (2009) Reconstructing faunal migrations using intra-tooth sampling and strontium and oxygen isotope analyses: a case study of modern caribou (*Rangifer tarandus granti*). *Journal of Archaeological Science,* 36**,** 1163-1172. However, given that this work was undertaken as a component of this doctoral project, the subject will be detailed in its entirety in this thesis.

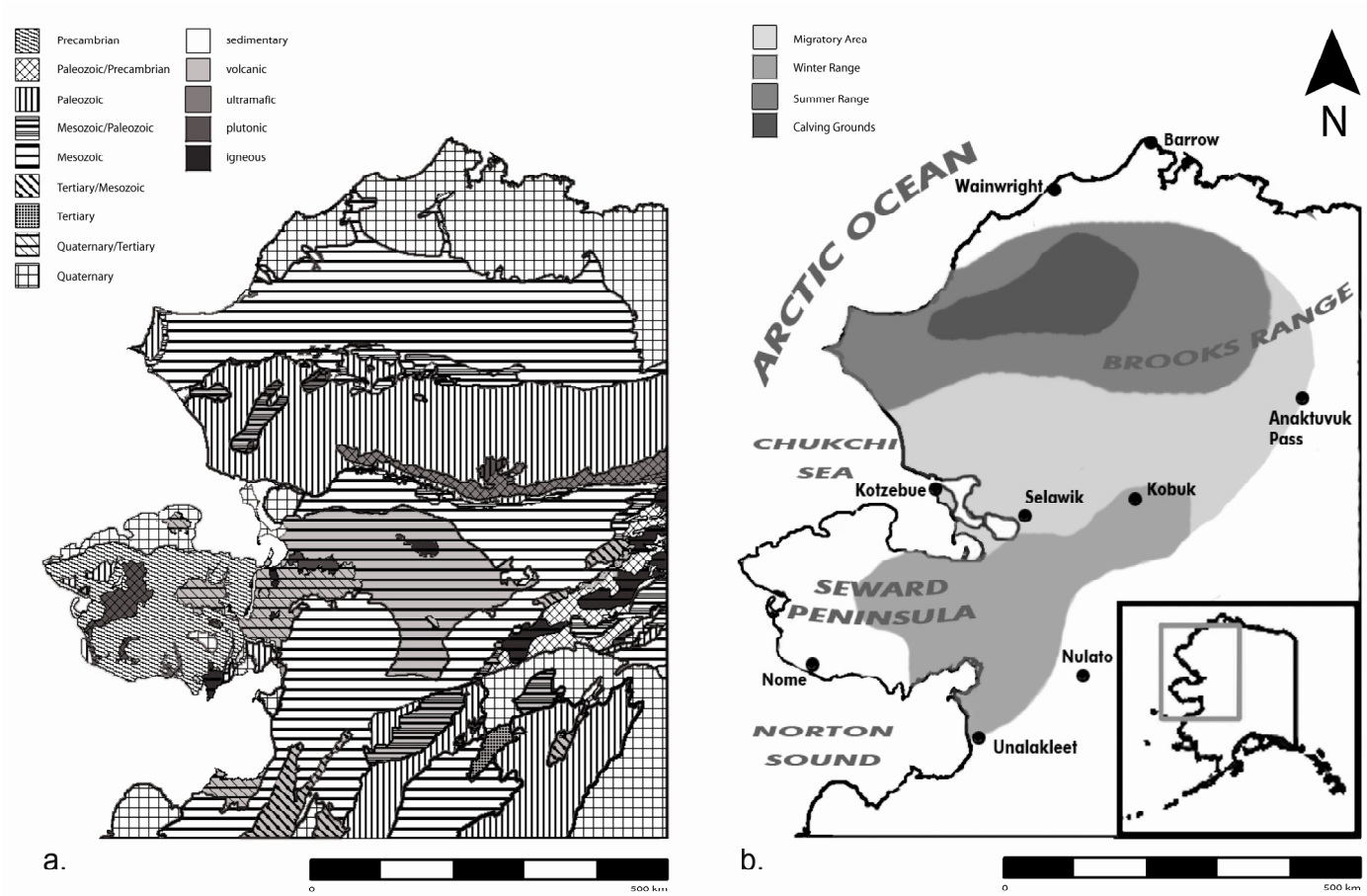


Figure 5.3 Geological map of northwest Alaska (based on Beikman 1980), b: Annual range and seasonal movements of the Western Arctic Herd (based on Dau 2003) (both taken from Britton et al. 2009: 1165, Figure 1).

As described in Chapter 2.2.3, basement geology only provides a general estimation for the range of bio-available strontium in an area. A previously published study comprising a small section of this area can give an indication of the geological-derived strontium available to plants and eventually to the local animal feeders (Keller et al. 2007). Soil values from this study (including only geologies found on the calving grounds and at surficial depths) were used to establish an approximate expected value for the calving grounds ($^{87}Sr/^{86}Sr = 0.7140\pm0.0045$, 1σ, n=40).

Like other caribou herds, cows of the Western Arctic herd give birth in late May and early June. Neonates and maternal cows then move west to the Lisburne Hills. Other individuals (non-maternal cows, males and yearlings) occupy a large area during this period, spreading across the foothills of the Brooks Range, west of the Trans-Alaska pipeline. This is an area of mainly Upper Cretaceous sedimentary geology, largely similar to that of the calving grounds (Figures 5.3a and 5.3b).

The herd aggregates during early July before moving rapidly southwest during the fall migration over a distance of more than 1200km. Individual migrations are rapid, although the autumn migration of the whole herd lasts several months (from late-September to mid-November), with some caribou arriving at the most southern extent of their range in the Nulato Hills and the Seward Peninsula before other animals have even begun to migrate. This area comprises a complex geology but mainly consists of Quaternary and Tertiary mafic volcanic with some areas of Precambrian and Palaeozoic marine sedimentary rocks (Beikman 1980; Patton and Moll-Stalcup 2000). Mean $^{87}Sr/^{86}Sr$ values for a proximal volcano field of similar geological composition are 0.7079 ± 0.0095 (1σ, n=30) (Moll-Stalcup and Arth 1991).

Fidelity to winter range may also vary in response to broad-scale climatic changes, fire and caribou grazing habits, influencing vegetation cover. As with many other

caribou herds, the preferred winter forage of the Western Arctic herd are fruticose lichens (*Cladina* sp.) and mosses (primarily *Sphagnum* sp.) (Joly et al. 2007: 201). Lichen cover is particularly prone to deterioration, leading to the need for individuals to look farther for winter forage. This has been observed in the Western Arctic herd as their winter range has expanded significantly between 1981 to 2005 (Joly et al. 2007). This expansion has included large areas of the Steward Peninsula and encroaches on the range of semi-domesticated reindeer (Dau 2003)

The mean annual precipitation in the winter range is 300-400mm, much of which falls as snow, and can persist as snow cover from November to May. Temperatures can drop as low as -45°C during the winter. Oxygen isotope values of local meteoric water ($\delta^{18}O_w$) at the most northern and southern extremes of the range vary seasonally and are universally higher in the southern winter territory than in the northern summer range/calving grounds. Two areas – central to (and deemed representative of) the two extents of the migratory route – were selected (65.7 N; -160.5W; ca. 550m a.s.l. and 69.5 N; -161.9 W; ca. 460m a.s.l. for the winter and summer ranges respectively). Mean monthly $\delta^{18}O_w$ values of local precipitation for these two areas were interpolated from existing literature, with seasonal values of -22.2‰ and -13.8‰ (winter and summer; winter grazing grounds) and -25.8‰ and -14.8‰ (winter and summer; summer grazing grounds). All values were calculated using the online OIPC tool (Bowen 2009). Given the limited nature of available measurements and the vast and varied area under scrutiny reported values using this interpolating tool may not always be accurate. However these values – along with estimations of $^{87}Sr/^{86}Sr$ soil and rock values from other studies – can provide a framework for expected intra-tooth values.

Provided mineralisation patterns and intra-tooth sampling can permit time-series dietary isotopic trends, a non-migratory animal living in such seasonal extremes in either portion of this range should exhibit the typical undulating/sinusoidal waves in

intra-tooth $\delta^{18}O$ observed at other high- and mid- latitude studies (Balasse et al. 2002; Balasse et al. 2005; Balasse et al. 2006; Fricke et al. 1998b; Gadbury et al. 2000). These patterns are not normally observed at lower latitudes, in tropical areas or in areas of very low rainfall (Copeland et al. 2009; Wiedemann et al. 1999). However, it is proposed that a seasonally moving thermostress migratory animal might demonstrate a different intra-tooth $\delta^{18}O$ trend compared to a non-migratory animal. It is suggested that such migrants would instead display a smoothed or buffered signal. In such circumstances, a reduced degree of intra-tooth variability would occur due to the escaping of climatic extremes at either end of the annual range (moving with the seasons and during the process of enamel formation and mineralisation). However, it must be noted that where mechanisms other than thermostress are the primary incentives for seasonal movement a very different pattern could be observed. Such incentives could include mechanisms such as predation avoidance, avoidance of insect harassment or forage availability. In these instances, movement may even serve to enlarge intra-tooth variability. Ascertaining the trends within and between the different caribou herds included in this study (and their associated migratory behaviours) should help to provide evidence supporting or negating this theory. Caribou ingest most of their water directly from their food, but will also occasionally drink from streams and small pools and are even known to eat snow (Jim Dau, personal communication). The input of snow and glacial melt in this arctic and sub-arctic areas and the effect of this on any intra-tooth seasonal signal of the animals enamel is not known.

Five individuals from this herd were selected for analysis (Table 5.2). The individuals lived and died within ten years of each other but are unlikely to represent the same birth cohort. The animals had died of natural causes and were collected by Alaska Department of Fish and Games officials or had been euthanised for purposes unrelated to this study. All individuals had been radio-collared for some period of their lives. Unfortunately, policies of the Alaska Department of Fish and Game

dictate that no animal under two years is collared and therefore the telemetry/GPS data cannot be directly correlated with that gained from the isotope analysis of enamel or dentine (given that enamel and dentine from M2 and M3 molars are secreted and mineralised within the first 18 months of life). Obviously a lack of detailed information on the movement of individuals could limit the degree to which data can be interpreted on the individual level. However, the collar data from the herd as a whole is still of great value and demonstrates a high degree of migration-route fidelity. This has been demonstrated in studies of other migratory (and sedentary) caribou herds (Schaefer et al. 2000).

Each individual was of prime age (5-9 years) with dentition demonstrating different degrees of wear. Crown heights were between 8.9mm and 11.9mm (M2), and 8.9mm and 10.5mm (M3). Samples were obtained by the Alaska Department of Fish and Game and were provided for this study care of Jim Dau (Alaska Department of Fish and Game).

Table 5.2 Samples from the Western Arctic caribou herd, Alaska.

Sample number	Sex (M/F)	Dentine	Enamel	Bone	Teeth sampled	Notes
WACH-2.210	F	X	X	X	M_2L, M_3L	Little wear
WACH-0.120	F	X	X	X	M_2L, M_3L	Little wear
WACH-2000	F	X	X	X	M_2R, M_3R	Slightly worn
WACH-2.230	M	X	X	X	M_2L, M_3L	Slight wear
WACH-153.180	M	X	X	X	M_2R, M_3R	Fairly worn

5.2.2 Leaf River (Rivière aux Feuilles), Québec/Labrador, Canada

The tundra of Northern Québec and Labrador (north of 52°N) is host to two of the largest migratory caribou herds in the world – the George River (Rivière George) and Leaf River (Rivière aux Feuilles) caribou herds. These herds are migratory woodland caribou (*Rangifer tarandus caribou*). Both herds have undergone cycles of scarcity and overabundance in the last 200 years and their herd ranges have expanded and contracted (Couturier et al. 2004: 1). The herds have been the focus of a small number of studies in recent years, exploring the demography, ecology, movement patterns and conditions of the animals. The George River and Leaf River herds have been the subject of extensive telemetry and radio collaring studies, as well as to tradition aerial observation survey approaches (Couturier et al. 1990; Couturier et al. 2004; Messier et al. 1988). The region has typically continental weather patterns, cool winters and warmer summers. Mean snow fall is 132±7cm (1973-2003 period) (Couturier et al. 2009: 448).

The Leaf River (or Rivière aux Feuilles) herd occupies a substantial range in Québec, stretching from the James Bay area to most northern parts of the Ungava Peninsula (Couturier et al. 2004: 25) (see Figure 5.4 and 5.5). Although demography and habitat use of this herd have been assessed in recent years using radio collars, radio tracking and aerial survey/photography (Couturier et al. 2004), knowledge of the Leaf River herd is limited. This is due to the fact that the herd (and calving ground) was only formally located in 1975 and preliminary observations of their ranging behaviour were not made until 1987 (Crête et al. 1990: 60).

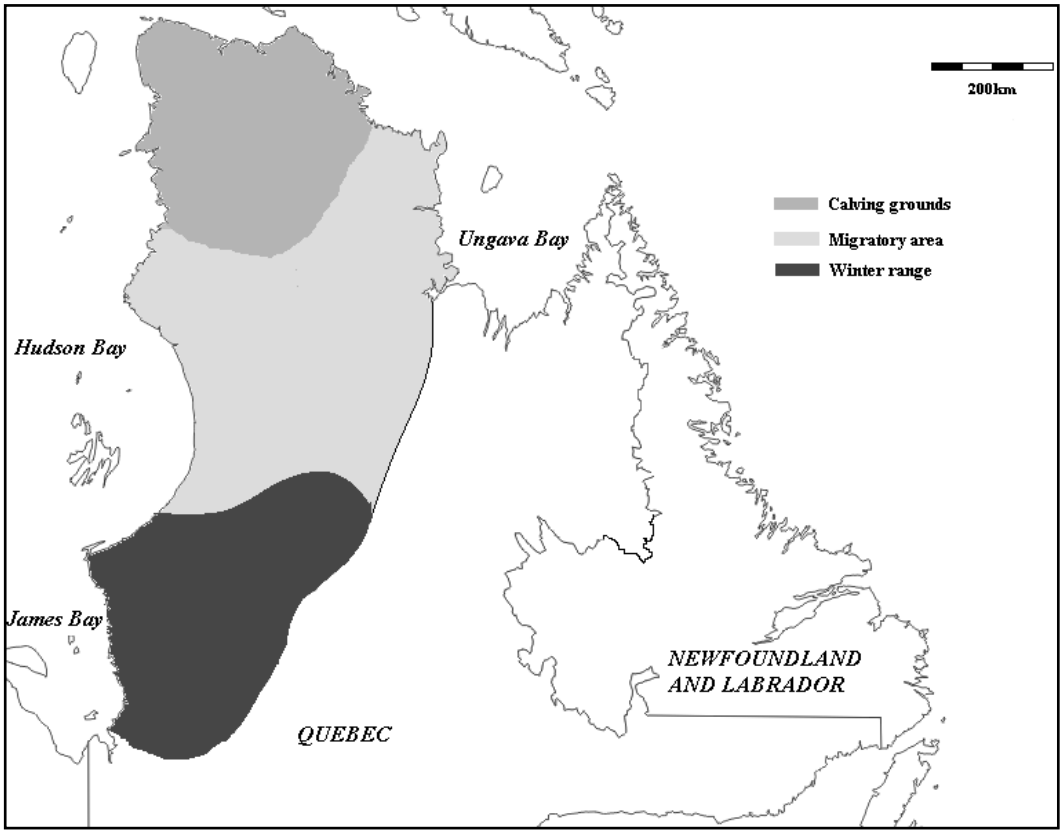


Figure 5.4 Annual herd range of the Leaf River herd (based on information and maps from CARMA 2009; Messier et al. 1988). This herd shows a higher degree of fidelity to seasonal use of the different portions of their range than the George River herd.

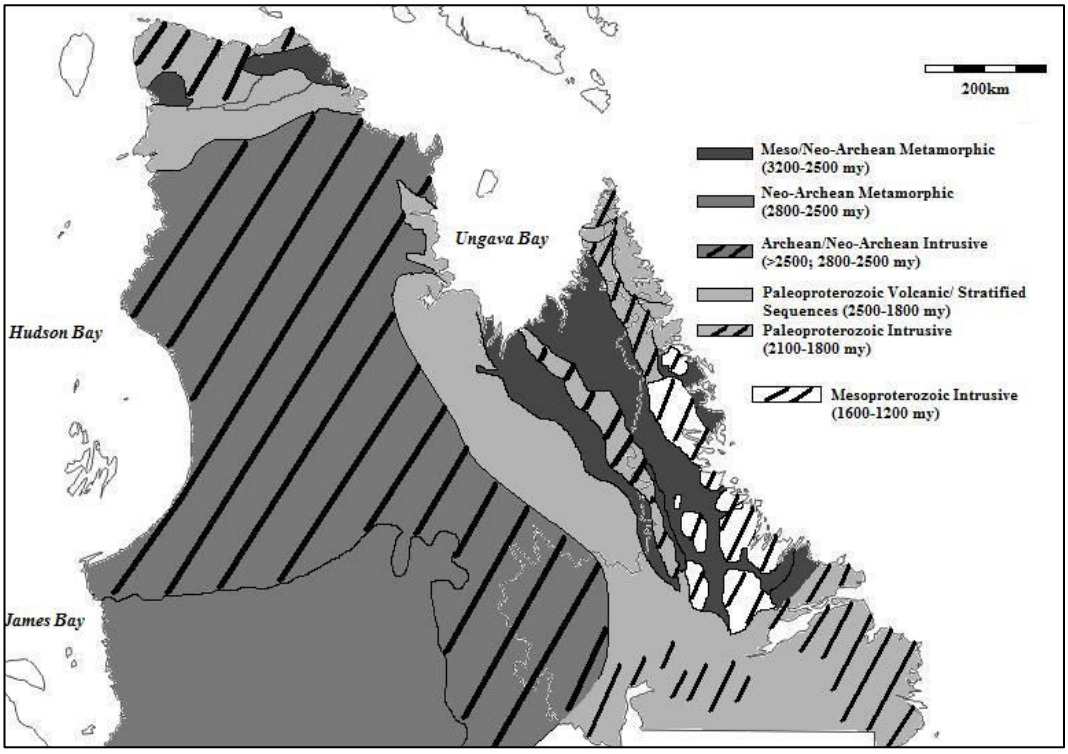


Figure 5.5 Basic geology of eastern Canada (Québec and Labrador) showing age and rock type (based on Wheeler et al. 1997).

This herd numbered 260,000 in the 1991 census (Couturier 1994) but has grown to 628,000 in recent years (Couturier et al. 2004: 23), although the physical condition of animals has deteriorated (Couturier et al. 2004: 25). As with other caribou herds, adult females of the Leaf River herd are philopatric to the traditional calving grounds of the herd. These grounds are believed to have been in use since the end of the 19th century, the calving ground has gradually moved further north and east into the highest parts of the Ungava Peninsula. This area is north of the tree line on a gently rolling plateau of barren-ground tundra (225 - 325m a.s.l.). Calving occurs in the first week of June (Crête et al. 1990; Crête et al. 1991). Following calving the herd disperse. At these times, density has been observed to be less than 1/km^2 (Le Henaff, 1975). The Leaf River herd migrates south in winter, to the James Bay area, south-west of Kuujjuaq (Boulet et al. 2007). In recent years, the winter range has gradually been shifting north, increased herd numbers and increased aggregation, most likely probably in response to changes in vegetation and predation (Bergerud and Luttich 2003: 173).

Annual precipitation on the Leaf River calving ground is 400-500mm, with a snow fraction of 35-40% and an mean annual temperature of <-7.5°C (Crête et al. 1990: 61). Oxygen isotope values of local meteoric water ($\delta^{18}O_w$) within the annual range vary seasonally. Locations representative of the summer range (59°N; -73.6°W, 275 a.s.l.) and winter range were (54.8°N; -74.1°W, 200 a.s.l.) used to generate interpolated meteoric water values ($\delta^{18}O_w$) using the OIPC tool (Bowen 2009). Mean seasonal values were -24.0‰ (winter) and -12.7‰ (summer) for the summer range and -21.8‰ (winter) and -10.7‰ (summer) for the winter range at the summer extreme of the area.

Ten individuals were selected for bone collagen analysis (Table 5.3), and dental tissue from three of these individuals was also sampled (M2 and M3s). All individuals were prime age female adults (5-9 years). Crown heights were 10.02-11.21mm (M_2) and

10.02-10.55mm (M_3). The animals were culled in June 2007 for purposes unrelated to this study and were provided by Stéphane Rivard, Faune Québec (Direction de l'aménagement de la faune du Nord-du-Québec) and Vincent Brodeur (Ministère des Ressources naturelles et de la Faune, Québec).

Table 5.3 Samples from the Leaf River (Rivière aux Feuilles) caribou herd, Canada.

Sample number	Sex (M/F)	Dentine	Enamel	Bone	Teeth sampled
AFR-1	F	X	X	X	M_2R,M_3R
AFR-5	F	-	-	X	-
AFR-6	F	X	X	X	M_2R,M_3R
AFR-7	F	-	-	X	-
AFR-10	F	X	X	X	M_2R,M_3R
AFR-13	F	-	-	X	-
AFR-14	F	-	-	X	-
AFR-15	F	-	-	X	-
AFR-16	F	-	-	X	-
AFR-18	F	-	-	X	-

5.2.3 George River (Rivière George), Québec/Labrador, Canada

The George River herd is found in Ungava, in the taiga of Labrador and Northern Québec. Like many of the great caribou herds of Canada and Alaska, this population has undergone a number of population cycles in known history, where periods of both rapid population increase and rapid decline have been observed throughout the 18th, 19th and 20th centuries (Messier et al. 1988). Over the last 60 years, the population has fluctuated from 5,000 individuals (Banfield and Tener 1958) to over 770,000 in 1993, which made it the largest caribou herd in the world at the time (Couturier et al 1996). However, the last census indicated numbers had reduced to 385,000 (Couturier et al. 2004: 23).

The total range of the George River herd covers much of the Ungava peninsula of Northern Québec and Labrador extending from the Hudson Bay to the Labrador Sea. The range size has increased dramatically in recent years from 422,000km^2 (Messier et al. 1988) to more than 900,000km^2, between latitudes of 54° and 61° N (Schmelzer and Otto 2003) (see Figure 5.6). The George River calving grounds lay on a hilly

plateau (500m-700m a.s.l.) and also cover some lowlands on the east side of the Rivière George valley (400m a.s.l. and less) (Crête et al. 1990; Crête et al. 1991). The underlying geology of this area is very ancient and mixed, including Archean metamorphic and Paleoproterozoic intrusive deposits (Figure 5.7). This is an area of barren-ground tundra north of the tree line with lichen-forest on the lower areas (Figure 5.8). Calving occurs within the first two weeks of June (Crête et al. 1991). As with other herds, after giving birth females disperse into the wider area and are joined by males and yearlings in large post-calving aggregations during the summer.

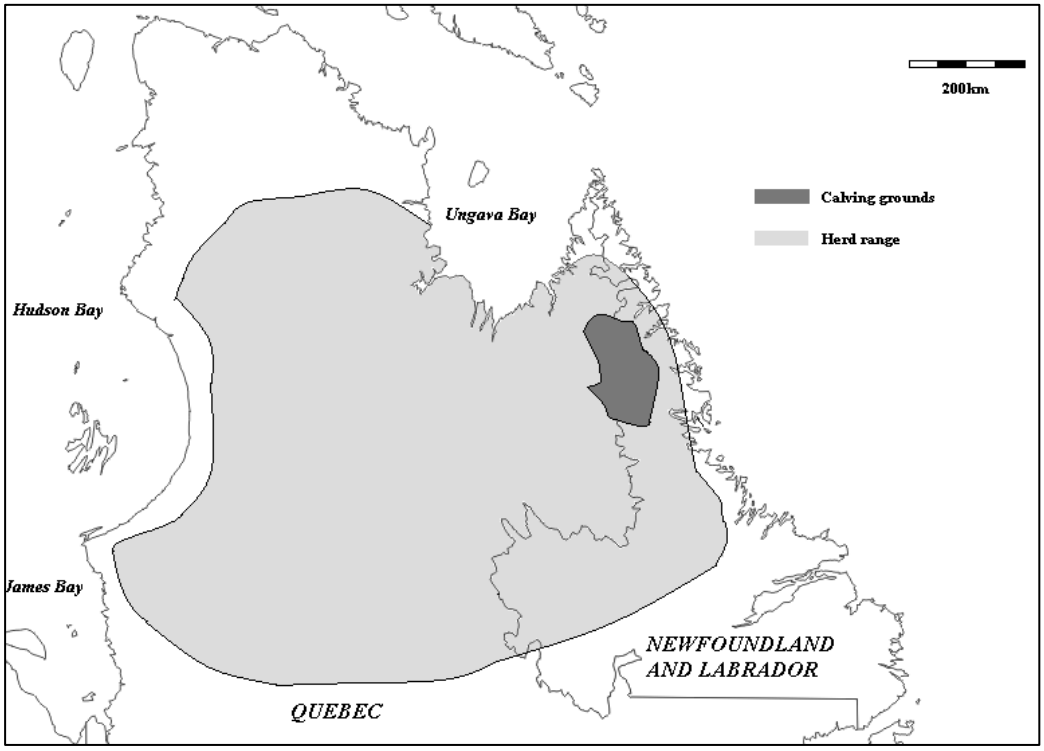


Figure 5.6 Herd range and calving area of the George River caribou herd (based on information and maps from CARMA 2009; Messier et al. 1988).

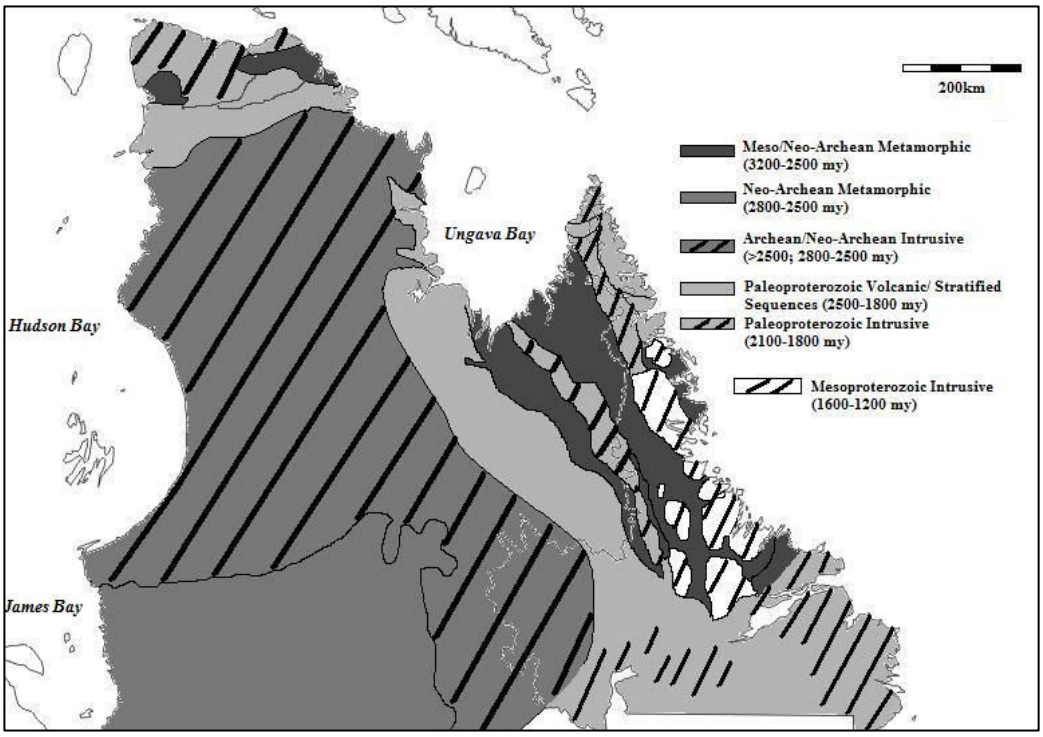


Figure 5.7 Basic geology of eastern Canada (Québec and Labrador) showing age and rock type (based on Wheeler et al. 1997).

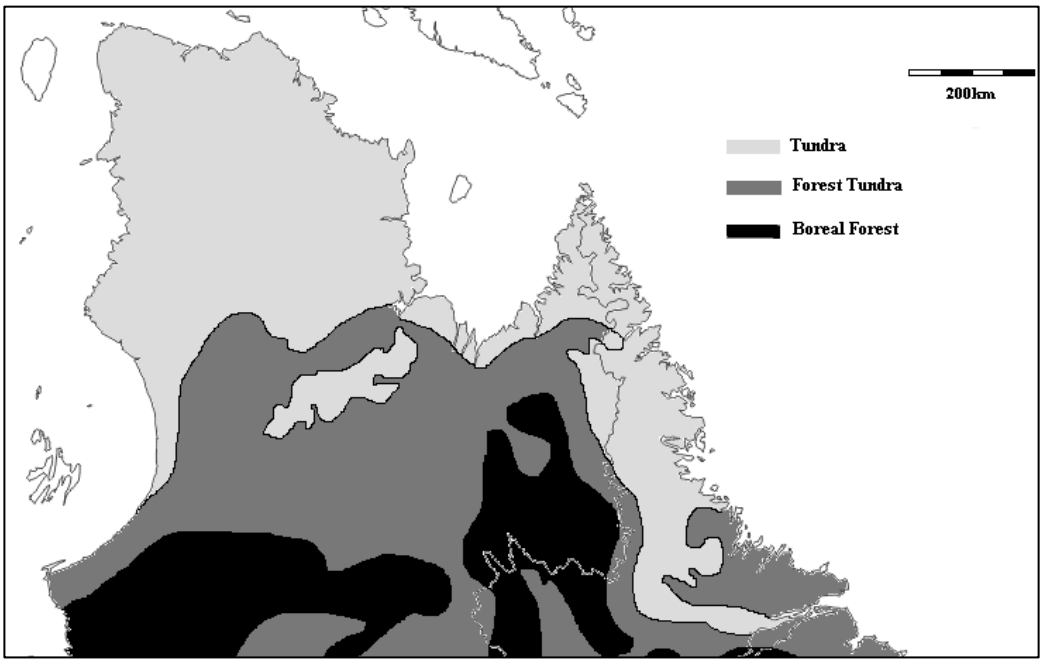


Figure 5.8 Biome distribution of northern Québec and Labrador (based on Crête et al. 1990; after Payette 1983).

The George River herd is extremely vagile and undertakes long-distance annual movements. Throughout the course of one year, these caribou travel an average distance of 3066km, up to 14.5km per day (Bergman et al. 2000: 367). However, although their range use is seasonal and includes movement between calving grounds and boreal forest in the southern extent of the range, the herd is widespread for much of the year (see Figures 5.6 and 5.9). This could lead to individuals being hundreds of miles apart, on different geological zones and in subtly different ecosystems for much of the year. Furthermore, a low degree of inter-annual fidelity has been displayed to the summer and winter ranges in recent years, with individuals demonstrating avoidance of previously-used areas (Schmelzer and Otto 2003). Messier et al. (1988) suggested that forage limitation was the primary regulation mechanism for the George River herd summer range selection. The winter range has also 'drifted' considerably in recent years and now incorporates large areas of Ungava and the James Bay region. This could be related to recent significant population fluctuations - as the exploding population placed new pressure on forage abundances (Schmelzer and Otto 2003). Shifting bear and wolf populations may also have influenced distributions along the Labrador coastline (Bergerud and Luttich 2003: 172). These changes can be described as the result of a necessary 'trade-off', between optimal foddering, avoidance of predators, landscape use and migratory behaviour and herd demography (Bergerud and Luttich 2003). An individual lack of consistency in inter-annual range selection could prove problematic for strontium studies in an area of mixed geology such as Labrador and northern Québec. The herd has now declined and, although the range has remained large, the condition of the caribou (e.g. body size, protein mass, percentage of fat reserves, etc) has improved (Couturier et al. 2004).

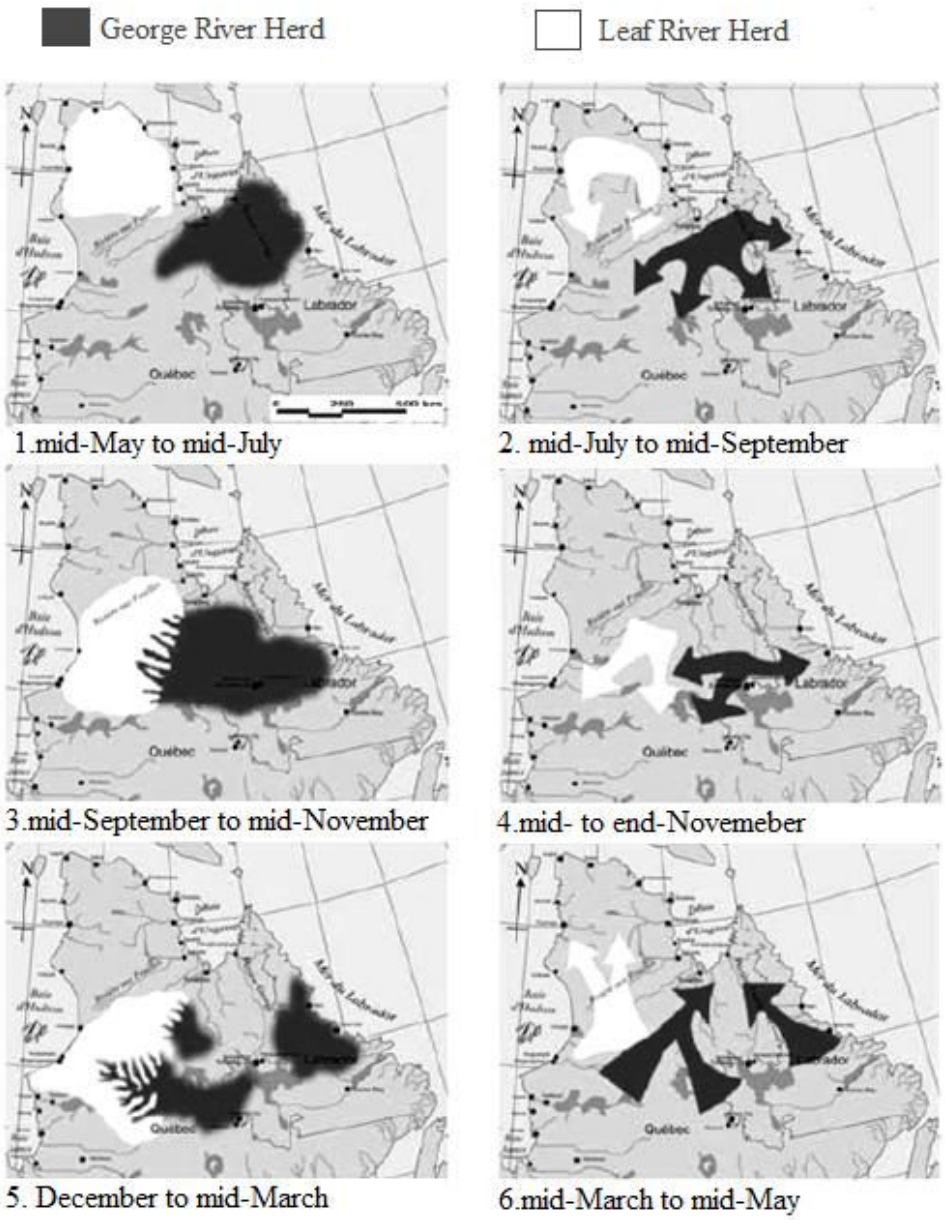


Figure 5.9 Seasonal movement patterns of migratory tundra caribou of Québec-Labrador, 1999-2001 (taken from Couturier et al. 2004: 6, Figure 1).

The George River caribou herd (indicated by the dark colour) have the largest and most dispersed range, covering much of Labrador and Québec. The winter range is notably dispersed (5) and members of the herd are found across the whole landmass in a number of distinct groups. The Leaf River herd (shown in white) have a smaller herd range and display a greater seasonal intra-herd fidelity to different areas of the range.

The annual precipitation of the calving ground is 500-600mm, the snow fraction being 35-40%. Mean annual temperature is <-7.5°C (Crête et al. 1990: 61). Given the dispersed nature of the herd throughout the year and its lack of seasonal fidelity to particular areas of the range (other than the calving ground), a single point central to its total range has been selected to establish predicted seasonal variation in the oxygen isotope values of local meteoric water ($\delta^{18}O_w$) using the OIPC tool (Bowen 2009). The area selected was Schefferville (54.8N; -66.8, 520m a.s.l.). The mean annual temperatures at Schefferville vary between 12.4°C (July) and -23.1°C (January) (Bergerud and Luttich 2003: 170). Mean seasonal values were -12.0‰ (summer) and -21.5‰ (winter).

Ten individuals were selected for bone collagen analysis (Table 5.4), with three of these individuals also being sampled for dental tissues (M2 and M3s). All individuals were prime age female adults (5-9 years). Crown heights were between 11.09-13.28mm (M2) and 10.79-12.54mm (M3). The animals were culled in June 2007 for purposes unrelated to this study and were provided by Stéphane Rivard, Faune Québec (Direction de l'aménagement de la faune du Nord-du-Québec) and Vincent Brodeur (Ministère des Ressources naturelles et de la Faune, Québec).

Table 5.4 Samples from the George River caribou herd, Canada.

Sample number	Sex (M/F)	Dentine	Enamel	Bone	Teeth sampled
GR-3	F	X	X	X	M_2R,M_3R
GR-5	F	-	-	X	-
GR-6	F	-	-	X	-
GR-7	F	-	-	X	-
GR-8	F	X	X	X	M_2R,M_3R
GR-9	F	-	-	X	-
GR-13	F	-	-	X	-
GR-15	F	-	-	X	-
GR-16	F	X	X	X	M_2R,M_3R
GR-17	F	-	-	X	-

5.3 Bison

5.3.1 Definition

Bison is a taxonomic grouping within the family *Bovidae* and subfamily *Bovinae*. There are two extant species and of the genus – American bison (*B. bison*) and the European bison or wisent (*B. bonasus*). American bison include two sub-species – the more common plains bison (*B. bison bison*) and the American wood bison (*B. bison athabascae*). There are also several extinct species, including *B. antiquus* and *B. priscus* (Meagher 1986).

5.3.2 Ecology, diet and behaviour

Modern bison are grazers who live in small, nomadic herds including bulls, yearling males, females and calves. These herds are known as 'cow groups' and their size varies from less than 20 to more than 50 individuals. Groups size may largely be related to habitat structure and the stability of such clans is largely unknown (van Vuren 1983). Adult males (over 4 years old) may also disperse from these groups, in bachelor herds or as loners until they gain access to females, with solitary males rejoining 'cow' herds during the rut. However, females of all ages, calves and the majority of males up to three years of age remain in mixed herd groups throughout the year (McHugh 1958). Although the later behaviour of adult bulls could influence the isotope values of developing tissues (thus making them distinct from other individuals in a herd), dentine and enamel formation occurs before this behaviour begins (see tooth formation section below, Chapter 5.3.3)

Most bison reach sexual maturity between the age of 2 and 4 years. The breeding season in most herds is a concentrated 2-week period, occurring between late June/early July and late August/early September (depending on the herd) (Fuller 1962). Gestation is around 285 days (Haugen 1974), with the calving season extending from mid-April to the end of May. The majority of births in most herds

occur in late April and the first two weeks of May, although out-of-season births (towards the end of summer) have also been observed (Lott and Galland 1985; McHugh 1958; Meagher 1986; Rutberg 1984). Cows nurse their calves for at least seven or eight months and weaning is normally completed before the end of the first year of life (McHugh 1958).

The bison's natural habitat is grassland but herds can also be found in mountainous areas, arid zones, semi-desert and forested areas. There are four types of North American grassland – tall, shortgrass, tallgrass and mixed grass prairie. Bison are herbivorous graminoid grazers in all seasons, their diet consisting of up to 98% grasses and sedges (Coppedge et al. 1998: 379). Warm season diet will include seasonal grasses, with a higher proportion of sedges in the cool season diet. The proportion of C_4 grasses consumed can be high, depending on the area and their seasonal prevalence. More sedges, which are cool-season graminoids suited to cooler, wetter conditions, will be selected in autumn/winter and in more mountainous or northern zones. Forbs (a group of plants including all non-woody *Dicotyledonae*) are also sometimes consumed, making up a varying (but normally very small) percentage of the diet (Coppedge et al. 1998). Bison ingest water daily and will even consume snow in freezing conditions (McHugh 1958; Meagher 1986; van Vuren 1984).

Modern bison herds are geographically isolated from one-another, within parks, preserves, public lands and on private ranches (Meagher 1986). Bison are also able to live at high altitudes, with occupations reported at over 3500m a.s.l. in the recent (see Meagher 1986) and archaeological past (e.g. Cannon 2007). Grazing on steep slopes, at higher altitudes than other grazers, is common behaviour in modern bison (Meagher 1986). Free ranging bison can be described as seasonal nomads. These movements can be directional and altitudinal but tend to be over short distances and are not always well-defined – unlike the long distances traversed seasonally by

migratory caribou. Factors influencing such movements will include access to forage, weather conditions, temperature, availability of water and snow fall (McHugh 1958; Meagher 1986). Movements are also made daily whilst feeding in the home range. The influence of size of parkland/preserve and the limitations this may place on movements cannot be estimated but can be presumed to be significant.

Prior to the arrival of European colonialists, it is estimated that there were between 30 and 60 million bison in North America (Shaw 1995). Bison were naturally widespread throughout the continent, throughout mainland USA, Alaska, Canada and northern Mexico. By 1900 there were only a handful of wild bison remaining in the USA, with approximately 1500 additional individuals known to exist in privately owned herds and in zoos (Meagher 1986). The bison had been exterminated through overhunting and the species neared extinction. Modern American bison herds have been deliberately revived from the small numbers left at the end of the 19th century in the wild and are no longer free-ranging or freely breeding (Berger and Cunningham 1994). This action resulted in an estimated population of 75,000 in 1983 (Jennings and Hebbring 1983 cited in Meagher 1986). It has been suggested that densities of bison would once have been very large in the grasslands of the Great Plains, which would have supported many millions of bison in the pre-contact past. There are accounts of substantial, seasonal movements and true migrations in these enormous historic American populations of plains bison (e.g. Bamforth 1987). However, other accounts of explorers and travellers have contradicted both north-south migratory movements in historic bison populations and the associated flash grazing. It has instead been suggested that the huge bison herds responded instead to fluxing weather conditions, fire and the intensity of previous grazing rather than to adhering to specific migration routes (Hart 2001). Furthermore, bison would also have lived in lower densities, in mountainous areas, in meadows and shrub-steppe communities (van Vuren 2001).

However, much that is understood about the 'natural' ecology of this ancestral species is inference. Furthermore, post-contact historic accounts must also be viewed with caution. Given this, little is known about the natural feeding and migratory ecology of this species. This renders the development of other methods for investigating the behaviour of this animal, such as isotope analysis, especially important (e.g. Chisholm et al. 1986; Gadbury et al. 2000; Hoppe 2006b; Larson et al. 2001). Such techniques could be used to provide insight into the foraging patterns, seasonal landscape use, herd fidelity, group size and total home range size (Larson et al. 2001: 27)

5.3.3 Dental development

Bison molariform teeth, like other mammalian teeth, form over several years (both enamel and dentine components). Bison, like many other herbivore taxa, experience reproductive synchronicity (Berger and Cunningham 1994). Birth is therefore a predictable event (each spring) and the same teeth from different individuals will yield isotopic data representing the same seasonal period (Gadbury et al. 2000). Eruption and attrition have been studied in bison (Frison and Reher 1970; Haynes 1984; Wegrzyn and Serwatka 1984) as well as domestic cattle (Brown et al. 1960). However, in order to undertake successful isotope studies, patterns of enamel and dentine development (when they form and mineralise, and not when they first appear in the jaw) must be considered. Currently, the best existing data on dentine and enamel formation/mineralisation comes from radiography studies and stable isotope studies incorporating controlled-feeding experiments or seasonality reconstruction.

Bison and cattle have very similar molariform teeth so cattle formation patterns can be useful indicators of bison tooth formation times (e.g. Brown et al. 1960). Eruption patterns in turn can provide an initial framework for understanding crown formation and development. Bison are born with a complete set of deciduous

dentition. At birth, this is covered with a thin, transparent film which is quickly sloughed off as the teeth go into wear (Fuller 1959: 343). All molariform teeth are permanent and in wear by the age of 5 (Fuller 1959). The second molar erupts and goes into wear by the age of 18 months whereas the M3 is not fully erupted or in wear before the third year of life (Fuller 1959; Hillson 2005).

However, as the majority of crown formation and mineralisation in high crowned teeth (hypsodontic) occurs prior to eruption, radiography or dissection methods are required to properly establish the timing of these processes. Gadbury et al. (2000) established a timeline of enamel formation (see Figure 5.10). This study assessed enamel density and therefore the phasing and direction of mineralisation, indicating sequential growth from the top of the crown to the cemento-enamel junction in the broadest sense (Gadbury et al. 2000: 81).

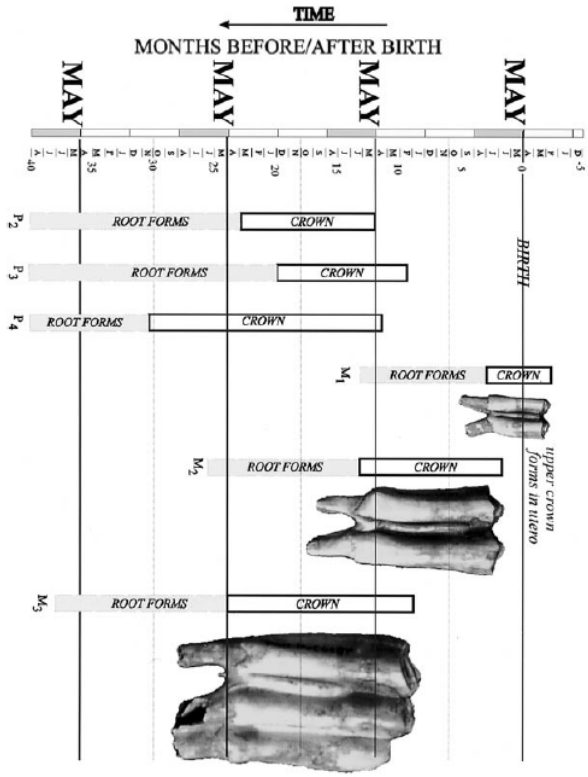


Figure 5.10 Modern bison enamel formation timeline (Gadbury et al. 2000: 81, Figure 1). Radiograph analysis indicates that enamel growth and mineralisation (seen as density increase gradient) begin at the top of the crown and proceed down to the cervix.

The enamel crown of the M2 and M3 form between birth and ~13 months and between 9 and ~24 months respectively (Brown et al. 1960; Gadbury et al. 2000: 81-82; see Figure 1). The mineralisation is therefore not entirely complete prior to eruption. Given the overlapping and elongated progress of enamel mineralisation in bison, analysis of enamel from bison M2 and M3 molars (where possible) from the same individual will theoretically represent a continuous record of carbon and oxygen isotopic inputs from just after birth to around the age of 2 years.

The dentine in cattle and bison teeth extends throughout the whole length of the tooth, covered at the crown by the enamel cap and coated with cementum at the root (Brown et al. 1960: 14). Dentine formation begins slightly earlier than crown formation initialises. In cattle, root formation is complete (i.e. dentine formation has ceased) by the age of 25-26 months in the second molar and 38-39 months in the third molar (Brown et al. 1960: 14; Gadbury et al. 2000) (see Table 5.5). Dentine from second and third molars of the same individual could therefore allow the reconstruction of a continuous dietary record for several years. The loss of both enamel and dentine through attrition could render the periods represented by complete molariform dental tissues to be shorter than their formation times.

Table 5.5 Crown and root formation times for second and third molars of bison/cattle (Brown et al. 1960, Gadbury et al. 2000).

Development	Second molar (months)	Third molar (months)
Crown formation begins	0-1	9-10
Crown formation completed	12-13	23-24
Root formation completed	25-26	38-39

5.4 Bison: Herds

5.4.1 Henry Mountains Wilderness, Utah, USA

The Henry Mountains is a semi-arid wilderness area, located in Garfield County, Utah (38°5'N, 110°50'W; Figure 5.11), rising above the Colorado Plateau to elevations up to 3500m (van Vuren 2001: 118). Although native to the area, bison

were reintroduced in 1941 due to over-hunting having exterminated the local populations. Today, the Henry Mountains herd is one of the few free-ranging herds remaining on public lands in North America (van Vuren 1983; van Vuren and Bray 1986). The area is characterised by a rugged topography and is very dry, typical of the montane environments in which bison are known to have occurred in recent history (Meaney and van Vuren 1993; van Vuren 2001).

The population numbered 340 in 2007 (Utah Division of Wildlife Resources 2007). The herd are not contained by any fences and are therefore effectively free-roaming. The total area currently in use by the bison population of the Henry Mountains is approximately 300,000 acres (~1214km^2) (Utah Division of Wildlife Resources 2007) (Figure 5.9). This large range may not only be due to the lack of fences but also to the relatively unproductive landscapes these individuals inhabit, especially in their rocky, fir-forest summer range. The terrain and extreme altitudinal movements may also explain the small group sizes and unstable social structure (van Vuren 1983: 331). Most individuals spend much of their lives at higher altitudes in the foothills or close to the summits of Mount Ellen and Mount Parnell. The herd show nomadic, seasonal movements, although such movements are invariably influenced by the occurrence of wildfire, and human and livestock land-use patterns (Utah Division of Wildlife Resources 2007). This herd of bison make a seasonal altitudinal migration, spending summers at high elevations (2500-3500m) on Mount Ellen and Mount Parnell (2350m), wintering to the south and south-west at around 1800m elevation – a distance of no more than 20km away (van Vuren 1983: 329; van Vuren and Bray 1983).

The geology of the Henry Mountains is mid-late Tertiary igneous (Figure 5.11). These relatively young (and thus less radiogenic) geologies form the upland areas that constitute the foot hills and three peaks of the mountain range (see Figure 5.11). The total range currently in use by individuals of the Henry Mountains bison also incorporates some lowland areas of older, sedimentary geology (Cretaceous) (Hintze 1974; Hintze et al. 2000).

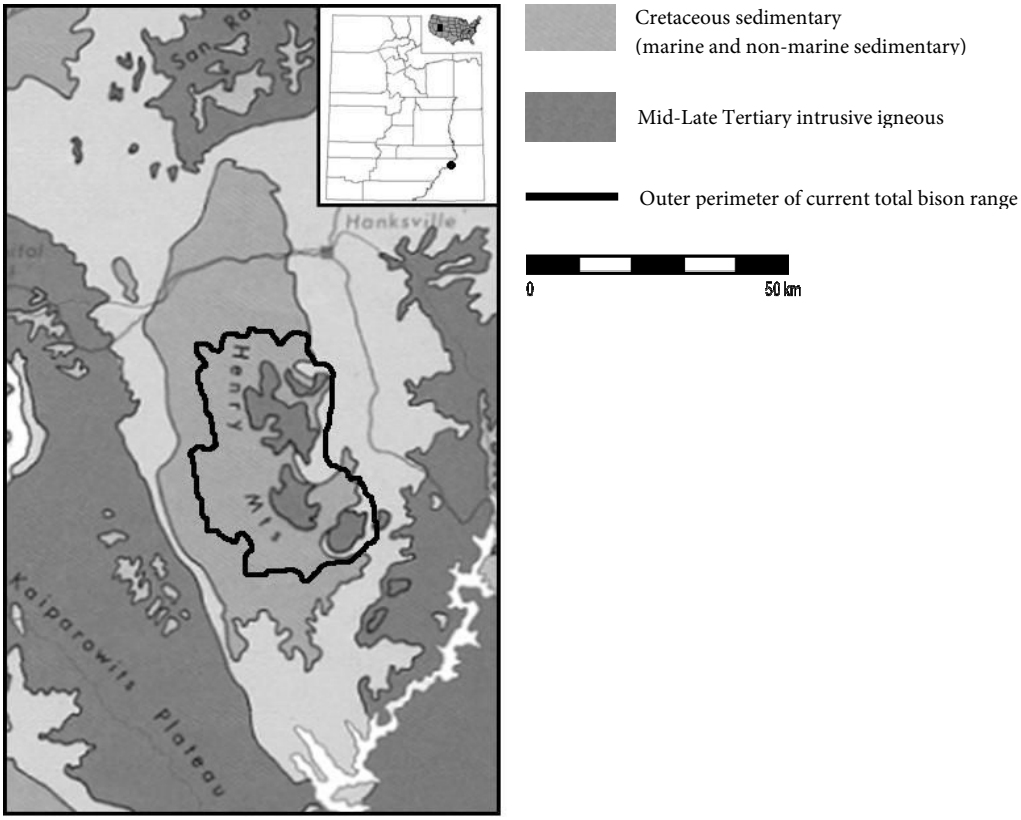


Figure 5.11 Geological map of the Henry Mountains, Utah.
The black line denotes the outer limits of the total area used currently by the free-range bison herds (290,025 acres). The animals spend the majority of their time at high altitudes close to the summit and the slopes of Mount Ellen and Mount Parnell. Geological map and units from Hintze (1974) and Hintze et al. (2000). Range from Utah Division of Wildlife Resources (2007).

There are vegetation changes with altitude. The lowest areas are the surrounding deserts, with pine (*Pinus edulis*) and juniper (*Juniperus* sp.) woodlands on the lower slopes (1500-2500m) and stands of Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea* sp.) and quaking aspen (*Populus tremuloides*) on the upper slopes (2500-3540m).

The woodland is not continuous, with stands of sagebrush (*Artemisia* sp.), perennial grasses such as bluegrass (*Poa* sp.) and needle grass (*Stipa* sp) forming openings for grazing (van Vuren 1983: 329). In some areas woodland clearing and seeding has provided additional forage areas for bison, including tracts of crested wheatgrass (*Agropyron desertorum*) – a C_3 plant – and the C_4 crop alfalfa (*Medicago sativa*).

Compositional analysis of bison faeces in the Henry Mountains reveal the late summer diet is made up chiefly of grasses and sedges (96%), forbs (4%) and few shrubs (trace). The majority of these were *Agropyron* sp., a genus of C_3 grasses. This summer diet dominated by C_3 should be identifiable using carbon isotope analysis. The winter diet, at lower altitudes, may incorporate more C_4 plants such as alfalfa (van Vuren and Bray 1983; van Vuren 1984).

As with other bison herds, weaning normally occurs by the end of the first year of life in the Henry Mountains herd. However, yearling suckling has been observed numerous times in this herd, thought to positively influence calf survival in this harsh terrain (van Vuren and Bray 1986: 505). This could influence stable light isotope values in some dental tissues, especially the nitrogen isotope chemistry of sampled dentine. However, as described above, this should not influence values observed in the M3.

The precipitation in this area varies between 150 and 500mm per year, increasing with elevation, with a mean of 204mm. The area has a low relative humidity of 49% and a mean annual temperature of 12.8°C (Hoppe 2006a). Given the close proximity of the summer and winter ranges, geographical differences in the oxygen isotope composition of meteoric water are not expected. However, an altitudinal effect (Dansgaard 1964) may be expected. $\delta^{18}O_w$ values at different altitudes at this location (38.0°N; -110.8°W) are shown in Table 5.6.

Table 5.6 Mean seasonal minimum and maximum oxygen isotope composition of meteoric waters at the Henry Mountains, Utah. Interpolated data was generated using the OIPC calculator (Bowen 2009).

Altitude (m a.s.l.)	July/August (δ^{18}Ow)‰	December/January (δ^{18}Ow)‰
1500	-9.6/-9.1	-16.2/-16.1
2500	-10.0/-10.5	-18.4/-18.2
3200	-11.4/-11.8	-20.6/-20.3

These seasonal ranges correlate well with locally-sampled river water, which has given a measured value of -13.8±0.7‰ (Dolores River, Cisco, Utah). Isotopic analysis of bulk enamel carbonates from Henry Mountains bison in the same study determined a $\delta^{18}O_{SMOW}$ value of 20.7‰ (Hoppe 2006a).

A single individual (M_3L) was sampled from this herd (FS-768). The individual (male; aged 6.6 years) was found deceased on the west slope of Mount Ellen at an elevation of 2804m on 10th September 1997. Maximum crown height was 39.15mm. The sample was provided by Ken Cannon (University of Nebraska).

5.4.2 Wind Cave National Park, South Dakota, USA

Wind Cave National Park is located close to Hot Springs in south-west South Dakota, USA, at the edge of the Black Hills and encompasses an area of 11,451 ha (or 114.51km^2) (Figure 5.12).

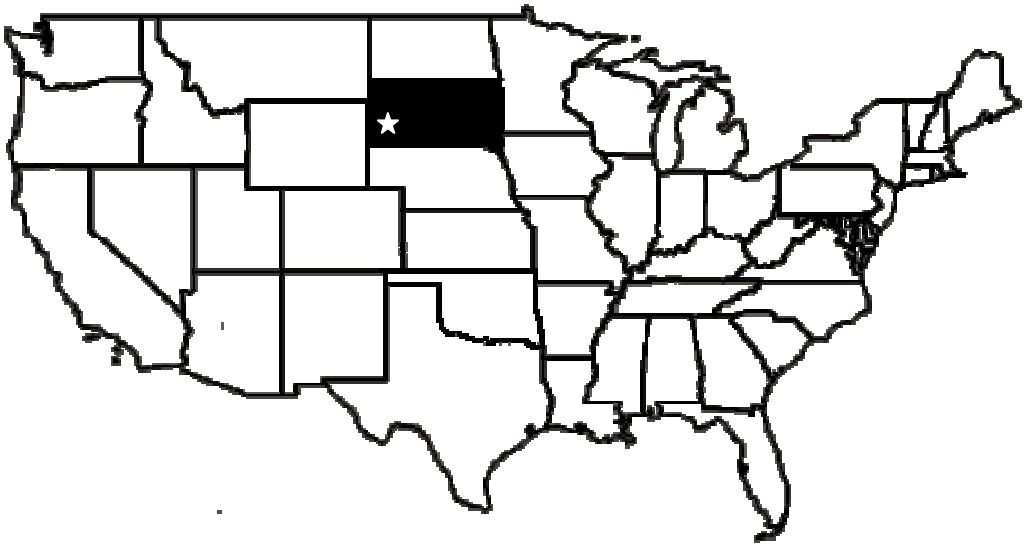


Figure 5.12 Location of Wind Cave National Park, South Dakota, USA.

The park was established in 1903 and like other parks and reserves in North America, herbivorous species were reintroduced to this area in order to try and re-establish local populations, including bison, Rocky Mountain elk (*Cervus elaphus nelson*) and pronghorn (*Antilocapra americana*) (Millspaugh et al. 2008). A perimeter fence limits the movement of animals within the park, including bison, ensuring they cannot move beyond Wind Cave Park boundaries (Millspaugh et al. 2008). The park includes elevations ranging from 1111 to 1528m. In recent years, the bison population at the park was around 300 individuals (Detling 1998: 439). Bison at Wind Cave demonstrate little systematic seasonal variation in habitat use, with individuals distributed throughout the prairies of the National Park throughout the year.

The geology of the park consists of gently rolling layers of sedimentary rocks including limestones and sandstones (Precambrian to Mesozoic) but there are areas of older geologies in the park. The oldest geologies exposed in Wind Cave are Paleo- and Meso-Proterozoic metamorphic and igneous rocks, including mica-rich

metamorphic and intrusive pegmatites. Although this herd do not undertake directed seasonal movements within the confines of the park, during normal foraging and ranging the bison could potentially traverse geologies with very different strontium isotopic signatures (from older, much more radiogenic geologies, to younger, less radiogenic, deposits) (Martin et al. 2004).

The vegetation at Wind Cave National Park includes mixed-grassland prairie with some shrubland and woodland. The vegetation is managed to create an environment similar to pre-contact wilderness (Millspaugh et al. 2008: 241). About 83% of the park is prairie, savannah and forest meadows, the remaining 17% of the park being pine-dominated forest. Grassland plants include western wheatgrass (*Agropyron smithii*), needle grass (*Stipa* spp.) and other grasses, along with sedges (*Carex* spp.) and forbs (e.g. *Artemisia* spp.). The year round diet of bison at Wind Cave is composed of these graminoids (Wydeven and Dahlgren 1985). As with other temperate grasslands in North America, the area contains different proportions of C_3 and C_4 grasses, with approximately 33% mean measured abundance of C_4 biomass (Hoppe et al. 2006: Figure DR1 (online supplement)). The abundance of these respective photosynthetic pathway groups is a function of temperature, and to a lesser extent of local topography and locally-available nutrients. In South Dakota, C_3 plants are the most common in wetter areas, whereas C_4 species are normally confined to drier and warmer areas of mixed-prairie (Barnes et al. 1983). This trend is also clear at Wind Cave, where C_4 are the most abundant on coarser, drier soils (Tieszen et al. 1988). Distribution and prevalence of C_3 and C_4 plants can also vary seasonally in temperate zones.

A previous isotope study at the park has incorporated the carbon isotope analysis of plants, animal faeces and bone collagen. Grass, sedges and forbs were collected from throughout the park, along with faecal material from elk, bison, mule deer, pronghorn and prairie dog. Bones were also selected from bison and elk. Faecal

analysis of bison determined $\delta^{13}C$ values of -22.0‰ to -28.0‰ (n=14) with a mean of -24.9±0.6‰ revealing a dominance of C_4 forage in the summer diet of bison (Tieszen et al. 1988). The $\delta^{13}C$ values for bison bone collagen was -18.7‰, with little variation between individuals, indicating an overall dietary mixture of C_3 and C_4 plant foods. Carbon isotope analysis ($\delta^{13}C_{PVB}$)of bulk enamel samples in a separate study also indicate a diet of mixed C_3 and C_4 plants (-7.9±0.3‰, 1σ, n=8) (Hoppe et al. 2006: Figure DR1 (online supplement)). This is in keeping with the ~33% of C_4 species at the locale and with the seasonal consumption of these grasses (Hoppe et al. 2006: Figure DR1 (online supplement)). The intra-tooth analysis of sequentially-sampled dentinal collagen and enamel carbonate may reveal seasonal dietary habits of the bison indicated by the faeces and bulk samples.

On grazed land, like Wind Cave, it is common that nitrogen concentration in defoliated shoots is higher than in ungrazed plants (Coppock et al. 1983). The exact causes of this effect are not known but have been attributed to the increased uptake of N in the plant, the relocation of mobile N in the plant and increased net N-mineralisation in grazed areas (Coughenour et al. 1990; Holland and Detling 1990; Jaramillo and Detling 1988). The increased N may be due to increased N availability in heavily grazed areas due to the presence and biological processes of the grazers themselves – due to the recycling of nitrogen in urine and dung. Nitrogen concentrations in urine patches are higher than in other areas (Detling 1998: 445). High concentrations of nitrogen in soils and plants have been related to the input of animal excreta in grazed areas, leading to ^{15}N-enrichment in the tissues of domestic animal grazers (e.g. Schwertl et al. 2005).

At Wind Cave, Coppock and colleagues measured concentrations of N in graminoids (both C_3 and C_4 species). Results determined that N-concentrations were significantly higher in all species on heavily grazed areas than in lightly grazed areas, with differences being most apparent on the oldest tracts of grazed land (e.g. prairie

dog colonies). The grazing of both prairie dogs and bison has been demonstrated to contribute to higher nitrogen levels in the shoots of growing plants at Wind Cave National Parks (Cid et al. 1991).

Where populations of bison and other grazing animals are large, and herd ranges are restricted, higher ^{15}N concentrations in tissues might be expected as stocking rate increases (Schwertl et al. 2005). High concentrations of total nitrogen in heavily-grazed areas have been measured at Wind Cave National Park (Coppock et al. 1983) and this could be true of other parks and wildlife refuges, and could leave to enriched ^{15}N in the tissues of animals sampled.

The area has a mean annual temperature of 8.1°C and 440mm of precipitation per year, with 70% of the annual precipitation occurring between May and September (Detling 1998: 439). The relative humidity was recorded as 62% (Hoppe 2006a: 409). Previous isotope studies have demonstrated a $\delta^{18}O_{smow}$ value of -16.2±0.2‰ for local environmental waters (sampled at Castle Creek, Hill City, South Dakota) (Hoppe 2006a: 409). These values correspond with seasonal interpolated oxygen isotope water data at this location (43.6°N; -103.5°W), from -9.6‰ (July) to -22.9‰ (January) at 1111m a.s.l and -10.2 (July) to -23.8 (January) at 1528m a.s.l.. Hoppe determined bulk $\delta^{18}O_{SMOW}$ values from bulk-sampled bison enamel at the Wind Cave National Park (21.3±0.7‰, 1σ, *n*=8) (Hoppe 2006a: 409).

Two individuals were sampled from the park, collected from bison remains found within the park (sex unknown; Table 5.7). Crown heights were not recorded. Samples were collected and co-ordinated by staff at the Wind Cave National Park.

Table 5.7 Samples from the Wind Cave National Park bison herd, South Dakota, USA.

Sample number	Sex (M/F)	Dentine	Enamel	Bone	Teeth sampled
WCNPB-2	-	X	X	-	M^3R
WCNPB-3	-	X	X	-	M^3R

5.4.3 Wichita Mountains Federal Wildlife Refuge, Oklahoma, USA

The Wichita Mountains Federal Wildlife Refuge is located in the south-west USA, within the granitic mountains of Comanche County, Oklahoma (Figure 5.13). The refuge is 59,000 acres (~240km^2), close to Cache, Oklahoma (Hebbring Wood 2000: 174) and includes areas of mixed grass prairie, oak woodlands and granite mountains (Shaw and Carter 1990). However, the grasslands prevail over most of the area (Crockett 1964). Elevations vary between from 457m and 756m a.s.l.

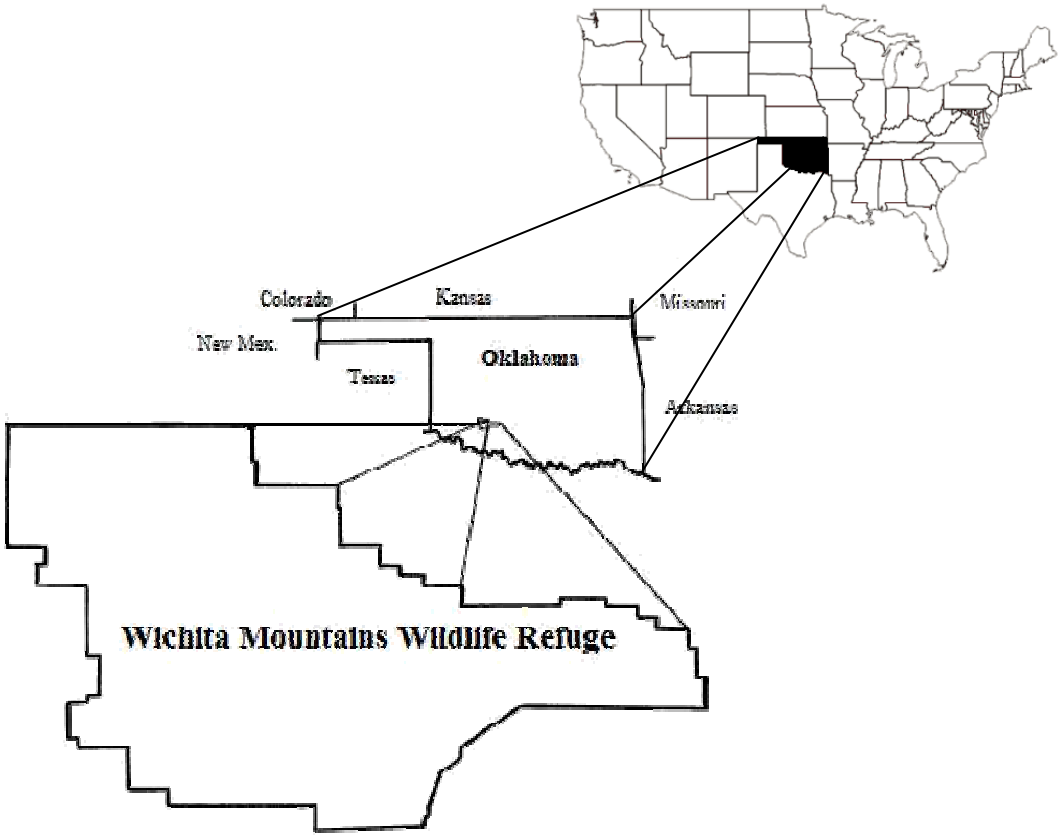


Figure 5.13 Location of the Wichita Mountains Federal Wildlife Refuge, Oklahoma, USA (adapted from Buck 1964: 336, Figure 1).

Wichita Mountains is a big game refuge and includes managed populations of antelope, bison, deer, elk and long-horn cattle (Halloran and Glass 1959). The bison herd was founded in 1907 through the efforts of the American Bison Society and the New York Zoological Society. Any wild bison herds that would have ranged in this area pre-contact were extinct long before the reintroduction (Halloran and Glass

1959). The Wichita Mountains bison herd is maintained at around 650 animals. The range is surrounded by a 2.6m high big game fence, ensuring animals cannot move beyond the boundaries of the park (Shaw and Carter 1990). The majority of this range consists of contiguous grassland, with outlying grasslands separated by granite deposits and forest. Studies of bison habitat-use at Wichita have demonstrated that most individuals spend the duration of the year on the traditional grassland annual range of the bison, with only a few instances of individuals making the 11km journey across the granite mountains to the outlying grasslands (Shaw and Carter 1990). Recent observations of the herd confirm this, with groups demonstrating no clear seasonal use of specific areas (Walter Munsterman, personal communication). The rutting season for the bison of Wichita Mountains is in late June and July. Calves are born the following year in late March/early April (Halloran and Glass 1959) and are commonly weaned before the end of the first year of life (Walter Munsterman, personal communication).

The whole area of the refuge lies within an uplifted area, the Precambrian, igneous core of a mountain system (Halloran and Glass 1959). The relatively small talus- (or scree-) sloped mountains are separated by rolling plains, the highest point being Mt. Pinchot at 2479ft (756m) and the lowest being the base of Mt. Scott at 1140ft (347m) (Crockett 1964). In addition to the Precambrian igneous geologies there are also sedimentary accumulations in the lowlands. The sedimentary material is mainly Paleozoic, with some Pleistocene and recent surficial deposits (Hoffman 1930). The soils are mostly influenced by the different local granitic parent materials (Carlton, Quanah and Lugert granite) and also demonstrate some influence from gabbroic rock (~3%) (Crockett 1964). The Lugert granite is medium-grained and pink in colour, and constitutes to approximately 58% of the area (Buck 1964).

The area contains a mix of tall, mixed and short grass prairies (Crockett 1964). Grassland flora include many species of C_4 prairie grasses (e.g. *Andropogon geradi*, *A.*

scoparius, etc) and forbs (flowering herbaceous plants). The measured abundance of C_4 biomass has been estimated as 84%, based on biomass measurements made at Lawton, Oklahoma (Hoppe et al. 2006: Figure DR1 (online supplement)). Common forb species at Wichita include ragweeds (*Ambrosia* sp.) and use the C_3 photosynthetic pathway (Crockett 1964). Like other bison, the herd at Wichita Mountains Wildlife Refuge graze on both grasses and, to a lesser extent, forbs. The dominance of C_4 plant foods in both the ecosystem and in the diet of the bison has been confirmed through the carbon isotope analysis ($\delta^{13}C$) of bulk enamel in Hoppe's previous study. Nine individuals measured had a mean $\delta^{13}C$ value of -1.9±0.7‰ (1σ) (Hoppe et al. 2006: Figure DR1 (online supplement)).

South-western Oklahoma has a typically continental climate (Buck 1964). The average annual rainfall is 788mm, with a relative humidity of 68% (Hoppe 2006a: 409). The average mean annual temperature is 16.5°C (Hoppe 2006a: 409), with a high of 82.1°F (27.8°C) in July/August and a low of 39.6°F (4.2°C) in January (Crockett 1964). In a previous study, local water samples were collected from the Washita River (Dickson, OK) and were determined to have oxygen isotope values of -3.5±0.7‰ ($\delta^{18}O_{SMOW}$). This value is ^{18}O-enriched compared to interpolated oxygen isotope data for meteoric water from this site (34.8°N; -98.6°W) with a range from -4.2‰ (July) to -10.3‰ (December) at elevation 347m a.s.l., and -4.8‰ (July) to -11.2‰ (December) at elevation 756m a.s.l.. One factor that may complicate oxygen isotope data from Wichita bison is that the wildlife reserve is dotted with artificial ponds and lakes, from which the bison regularly drink (Walter Munsterman, personal communication). Hoppe's isotope study also determined that bulk enamel carbonate oxygen isotope values from Wichita bison ranged from 26.9‰ to 29.6‰ with a mean of 28.3±0.8‰ (n=9, 1σ) ($\delta^{18}O_{SMOW}$).

Five individuals were sampled from the Wichita Mountains herd (Table 5.8), of which two were sampled for their dental tissues. Crown heights were between

37.69mm and 49.28mm (M_3). Samples were provided by the Wichita Mountains Federal Wildlife Refuge, and collected and co-ordinated by Joe Kimball and Walter Munsterman (US Fish and Wildlife Service).

Table 5.8 Samples from the Wichita Mountains Federal Wildlife Refuge bison herd, Oklahoma, USA.

Sample number	Sex (M/F)	Dentine	Enamel	Bone	Teeth sampled
WMB-11	-	X	X	X	M_3R
WMB-12	-	X	X	X	M_3R
WMB-13	-	-	-	X	-
WMB-14	-	-	-	X	-
WMB-15	-	-	-	X	-

5.5 Summary

In order to assess the potential of stable isotope analysis to explore the foraging and migratory behaviours of extinct and ancestral archaeological fauna, modern herbivores from two species and multiple geographical areas have been selected. The location and ranges (where applicable) of each herd is shown below in Figure 5.14.

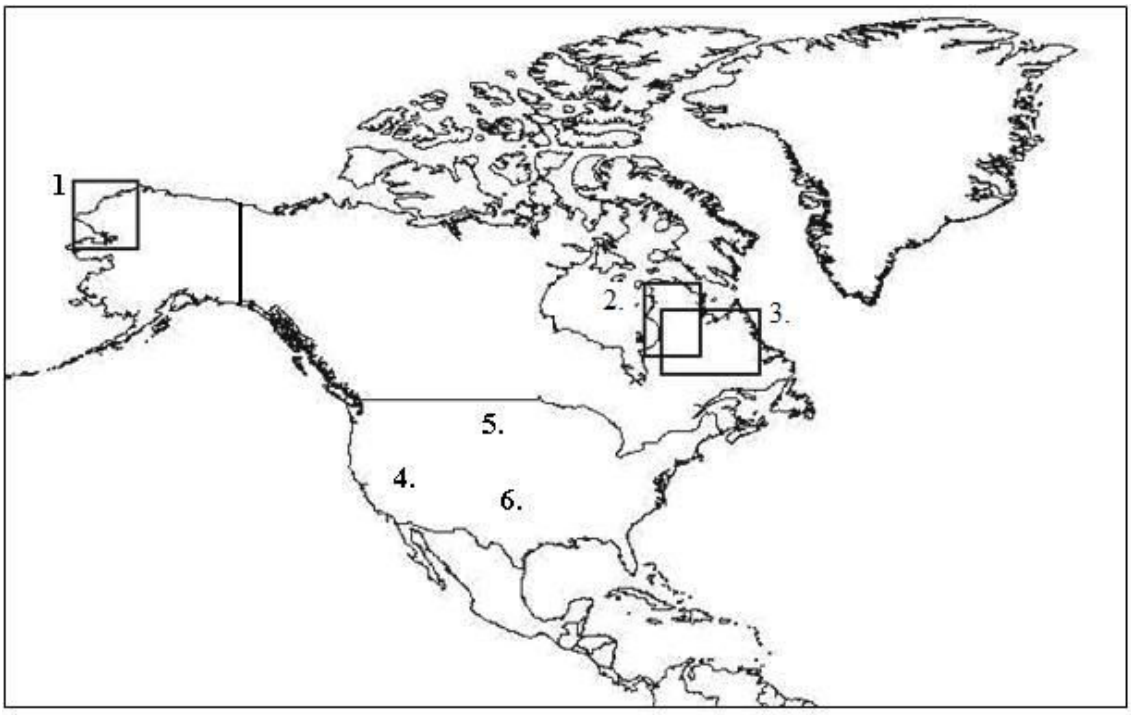


Figure 5.14 Geographical origin and range of each herd under investigation.

Herds include 1. Western Arctic caribou, Alaska, USA; 2. Leaf River caribou, Québec; 3. George River caribou, Québec/Labrador, Canada; Canada; 4. Henry Mountains bison, Utah, USA; 5. Wind Cave bison, South Dakota, USA; 6. Wichita Mountains bison, Oklahoma, USA.

The documented movements and seasonal dietary behaviours described above, along with the descriptions of tissue development times, allow certain predictions concerning the likely results of isotope analysis. Given the scope of isotope systems under investigation, these methods have the potential to assess the migratory (strontium and sulphur), dietary (carbon and nitrogen) and seasonal behaviours of the modern individuals under analysis (summarised below in Table 5.9). Stable isotope ratios will be determined from incrementally-developed tissues (dentine and enamel) and, where possible, bone for individuals from these different herds. These values will be compared to the environmental, dietary and mobility information described above. The use of multiple-isotopic analyses and multiple archaeologically-available analytes will be evaluated and the applicability of these methods to the reconstruction of behavioural and feeding palaeoecology will now be assessed.

Table 5.9 Summary of modern herbivores sampled for isotope analysis.

Species	Herd	Summary
Rangifer tarandus	All herds	• M_2 and M_3 should represent 1+ year of isotopic inputs in enamel and even more for dentine • Philopatry in females should ensure first forming parts of M_2 have calving ground/proximal summer range $^{87}Sr/^{86}Sr$ signal • Long-distance, north-south ('thermostress') migration is a form of environmental buffering and should lead to smoothed $\delta^{18}O$ signals • ^{13}C-enrichment in winter and depletion in summer (seasonal lichen consumption) • ^{15}N-enrichment in winter and depletion in summer (due to seasonal weight loss and low-protein winter forage) • Bone collagen from individuals within the same herd may have a similar isotope chemistry ($\delta^{34}S$, $\delta^{13}C$ & $\delta^{15}N$) and may be distinguishable from other (even geographically proximal) herds
R.t.granti	1.Western Arctic (Alaska)	• M_2 and M_3 (+bone) • Stable herd behaviour (high level of intra-herd isotopic homogeneity) • Regular movement from older (more radiogenic) geologies (calving ground/summer range) to younger deposits (less radiogenic; winter range) • Long-distance, north-south seasonal migration (smoothed $\delta^{18}O$?)
R.t.caribou	2. Leaf River (Canada)	• M_2 and M_3 (+bone) • Very old geologies (more radiogenic; higher $^{87}Sr/^{86}Sr$ values) • Relatively stable herd behaviour (high level of intra-herd isotopic homogeneity) • North-south migration (smoothed $\delta^{18}O$?) • Bone collagen from multiple individuals (n=10) should have similar isotope chemistry ($\delta^{34}S$, $\delta^{13}C$ & $\delta^{15}N$) and be comparable to George River herd
R.t.caribou	3. George River (Canada)	• M_2 and M_3 (+bone) • Very old geologies (more radiogenic; higher $^{87}Sr/^{86}Sr$ values). Also some younger, varied geologies • Recently erratic herd movements (low intra-herd fidelity

		and therefore low degree of homogeneity?) especially spatially-dependant $^{87}Sr/^{86}Sr$ • Bone collagen from multiple individuals (n=10) should have similar isotope chemistry ($\delta^{34}S$, $\delta^{13}C$ & $\delta^{15}N$) and be comparable to George River herd
Bison bison	All herds	• $\delta^{18}O$ may be varied – purely seasonal (due to no movement), influenced by altitude (leading to ^{18}O-depletion?) or artificial ponds • Where applicable, inclusion of C_4 plant foods in the diet should be visible and may be even seasonal
B.bison	4. Henry Mountains (Utah)	• A single individual (M_3) – no possibility to explore intra-herd homogeneity • Younger, less radiogenic geologies. Small-scale movements on geological similar area should lead to constant intra-tooth $^{87}Sr/^{86}Sr$. • Local animal, high seasonal $\delta^{18}O$ variation? Summer at higher altitudes, dampening effect? • Varied C_3/C_4 composition of diet, will influence $\delta^{13}C$
B.bison	5. Wind Cave (South Dakota)	• One M_2 + one M_3 (different individuals) • No clear seasonal use of space but varied movements across geologies of mixed ages (could lead to variable $^{87}Sr/^{86}Sr$) • $\delta^{18}O$ in enamel should reflect local seasonal variation • Mixed C_3 and C_4 diet (more C_4 in summer diet, should be visible in intra-tooth $\delta^{13}C$ (dentine and enamel) • ^{15}N-enrichment due to intensive grazing?
B.bison	6. Wichita Mountains (Oklahoma)	• Multiple individuals (M_3 +bone) • No clear seasonal use of space, potentially homogenous $^{87}Sr/^{86}Sr$ • $\delta^{18}O$ in enamel should reflect local seasonal variation (artificial ponds could dampen/homogenise signals) • Dominance of C_4 grasses should lead to less negative $\delta^{13}C$ values in dentine, enamel and bone • Isotope chemistry of bone collagen ($\delta^{34}S$, $\delta^{13}C$ & $\delta^{15}N$) from multiple individuals (n=5) should be fairly homogenous across this small area and reflect their feeding niche/local geology

CHAPTER SIX METHODS

6.1 Sample preparation: modern bone

Modern bones samples were taken from the mandible of each animal (where available). Small sections ($1cm^2$) were cut from each individual using a diamond coated circular drilling disc. Any adhering matter was cut away using a scalpel and discarded.

De-greasing the modern bone was imperative as whole fresh bone contains 1-2% lipids (Wuthier 1968) and lipids have carbon isotope values up to 7‰ more negative compared to bone collagen (DeNiro and Epstein 1978; Smith and Epstein 1971), therefore later influencing carbon isotope measurements (Liden et al. 1995). Some studies have utilised sodium hydroxide (NaOH) during collagen extraction in order to remove both lipids and humic acids (Ambrose 1990: 432). However, other studies have demonstrated this to be not only ineffective in removing lipids but also detrimental to collagen yield (Liden et al. 1995: 325-326). Alternatively, solvents can be used to remove lipids prior to collagen extraction. Most commonly, solvent mixtures of methanol (CH_3OH) and chloroform ($CHCl_3$) are used and have been applied to both hair/wool and bone (Hedges et al. 2005; Liden et al. 1995; O'Connell et al. 2001), with polar and non-polar lipids being removed by chloroform and methanol respectively (see discussion in Jay 1999: 25-27). Due to differences in the polar/non-polar lipid composition of marrow fats and bone matrix, it has been argued that a solvent higher in methanol (corresponding with the high non-polar lipid content of marrow fats) may be more suitable for de-greasing fresh bone (Jay 1999: 25-27). Therefore, samples were soaked in methanol and chloroform (2:1 v/v) for 10-14 days. A laboratory carousel was used to maintain movement and the solvent was replaced every 3-4 days. Degreased samples were then rinsed in deionised water and left to dry overnight in a clean ventilated environment.

Samples of bone were then sub-sampled (if necessary) into smaller sections and any trabecular bone and remaining adhering materials were removed using air-powder power abrasion. During this process, aluminum oxide powder is blasted against the sample, removing trabelcular bone, surficial layers and any attached dirt and contaminating material. Trabecular bone is porous and thought more susceptible to diagenesis than cortical bone (Rao 2005: 6). Each bone sample was approximately 200-400mg and was broken into smaller sections. This was done in order to increase the total surface area of the segments of bone and to decrease the average demineralisation time. Given that the average collagen content of fresh bone is around 17%, collagen yields in the modern bone were expected to be high. During the analysis of archaeological material it is often required to utilise more analyte, depending on the preservation condition of the bone (or dentine), its age and degree of degradation. Demineralisation, collagen extraction and analysis proceeded as detailed below (Chapter 6.3)

6.2 Sample preparation: intra-tooth sampling

Mature hemimandibles or loose molars from caribou (*Rangifer tarandus* spp.) and bison (*Bison bison*) were selected for isotope analysis. All teeth sampled were selected for carbon and nitrogen isotope analysis of dentine serial sections. Strontium and carbonate (oxygen and carbon) isotope analysis was also carried out for the majority of samples.

Where still in jaws, molars were extracted from the bones, brush-cleaned with water and then left to dry overnight. Whole teeth were mechanically abraded using a tungsten carbide burr (NTI-Kahla, Germany) to remove surficial enamel and any adhering material. Teeth selected to be analysed were chosen according to the predicted chronology of dental development and eruption in *Rangifer* and *Bison* respectively (see Chapters 5.1.3 and 5.3.3 respectively)

Intra-tooth sampling for both enamel and dentine was performed using flexible, stainless steel diamond-coated superfine circular bits (NTI-Kahla, Germany). Individual bits were cleaned prior to every use and between each sample. This was especially important during serial-sampling to avoid powder cross-contamination. Dental tools were first dipped in a weak nitric acid (<0.3M) in order to dissolve any adhering mineral material. Tools were then rinsed in Millipore Alpha Q H_2O before being ultrasonicated for 5 minutes in fresh Millipore Alpha Q H_2O. Tools utilised for dentine sampling were then swabbed with acetone to ensure no protein or lipid contamination. Tools were left to dry fully in a clean environment before use .

Each tooth was initially dissected using the circular drills bits. In order to ensure data were comparable (where possible) enamel was removed from the buccal face of the anterior loph for analysis in each individual. Dentine was removed as a vertical column from the area adjacent to location of enamel removal, usually incorporating one-quarter of the anterior loph on the lingual face (Figure 6.1). Serial-sampling of both enamel and dentine is summarised in Figure 6.1 and described in detail below (Chapter 6.2.1 and 6.2.2). Some cleaning procedures (such as extensive surficial cleaning) may have been superfluous for the analysis of modern materials (where diagenetic alteration of surfaces is unlikely). However, this was done to ensure that all sampling and analytical procedures would be applicable to archaeological materials and could be replicated in entirety. This would maintain consistency, limit variability and ensure data comparability.

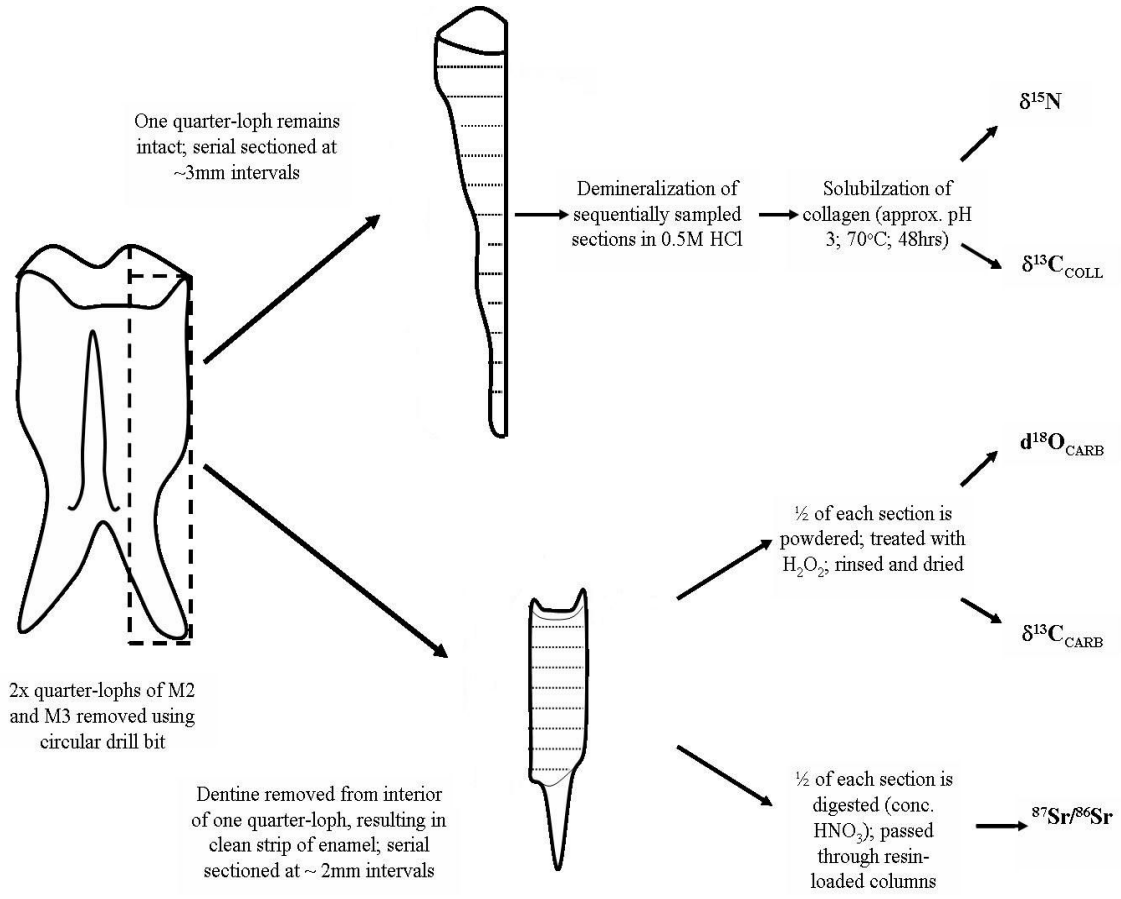


Figure 6.1 Schematic summary of tooth sampling, serial-sectioning and subsequent laboratory preparations and isotopic analysis.

6.2.1 Enamel

The buccal face of the anterior loph of each tooth was removed using flexible stainless- steel diamond-coated superfine circular drill bits. This was selected for analysis due to its normally slightly thicker enamel than the lingual face. Any adhering dentine was removed using a tungsten carbide burr. Similar tungsten carbide burrs and stainless steel saws have been demonstrated to introduce no measurable quantity of contaminating Sr when subjected to strong acid leaching and Sr isotope analysis (Montgomery 2002: 131-132).

Interior surfaces of enamel were also mechanically cleaned in this way after dentine removal, further abrading enamel from the dentine-enamel junction. This was done

to ensure only enamel would be analysed and not dentine (which forms at different rates to enamel and has a different structure). Furthermore, this ensured that the method could be replicated on archaeological samples (where the diagenetic alteration of dentine and surficial enamel could be likely).

Complete enamel faces were then marked for horizontal sectioning at ~1.5mm (*Rangifer*) or ~2.5mm (*Bison*) intervals and then ultrasonicated for 10 minutes and dried at room temperature. This was done to ensure all adhering powder produced during the cutting and cleaning process had been removed to limit sample cross-contamination or contamination from dentine power. Sections were then cut from the clean, dried vertical pieces of enamel using diamond-coated circular bits. Each individual section was also individually ultrasonicated in Millipore Alpha Q H_2O for approximately 5 minutes to remove adhering enamel powder. Sections were given numerical assignments, commencing from the cemento-enamel junction to the apex (e.g. M2-1, M2-2, M2-3, etc).

Sections were split longitudinally, with ~5mg of enamel reserved for each type of isotopic analysis (strontium and carbonate). As previously noted, sequential-sampling in this way serves to homogenise enamel of each section into one datum point. Given the potentially rapid rates of mineralisation (especially in low crowned herbivores such as *Rangifer*) this may limit the time resolution achievable.

6.2.2 Dentine

Prior to dentine sampling, each tooth had been thoroughly cleaned, dried and enamel had been removed from the buccal face of the anterior loph (see above).
Dentine was removed as a vertical column from the area immediately adjacent to the site of enamel removal (see Figure 6.1) using the circular drill bits.

Vertical sections were then ultrasonicated in Millipore Alpha Q H_2O for 5 minutes and left to dry in order to remove excess powder. Sequential sampling of ~2-3mm sections was then performed from the apex to the root of the tooth (Figure 6.1). Individual sections therefore included both dentine and adhering enamel components prior to demineralisation. Individual sections were ultrasonicated in clean Millipore Alpha Q H_2O for 5 minutes and left to dry before demineralisation (see below). Although previous literature has specified decalcification can be carried out prior to sequential-sectioning (Balasse and Tresset 2002), in this case sections were made prior to demineralisation serving to reduce demineralisation time from two months to approximately two weeks. Sections were given numerical assignments, commencing from the root tip to the apex (e.g. M2-D1, M2-D2, M2-D3, etc).

6.3 Collagen extraction

Bone and dentine samples were prepared for collagen extraction following protocols based on the Longin method (Longin 1971) with modifications based on the recommendations of Collins and Galley (1998) and the addition of an ultrafiltration step (Brown et al. 1988). Essentially, this method (after Longin 1971) converts the protein fixed in the mineral matrices of biogenic calcified tissues to gelatine and includes steps to eliminate humic substances and other contaminants (Brown et al. 1988).

There is now broad agreement in the archaeological sciences concerning the best methods for extracting collagen from ancient materials and differences between the methods (in terms of isotope data) are small (Jørkov 2007). In general, methods involve the initial removal of the mineral component using a acid solution (normally hydrochloric acid, HCl) and the solubilisation of collagen at a high temperature under weakly acidic conditions. This is then followed by a lyophilisation (freeze-

drying) phase, the solid product of which is then available for analysis (Jørkov 2007). Some modifications include the use of a sodium hydroxide (NaOH) solution prior to gelatinization (DeNiro and Epstein 1981) to remove organic contaminants such as humic acids, the use of EDTA (ethylenediaminetetraacetic acid) to demineralise samples instead of HCl (Tuross et al. 1988) and the use of ultrafilters to purify the gelatinised collagen (Brown et al. 1988). The ultra-filtration step is an important modification as it separates longer chain protein molecules (>30,000 kDalton or >10,000 kD depending on the filter selected), ensuring longer chain molecules (most likely Type I collagen) and not shorter chain potential contaminants are preserved. This has been performed in all instances with modern and archaeological samples in order to make data comparable. Unless specified, >30,000kD filters were used.

Once prepared and cleaned, bone samples were broken into smaller sub-samples. This was done along the grain of the bone in order to preserve the length of the collagen fibrils. Thin, long sections of bone were preferable as this ensured acid could move around the bone during demineralisation and maximise surface area, reducing the time taken to decalcify the bone. Tooth samples were preserved in whole pieces. Samples were then weighed in clean test-tubes to the nearest milligram - usually between 200 and 400mg for bone and 30 and 150mg for dental sub-samples. During this process all areas were kept clean and free from bone/tooth dust in order to avoid sample cross-contamination.

6.3.1 Demineralisation

The mineral phase of the bone was removed using a weak acid solution in order to dissolve the bone mineral (Longin 1971). Hydrochloric acid (HCl) was used for this purpose. 0.5M refrigerator-cooled HCl (approximately 4°C) was poured into the test-tubes containing samples up to the neck of the test-tubes. A cooled solution was used in order to ensure the rate of reaction would not be too rapid. The demineralisation

process not only results in the decalcifying of biogenic mineral tissues but will also inevitably cause some damage to collagen.

The longer samples are left in acid or the more aggressive the acid treatment (with a higher pH or a higher reaction temperature) the more likely an unacceptable level of damage will occur. This could potentially decrease the yield of collagen then available for isotope analysis. Storage in the refrigerator served to slow the rate of the demineralisation reaction and also the associated hydrolysis of the collagen, maximising yield (Collins and Galley 1998). Racks of tubes (containing 0.5 M HCl and individual samples) were covered loosely with foil, allowing carbon dioxide (CO_2 produced during the acid-apatite reaction) to escape and also protecting the contents of each tube from potential sources of contamination. Samples were then stored in a refrigerator for the duration of demineralisation.

The period of demineralisation varied between a few days and a couple of weeks, depending on the bone, preservation (in archaeological samples) and the quantity of bone. Depending on the condition of the sample, the acid was removed and replaced with fresh acid one or more times during the demineralisation process. It was necessary to replace and renew acid in these instances when original acid had entirely reacted but bone mineral had not completely dissolved. In these cases, spent acid was carefully removed (either using disposal pipettes or poured off directly), leaving the respective sample in the tube, then re-filling with additional 0.5M HCl and returning to the refrigerator. On average, this occurred every 3-5 days.

In general, fresh modern bone and dentine took more than a week to demineralise. Bone and dentine were deemed to be demineralised when samples became soft and gelatinous. Samples were assessed individually, with demineralisation deemed complete when bone became soft and pliable, CO_2 production (visible as effervescence) had largely ceased and (in some cases) when samples floated to the top

of their respective test tubes. The period of demineralisation varied between samples – with smaller, flatter samples with a larger surface area (and therefore larger reaction areas) taking often significantly less time than larger samples. The rates of demineralisation were generally faster for archaeological bone (compared to de-greased modern bone), taking up to 10 days, with the demineralisation period for modern bone and dentine extending to 12-16 days.

After demineralisation, samples were taken from the refrigerator and the spent acid was removed (again, either using disposable pipettes or poured off directly). Samples were then rinsed with deionised water three times, and tubes were then filled with deionised water, resulting in a near-neutral solution. Where samples were fragmentary, disposable glass pipettes were used for this and samples were centrifuged between rinses in order to preserve the sample. Regular pH tests using indicator paper ensured that samples were being rinsed successfully. Screw lids were placed on test tubes for refrigerated storage.

6.3.2 Gelatinization

After demineralisation, it was necessary to gelatinize the samples. During this process proteins are freed into solution under the effects of high temperatures and low pH. This separates the 'collagen' from any remaining bone matrix or other contaminant materials and facilitates the successive filtering steps. Prior to this it was first necessary to drain the samples, replacing the water with fresh deionised water. This was done in order to remove contaminants which may have entered the water during storage (between initial rinsing after demineralisation and the heating stage).

The screw-top test-tubes were filled all the way to the top with the water. This was done to avoid oxidation in the heating phase. A pH of approximately 3 was achieved by the addition of a few drops of 0.5M HCl. The maintenance of the low pH level

avoids dissolving any non-acid soluble contaminants – ensuring only denatured and partially hydrolyzed collagen is rendered soluble (Chisholm et al. 1983: 357). Acidity was assessed using pH indicator paper periodically in order to ensure the correct number of drops was being added to the samples in water.

The rinsed samples in sealed test tubes (in refreshed deionised water containing acid drops) were placed in a heater block at 70°C. Samples were wrapped securely in double-layered foil in order to insulate them and processed for 48 hours. The fibril structure of collagen denatures at approximately 58°C and studies have demonstrated that yields stabilise at this and at higher reflux temperatures (Brown et al 1988).

6.3.3 Filtering and ultrafiltering

After removing samples from the heater block, solutions were filtered in two steps. First, samples remained sealed and were allowed to cool. The first phase of filtering involved the use of 5-8μm Ezee® mesh filters (Elkay Laboratory Products). Samples were poured from screw-top tubes into clean test-tubes. Care was taken to ensure any residual debris or solid material remained in the screw-top test-tubes. Ezee® filters were inserted and pushed gently into the tubes. The filtered liquid was then poured into another clean, labelled test-tube. Tubes were covered with fresh, clean foil and refrigerator-stored until the ultrafiltration step.

For the second phase of filtering, >30,000kD filters were used. Prior to use, it was necessary to clean and rinse ultrafilters. This was done using a 0.5M sodium hydroxide solution (NaOH) in order to remove any potential organic contaminants, including glycerine which is routinely added during the manufacturing process. Ultrafilters were filled with the dilute NaOH and centrifuged for approximately 20 minutes in order to wash through any contaminants into the bottom of the filters.

This process was then repeated three times with deionised water to remove any traces of the NaOH. The cleaning of filters was carried out immediately before they were required to ensure they did not become blocked before sample filtration.

Filters were then filled with the liquid samples. Samples were centrifuged for a short time at first in order to establish how quickly samples were passing through the filters. This varied between samples meaning that every batch and every individual sample required close attention. Samples were centrifuged until the liquid had reduced down to the mesh section of the filter (around or slightly above the 500µl line in the filters used). When some solution had passed through, the waste filtrate was discarded from the base of the filter. More of the sample was added to the top of the filter until the entire sample had been filtered. Concentrated liquid samples were removed carefully using a pipette, avoiding touching the mesh filter itself which may have loosened trapped debris. The filtered samples were then moved to fresh test-tubes. Deionised water was then carefully poured into the filter to the 500µl line and removed using a pipette. This was added to the sample and was done to ensure that as much of the collagen as possible was preserved from the filter. Test-tubes were then covered with Parafilm® M Barrier Film.

6.3.4 Freezing and freeze-drying

Freeze-drying (lyophilisation) was necessary in order to precipitate and isolate the 'collagen' in solution in the filtered samples. It was necessary to freeze samples prior to freeze-drying. Samples were frozen at an angle in order to increase the surface area of the sample within the test-tube and to facilitate the freeze-drying process. The Parafilm® covering the samples was punctured (in order to let gas escape while in the freeze-drier) and samples were left in the freezer for at least 12 hours until they were frozen solid. Frozen samples (sealed with punctured Parafilm®) were quickly moved between the freezer and the freeze-drier to ensure samples did not defrost before they

became dehydrated. During this 48 hour phase, water was removed (through the sublimation of the ice), resulting in dry, white to pale brown 'collagen'.

Once removed from the freeze-drier, tubes were resealed in order to prevent the rehydration of the samples from atmospheric water vapour or weighed immediately into microtubes. The total freeze-dried product of every sample was weighed to calculate 'collagen' yields. 'Collagen' yields are expressed as weight percentages or as weight ratios (mg/g). Modern fresh bone contains about 22 wt % collagen, but this drops steadily during burial (van Klinken 1999: 689). Low-'collagen' archaeological bones (i.e. where yield was less than 1%) were given extra consideration for 'indications of breakdown of sample integrity' (van Klinken 1999: 689).

6.3.5 Collagen analysis: CF-IRMS

The 'collagen' was weighed into tin capsules for isotope analysis. For carbon and nitrogen analysis, only very small amounts were required for analysis. A microbalance was used to weigh 0.45-0.55mg of each sample into tin capsules. This was done using metal tweezers, which were cleaned between each sample using methanol. Capsules were pressed closed and shaped into small balls. Two sub-samples were prepared per sample in order to gain isotopic measurements in duplicate. The mass of each sub-sample was recorded individually.

International and laboratory standard materials were included in every isotopic run. For carbon and nitrogen, these included the amino acid methionine and Bovine Liver Standard (BLS) 1577b. These standards serve to calibrate the machine and as checks against the carbon and nitrogen data respectively. Carbon and nitrogen isotopic measurements were performed in duplicate using a continuous-flow isotope ratio mass spectrometer (CF-IRMS) with attached elemental analyser in the Department of Human Evolution, Max Planck Institute for Evolutionary

Anthropology. Leipzig, Germany. Specifically, samples were combusted in a Flash EA 2112 (the elemental analyzer) interfaced with a Delta XP (the mass spectrometer) (Thermo-Finnighan®, Bremen, Germany). Machine standard error (1σ), calculated from the long-term repeat analysis of international and in-house reference materials for this laboratory is ±0.1‰ or better. The analysis of 'collagen' samples in duplicate (in different batch runs, on separate days) could also be used to calculate the mean analytical error, which was routinely 0.2‰ (1σ) or better across all analyses.

The analytical technique used for sulphur isotopic measurements is detailed in full in Nehlich and Richards (2009). Approximately 10mg of collagen was weighed into tin capsules and mixed with 1mg of vanadium pentoxide (V_2O_5) (Microanalysis, UK). The V_2O_5 catalyses the combustion and helps to reduce variability between samples (Morrison et al. 2000). Due to the necessary larger sample size (~10mg), sulphur isotope measurements were not made in duplicate. Collagen samples for sulphur isotope analysis were combusted in a Heka EuroVector elemental analyser (HeKaTech, Wegberg, Germany) and analysed using a Delta V plus (Thermo-Finnigan, Bremen, Germany) (Giesemann et al. 1994; Kester et al. 2001; Nehlich and Richards 2009). $\delta^{34}S$ values were measured against a sulphur gas standards and were corrected for oxygen isotope mass variations (Coleman 2004). International and in-house laboratory standards accompanied sulphur isotope runs. Inorganic and organic international standards were included in every run, including NBS127, IAEA-S1, IAEA-S2 and IAEA-SO-5 (inorganic) and NIST Bovine Liver Standard (BLS) 1577b and IVA protein casein (organic). Analytical precision for standards was ±0.4‰ or better, with a standard error (1σ) of 0.3‰ or better. Internal bone collagen standards for the laboratory were run periodically and calculated a standard error of ±0.6‰ or better (Nehlich and Richards 2009). Given the quantities of sample required for analysis, it was not possible to measure samples in duplicate and no independent calculation of error could be made during this study.

Isotope data were evaluated prior to their use on the basis of the collagen quality criteria discussed in Section 4.3.2. All modern bone and dental collagen data met the relevant established criteria for carbon and nitrogen (DeNiro 1985; van Klinken 1999) and sulphur (Nehlich and Richards 2009). The quality of the archaeological bone collagen is discussed in a separately in Chapter 8.5.3.

6.4 Bioapatites

6.4.1 Carbonate preparation

Enamel samples for carbon and oxygen isotope analysis were prepared following the methods outlined in Koch et al. (1997) with some modifications. Enamel sub-samples of around 5mg (approximately half of every serial-sample, snapped in half using gloved hands) were crushed and powdered using an agate pestle and mortar. Care was taken to evenly and finely grind the enamel samples, in order to homogenise the enamel sub-samples and to produce a mixture with a large surface area for the later acid reaction (during the isotope analysis). Samples were then removed from the mortar using a metal spatula and weighed onto laboratory weighing paper and then transferred into microsample tubes. All implements and the pestle and mortar were rinsed with a weak nitric acid solution (~0.3M), followed by a rinse with deionised water and dried between every sample in order to prevent cross-contamination.

Given the small quantity of organics in biogenic hydroxyapatite (and any exogenous organic materials that may be contaminating archaeological materials), it was necessary to pre-treat samples with a basic solution. Chemicals commonly used to oxidise organic matter in enamel preparation are sodium hypochlorite (NaOCl) and hydrogen peroxide (H_2O_2). 30% H_2O_2 (room temperature) was used in this study, with 40µl per 1mg of sample being added to the respective microtubes. These were left for 24 hours to ensure organics were removed (Koch et al. 1997). After this time,

powder samples were then rinsed five times with deionised water. This was done using a centrifuge and disposable pipette tips. Samples were then dried for 48 hours in a clean environment under constant air flow.

6.4.2 Carbonate analysis: CF-IRMS

Samples were measured for carbonate oxygen and carbon in several different laboratories. Although this is undesirable, mechanical issues and factors beyond the author's control made this unavoidable. The universal use of international standards (NBS 18 and NBS 19) at the different laboratories allows data to be comparable. In addition to the international and in-house standards used at each laboratory, a third type of standard was used during analysis to help to recognise inter-laboratory analytical error. A highly-homogenised enamel powder from the teeth of a modern horse ('DOBIN') was used for this purpose. Multiple independent preparations of this material (both treated and untreated) were made and analysed at the separate laboratories. Furthermore, several preparations of this material were made in every batch of samples prepared (1 per 10 samples).

Measurements were made at the Department of Earth Sciences, Durham University; the Stable Light Isotope Facility, University of Bradford and at Iso-Analytical Ltd, Sandbach, Chesire, UK. Dried samples were placed in individual vessels in a Thermo-Finnigan Gasbench for reaction with ortho-phosphoric acid at 70°C and 80°C (Bradford and Durham respectively). CO_2 was obtained by cryogenic distillation and analysed for $^{18}O/^{16}O$ and $^{13}C/^{12}C$ ratios using CF-IRMS, specifically a Thermo-Finnigan MAT253 mass spectrometer (Durham) and a Thermo Delta V Advantage mass spectrometer (Bradford). At Bradford, an in-house calcium carbonate standard (Merck $CaCo_3$) and the international standard NBS-19 were analysed with the samples. In Durham, the international standards NBS-18 and NBS-19 were analysed along with an in-house calcium carbonate standard (DCS01).

At Iso-Analytical Ltd, samples and reference vials were placed in a drying oven for 24 hours prior to caps being fitted to ensure no moisture was present. The vials then had their headspaces flushed with pure helium (99.995%). After the flushing, phosphoric acid was injected into the vials and mixed with the sample powder (Coplen et al. 1983). Samples were left to react at 24hrs at ambient temperatures then heated to 80°C for 20 mins in order to ensure complete conversion to CO_2. The CO_2 gas was then analysed using CF-IRMS (Europa Scientific 20-20 IRMS). Reference materials included an in-house laboratory calcium carbonate standard (IA-R022), which is traceable to the international standard NBS-19. During analysis the International Atomic Energy Agency (Vienna) reference standards, NBS-18 and NBS-19 were also analysed. Isotope ratios were given relative to the V-PDB standard, and oxygen isotope ratios were converted to V-SMOW using the published conversion equation (Coplen et al. 1983):

$$\delta\ ^{18}O_{V\text{-}SMOW} = 1.03091 \times \delta\ ^{18}O_{V\text{-}PDB} + 30.91\ ‰$$

In-house analytical precision was good in all labs (normally <0.2‰), inter-laboratory variation was assessed using the repeated measurements of the NBS-19 standard and the homogenized modern horse standard in all laboratories. This data is summarised in Table 6.1.

Table 6.1 Carbon and oxygen isotope ratios of NBS-19 and the in-house horse enamel standard ('DOBIN') at Durham, Bradford and Iso-Analytical Ltd.

Values are given ±1σ. The accepted values for NBS-19 are taken from Coplen et al. 1983 and Coplen 1995. $\delta^{18}O_{V\text{-}SMOW}$ values were calculated using the equation above (Coplen et al. 1983).

	NBS-19		horse enamel 'DOBIN'	
	$\delta^{13}C_{V\text{-}PDB}$ ‰	$\delta^{18}O_{V\text{-}SMOW}$ ‰	$\delta^{13}C_{V\text{-}PDB}$ ‰	$\delta^{18}O_{V\text{-}SMOW}$ ‰
University Durham	1.95±0.50 (*n*=14)	28.73±0.23	-16.35±0.12 (*n*=8)	23.20±0.14
University of Bradford	1.99±0.10 (*n*=4)	28.66±0.07	-15.15±0.03 (*n*=3)	23.46±0.18
Iso-Analytical Ltd	1.80±0.21 (*n*=4)	28.38±0.10	-16.11±0.24 (*n*=19)	22.20±0.40
Accepted value	1.95	28.6	no value	no value

Analysis of the NBS-19 standard across laboratories was approximately the same as in-house error (~0.2‰, 1σ), allowing all measurements to be comparable between laboratories. However, it must be noted that measurements gained from the comparative analysis of the horse enamel standard reveal a larger error. Unfortunately, correction of data was not possible using this standard, given that there is no accepted single value. However, as herd groups were generally measured at the same laboratories (see data tables in Appendix for full details), it was not deemed necessary to correct data for intra-group comparisons and no inter-group comparisons were drawn between absolute intra-tooth oxygen isotope values. However, this does highlight the importance of utilising the same mechanical and analytical conditions in order to gain comparable data, and also emphasises the importance of biogenic hydroxyapatites as standards for this type of analysis. The international standards are currently calcium carbonate rock standards (e.g. NBS-18, NBS-19). Biogenic hydroxyapatites such as bone and tooth enamel contain only a small amount of carbonate (~5%) and could be influenced in different ways by the different protocols and equipment used in different laboratories. More work is needed to better control for the analysis of enamel, to regulate and standardise data from multiple laboratories. This is, however, beyond the scope of this study.

6.4.3 Strontium solution chemistry (ion exchange method)

Enamel samples for strontium isotope analysis were prepared for solution MC-ICP-MS following the methods detailed by Deniel and Pin (2001) with some modifications. The procedure took place in the clean laboratory and MC-ICP-MS facility at the MPI-EVA.

Clean enamel sub-samples (the remaining portion of the serial-samples; ~5mg or more) were weighed into microtubes. An additional cleaning step was carried out after samples had been taken from the sample preparation laboratory to a clean

laboratory at the Department of Human Evolution, MPI-EVA, Leipzig, Germany. The samples were rinsed three times with high-purity deionised (18.2MΩ) water (Milli-Q® Element A10 ultrapure water purification system, Millipore GmbH, Schwalbach, Germany). Samples were then rinsed with an ultrapure acetone (GR for analysis grade, ≥99.8%, Merck KGaA, Darmstadt, Germany). These were then dried overnight in a clean, closed environment under constant airflow.

Each enamel section was then weighed into clean 3ml Savillex™ beakers (Minnetonka, MN, USA) and dissolved in 1ml of 14.3M HNO_3 in closed vessels on a heater block (120°C). Samples were then evaporated to dryness. The resulting residue was dissolved in 1ml of 3M HNO_3 before being loaded into clean, pre-conditioned 2ml columns containing Sr-spec™ resin (EiChrom, Darien, IL, USA). Columns (with frits) had been stored in 6M HCl prior to use. Columns were then rinsed twice with Milli-Q® ultrapure water. Clean Sr-spec™ resin was then loaded into each column (approximately 0.5cm per column). Several column volumes of 3M HNO_3 were then passed through, pre-conditioning the columns and the resin. Resin had been cleaned prior to use (following Charlier et al. 2006). The resin had a bead-size of 50-100μm and was suspended in ultrapure deionised water after the cleaning process.

Samples were loaded into the pre-conditioned columns, passed through and recollected. During this process strontium from the sample adheres to the resin. This was repeated three times in order to maximise the amount of Sr obtained from the sample, although in-house experiments have since demonstrated that two repeats may be sufficient. After several washes with 3M HNO_3, strontium was then eluted from the resin in ultrapure deionised water and passed into clean Savillex™ beakers. Samples were dried down and then re-dissolved in 3% HNO_3, ready for MC-ICP-MS analysis. All acids used were made from SupraPur™ grade stock solutions (Merck KGaA) and diluted using ultrapure deionised water.

6.4.4 Strontium analysis: MC-ICP-MS

Strontium isotope data were produced using a Thermo Fisher Neptune™ (Thermo Fisher Scientific, Inc. Dreieich, Germany) MC-ICP-MS instrument at the MPI-EVA. Solutions were diluted in 3% HNO_3 to give ^{88}Sr signal intensities of 20-25V. Solutions were introduced into the plasma source using a 100µl/min self-aspirating capillary and Microflow PFA (perfluoroalkoxy) ST-nebuliser (Elemental Scientific Inc., Omaha, NE, USA). During analysis, baselines were established for 30s, followed by data collection in 50 cycles of 2 seconds. Corrections were made for interference from krypton (Kr) and rubidium (Rb) and normalised for instrumental mass bias to $^{88}Sr/^{86}Sr$ = 8.375209 (exponential law). Analysis of the international strontium isotope standard NIST SRM987 (National Institute of Standards and Technology, Gaithersburg, USA) during each analytical session was used for external normalisation of the data. The long-term $^{87}Sr/^{86}Sr$ value was 0.710273±0.000033 (46ppm, 2σ, *n*=97). All values of $^{87}Sr/^{86}Sr$ were then adjusted to SRM987 = 0.710240, a published TIMS $^{87}Sr/^{86}Sr$ value (Johnson et al. 1990; Terakado et al. 1988). The average internal error of any given measurement was 0.000006±0.0000004 (8ppm, 2σ, *n*=97). This typically involved a data correction factor of -0.00002. Strontium concentrations of the samples were also determined and were accurate to within ±31ppm (1σ, *n*=14) (Copeland et al. 2008a). Strontium concentrations for the modern fauna were comparable to published values from modern and archaeological fauna (Britton et al. 2009; Evans et al. 2007). Strontium concentrations and values in archaeological dentine can be expected to vary from enamel from the same teeth where diagenetic alteration has occurred (Budd et al. 2000; Hoppe et al. 2003; Montgomery 2002; Trickett et al. 2003), this is assessed in Chapter 8.5.2.

CHAPTER SEVEN RESULTS AND DISCUSSION

7.1 Introduction

This chapter will detail all isotopic results from the analysis of the modern materials. Given the volume of data and various levels of investigation (incorporating multiple species, herds, individuals, tissues and isotopes), results and data analysis will initially be divided by herd. A discussion of the data, on a herd by herd basis, will accompany the presentation and summary of results. The results of all analyses will then be discussed together with specific reference to the aims of this study and the implications of this research for the reconstruction of herbivore palaeoecology. All data tables can be found in the Appendix.

7.2 Western Arctic caribou, Alaska, USA[2]

The results of the isotopic measurements of enamel ($\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr/^{86}Sr$) from caribou of the Western Arctic herd are summarised in Table A.1 (see Appendix). Sequential strontium and oxygen isotope data from all five individuals are shown in Figures 7.1 and 7.2 respectively. Corresponding sequential carbon isotope data (enamel) are shown in Figure 7.3.

The results of the isotopic measurements of dentine ($\delta^{13}C$ and $\delta^{15}N$) from this herd are summarised below in Table A.2. These data is shown in Figures 7.5a-e for each individual. Data from the stable isotope analysis of bone ($\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$) from the same individuals are shown in Table A.3. These data are presented and discussed in Section 7.5, with the other caribou herds from which bone was obtained (George River and Leaf River herds).

[2] The data presented and analysed in this section, and the subsequent discussion, were published in a recent paper by the author. Britton K et al. (2009) Reconstructing faunal migrations using intra-tooth sampling and strontium and oxygen isotope analyses: a case study of modern caribou (*Rangifer tarandus granti*). *Journal of Archaeological Science,* 36**,** 1163-1172.

The total isotopic range for all intra-tooth data from this herd (all samples and all animals) was 0.7090-0.7129 ($^{87}Sr/^{86}Sr$), 12.8‰-18.5‰ ($\delta^{18}O_{V\text{-}SMOW}$) and -13.1‰ to -9.3‰ ($\delta^{13}C_{V\text{-}PDB}$) for enamel and -21.3‰ to -19.1‰ ($\delta^{13}C$) and 2.2‰-5.4‰ ($\delta^{15}N$) for dentinal collagen. Strontium concentrations range from 68ppm to 197ppm, with a mean of 124ppm, values which are comparable to published values from domestic herbivores (Evans et al. 2007). Whole bone collagen values from the same five individuals ranged from 2.6‰-9.0‰ ($\delta^{34}S$), -20.5‰ to -19.7‰ ($\delta^{13}C$) and 2.0‰-3.8‰ ($\delta^{15}N$).

7.2.1 Strontium

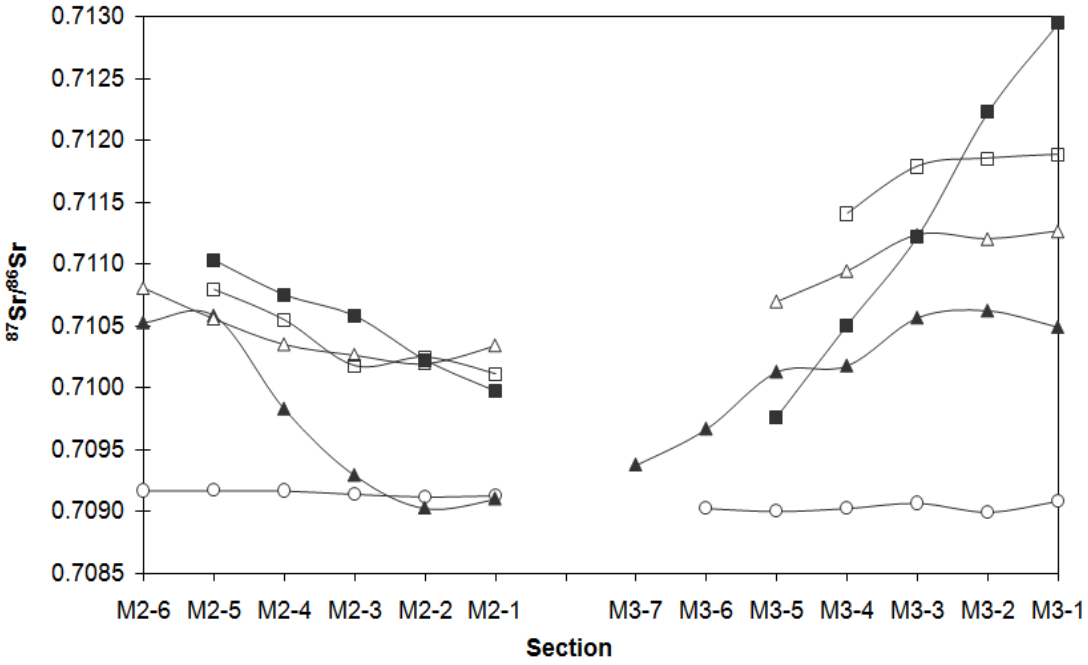


Figure 7.1 Plot of all strontium isotope data ($^{87}Sr/^{86}Sr$) from intra-tooth sections from M2 and M3 enamel of each of the five animals analysed from the Western Arctic caribou herd, Alaska. Open symbols are female (triangle = WACH-2.210, square = WACH-2000, circle = WACH-0120) and solid symbols are male (triangle = WACH-2.230, square = WACH-153.180) (e.g. Fizet et al. 1995).

With the exception of individual WACH-0.120, all individuals demonstrate intra-tooth strontium isotope ratio variation in the second or third decimal place. To allow the comparison of multiple individuals data have been aligned from the last-forming sections of each tooth (M2-1 and M3-1 respectively) (Figure 7.1). These portions are closest to the cemento-enamel junction (CEJ). The arrangement of data from occlusal surface to CEJ in both teeth allows the construction of an isotope profile through time, and allows multiple individuals to be compared. These four individuals display a similar overall trend in strontium isotope values – from more elevated values (0.7101±0.00007 (1σ) at point M2-5), to lower values (0.7099±0.0005 (1σ) at point M2-1) and a return to more elevated values (0.7108±0.0005 (1σ) at point M3-4 and 0.7116±0.0010 (1σ) at point M3-1) over a distance inferred to represent approximately one year of life (Brown and Chapman 1991a, 1991b). The intra-tooth (i.e. temporal) variation in strontium isotope ratios agrees with the herd's known patterns of movement in these individuals (WACH-2.210, -2000, -2.230 and -153.180) and the range of values observed in all specimens (0.7090–0.7129) is within the range of expected values for the region indicated from the literature (0.7079-0.7140; Keller et al. 2007; Moll-Stalcup and Arth 1991).

The inter-individual similarities in the earliest-forming portions of the M2 (e.g. point M2-5) indicate spatial proximity in the first few months of life. This likely corresponds with the latter phases of infancy on and around the calving grounds and the summer range. This philopatry is characteristic of many female caribou (Schaefer et al. 2000). However, by comparison, the intra-tooth strontium isotope profile of WACH-0.120 demonstrates very little variation, with a mean value of 0.7091±0.0001 (1σ) for all sections taken from both teeth (n=12). This appears to indicate that this individual, in contrast to other individuals, consumed an isotopically homogenous diet during M2 and M3 formation. Therefore, we can infer that this individual – unlike the others – remained on a geological homogenous area and did not undertake the same seasonal migration as other members of the herd. The $^{87}Sr/^{86}Sr$

values appear to indicate that the animal was born on less radiogenic soils – such as those found at the southern extent of the range – and not on the traditional Utukok Upland calving grounds at the northern extremes of the summer range. This individual then spent the duration of M2 and M3 formation on this less radiogenic geology or a similar one.

7.2.2 Oxygen

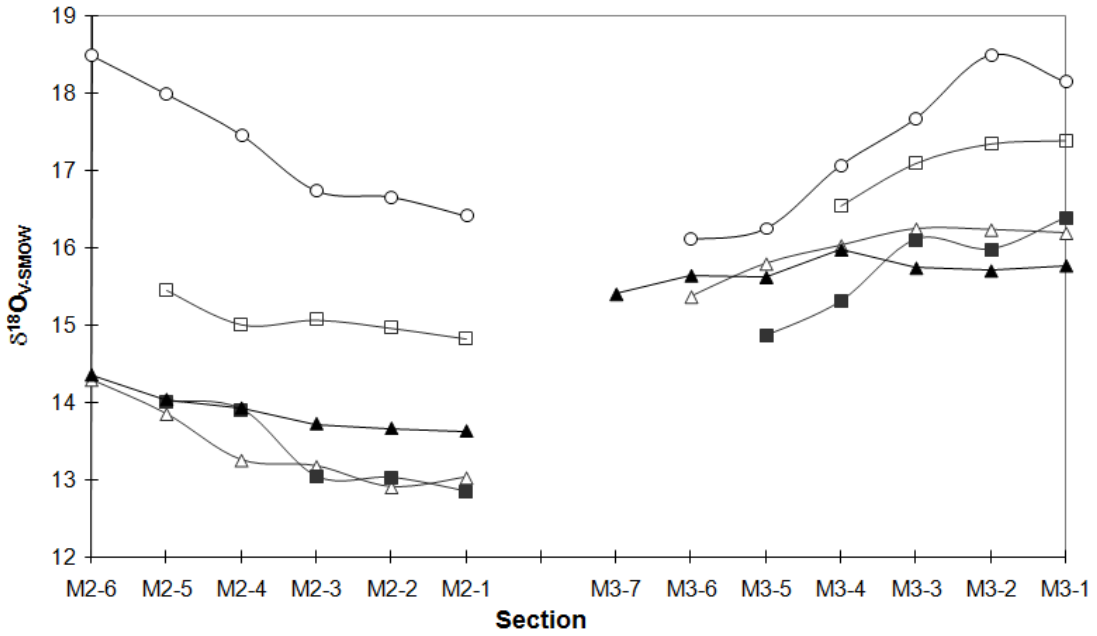


Figure 7.2 Plot of all oxygen isotope data ($\delta^{18}O_{V\text{-}SMOW}$) from intra-tooth sections from M2 and M3 enamel of each of the five animals analysed from the Western Arctic caribou herd, Alaska. Open symbols are female (triangle = WACH-2.210, square = WACH-2000, circle = WACH-0120) and solid symbols are male (triangle = WACH-2.230, square = WACH-153.180) (taken from Britton et al. 2009: 1168, Figure 2).

Oxygen values for the five individuals also display a similar trend through time, from higher values, to lower ones, before a return to higher $\delta^{18}O$ values (Figure 7.2). Given the periods of time involved, it is likely that these fluctuations are the product of seasonal variations during tooth enamel formation, with lower values corresponding to winter and higher values corresponding with summer. These trends are generally consistent with the interpolated water isotope data for these areas. However, some attenuation is clear. This dampening effect can be expected during intra-tooth isotope analysis and is thought to be a product of the various phases and directions

of mineralisation, combined with the direction and strategy of sampling, which can serve to homogenise these phases (and their potentially varied isotopic signals) (Balasse 2002; Kohn 1996; Kohn et al. 1996, 1998; Kohn 2004; Passey and Cerling 2002; Zazzo et al. 2005). Although some methods are in place to inversely model primary inputs and remove the effects of attenuation from intra-tooth isotope data (e.g. Passey et al. 2005), no such methods have been utilised to analyse data here unless otherwise specified.

Intra-tooth oxygen values in WACH-2.210, -2.230 and -153.180 are similar – in terms of overall trend and absolute values. These values vary from 14.0‰±0.4 (1σ) at point M2-5 to 13.2‰±0.4 (1σ) at point M2-1, to 15.8%±0.4 (1σ) at point M3-4 to 16.1‰±0.3 (1σ) at point M3-1. This indicates that these animals consumed water from similar sources during dental development, perhaps demonstrating that they were born during the same season and shared similar terrains throughout the year. The same trend is visible in individual WACH-2000, although the absolute values are slightly higher. This could be due to annual water fluxes in the local environment, or possibly due to small variations in dietary behaviour and the isotopic composition of food and water ingested. Such fluctuations can be common where environmental conditions are extreme (e.g. at the extreme northern latitudes of the Western Arctic herd range) (Ayliffe and Chivas 1990; Ayliffe et al. 1992; Cormie and Schwarcz 1996; Iacumin and Longinelli 2002; Kohn et al. 1998; Longinelli et al. 2003). All four individuals (WACH-2.-210, -2.230, -153.180 and -2000) appear to demonstrate a greater amount of oxygen isotope variation between teeth than within teeth. Given the similarities in strontium values in the latest forming portions of the M2, and the earliest forming enamel in the M3, it seems unlikely that this is due to a large amount of 'missing' isotopic data (due to wear or differences in the geometry of enamel apposition in the two teeth). It is suggested that the intra-tooth oxygen isotope variation here is due to the mixed influence of overall seasonal isotopic changes in meteoric water across the study area; the differences between the summer and winter

ranges; the rate with which these seasonal/geographical variations occur and the rate with which the animals move during enamel formation. As described above, some attenuation or signal 'dampening' can be expected in such intra-tooth approaches and this has previously been attributed to species-specific physiological and metabolic influences (Fricke et al. 1998b; Kohn 1996; Kohn et al. 1996); mineralisation rates and phasing (Balasse 2002; Passey and Cerling 2002; Zazzo et al. 2005, 2006); and sampling strategy (Hoppe et al. 2004b; Zazzo et al. 2005, 2006). Here, it is proposed that an additional factor could be influencing the oxygen isotope values observed in the teeth. It is suggested that the rapid, seasonal migratory behaviour of the animals themselves may produce this further dampening. This herd originates from an area of extreme northern latitude and seasonality, and these individuals undertake the most extensive seasonal migrations of any of the herds under analysis in this study (~1500km bi-annually on a roughly north-south trajectory). These caribou are true thermostressed migrants, and this long-distance migration allows them to escape climatic extremes at either end of the range, the movement itself ensuring a greater continuity of external conditions in an area of hyper-seasonality. This trend is not seen in all of the caribou herds under analysis here (see below) and is therefore unlikely to be a product of caribou development, morphology, physiology or the sampling/analytical techniques used here.

As with the strontium isotope profile, a different trend in oxygen isotope ratios is observed in WACH-0.120 throughout tooth formation. This individual demonstrates greater intra-tooth variation than the other animals (18.5‰ to 16.4‰ in the M2 and 16.1‰ to 18.2‰ in the M3). Values fluctuate gradually throughout both teeth, with summer peaks and winter troughs, demonstrating both the seasonality of birth and also the period of growth in question. Values in the latter forming parts of the M2 and earliest forming parts of the M3 have similar values (16.4‰ and 16.1‰ respectively), indicating an isotopically homogenous source of drinking water during this period and therefore the lack of any significant

movement. Therefore both the strontium and oxygen evidence indicate that this animal, although born in the spring/summer, was not born on the herd's calving grounds of the North. Furthermore, it appeared to spend the duration of the first winter and following summer of life on isotopically similar terrain. These less radiogenic strontium values better correlate with values measured in geological samples from the southern extent of the range (Moll-Stalcup and Arth 1989, 1991), as well as with the 'winter' values observed in the other caribou. Interestingly, all $\delta^{18}O$ values measured in this individual are higher than the rest of the Western Arctic herd. This could further support the suggestion that this animal was born in the southern extent of the range and spent the duration of (at least) the first year and a half of life sedentary in this area. Several scenarios could explain these values. For example, it could be possible that a pregnant female did not migrate north to the calving grounds and instead gave birth in the winter range – its offspring then also choosing again not to migrate the following year. Although behavioural outliers have been noted in some wild herbivore populations (e.g. Hoppe 2006b; Hughes 2003) such variation across successive generations does not seem likely. A scenario that may be far more likely is that WACH-0.120 is a reindeer (*R. tarandus tarandus*). Domesticated reindeer have been managed for over 100 years in the Seward Peninsula. Over the last few decades, productive lichen tracts have attracted wild caribou, causing the Western Arctic herd to expand and shift their winter range onto the eastern half of the Seward Peninsula and the reindeer range (Finstad et al. 2002). The shorter-limbed, slower moving reindeer are bred to be sedentary and to group when frightened. However, when interacting with caribou, reindeer become difficult to control, can quickly disperse and even migrate far from their ranges, joining wild caribou herds. Since 1990 two-thirds of reindeer herds on the Seward Peninsula have lost more than half of their herds to the caribou through emigration or through the associated wolf predation (Dau 2000; Finstad and Prichard 2000; Klein 1980). It is suggested that WACH-0.120 is one such individual. Unfortunately, given the skeletal components available (mandibles and cheek-teeth) sub-species determination using

traditional morphological analysis is not possible. Furthermore, sub-species identification through microsatellite DNA analysis (e.g. Cronin et al. 2003) is beyond the scope of this study. However, the data from the sulphur isotope analysis of the bone collagen of this individual (see below, Chapter 8.5) also gives support to this premise. WACH-0.120 had a $\delta^{34}S$ value of 9.0‰, which is much higher than the other members of the herd (mean = 3.37‰±0.96, n=4, 1σ). This value indicates that WACH-0.120 spent the majority of its life feeding on soils in a different geographical area.

7.2.3 Carbon (carbonate)

Intra-tooth carbon isotope data from sequentially-sampled enamel from the five individuals display a similar overall trend – from lower $\delta^{13}C$ values, to higher ones, before a return to lower values. Absolute values at any given point display a fairly large degree of inter-individual variation (e.g. more >2‰ at point M3-6) (Figure

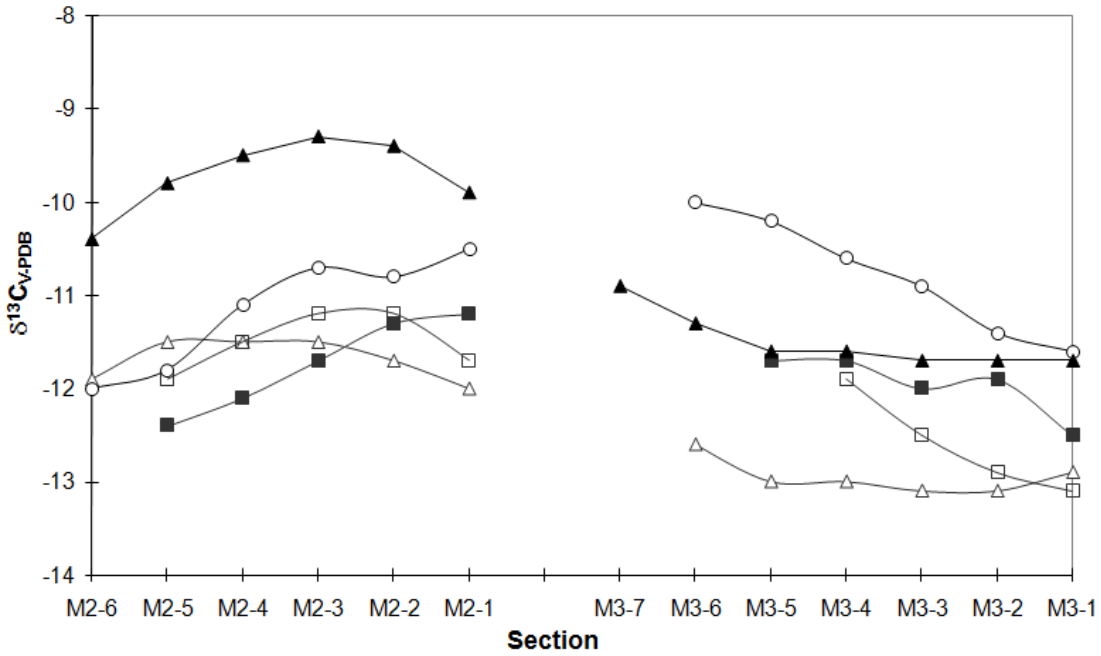


Figure 7.3 Plot of all carbon isotope data ($\delta^{13}C_{V\text{-}PDB}$) from intra-tooth sections from M2 and M3 enamel of each of the five animals analysed from the Western Arctic caribou herd, Alaska.

Open symbols are female (triangle = WACH-2.210, square = WACH-2000, circle = WACH-0120) and solid symbols are male (triangle = WACH-2.230, square = WACH-153.180).

7.3).

Carbon isotope values in tooth enamel should reflect the carbon isotopic composition of the whole diet. Unlike the production of proteins, there should be little metabolic delay or diet-tissue turnover time with the biological synthesis of apatites. The same is true of strontium and oxygen ingested from food and water. The highest $\delta^{13}C$ values occur at the same intra-tooth points as the lowest oxygen and strontium values (see Figures 8.2 and 8.1 above respectively), indicating that this ^{13}C-enrichment is coinciding with the cool season on less radiogenic winter range at the southern extent of the range. Given that carbon isotope ratios in tissues will reflect those of plants consumed, it is clear that there is a seasonal shift in the carbon isotope composition of the diet. There are several possible explanations for this – the change of location, seasonal variations in the isotopic composition of growing plants and the consumption of a seasonally-variable diet. The first explanation is possible as these caribou are migratory (occupying distinct and geographically-distant seasonal ranges) and geographical 'baseline' changes in the isotopic composition of plants and soils have been noted in purely-C_3 environments (e.g. Jay 1999; van Klinken et al. 2000). Furthermore, intra-annual carbon isotope variations have also been measured in plants, both at the same location and even of the same species (Heaton 1999; O'Leary 1981; O'Leary 1995). These seasonal changes in apatite carbon isotope values could also be due to a change in foraging behaviour during winter such as the consumption of lichen and mushrooms. These caribou – like other herds – are known to have seasonally variable diets, including large volumes of lichen in winter. These plants (especially lichens) are enriched in ^{13}C compared to other C_3 plants and the consumption of these winter forage foods likely accounts for the less negative $\delta^{13}C$ values exhibited seasonally.

7.2.4 Carbon and Nitrogen (dentinal collagen)

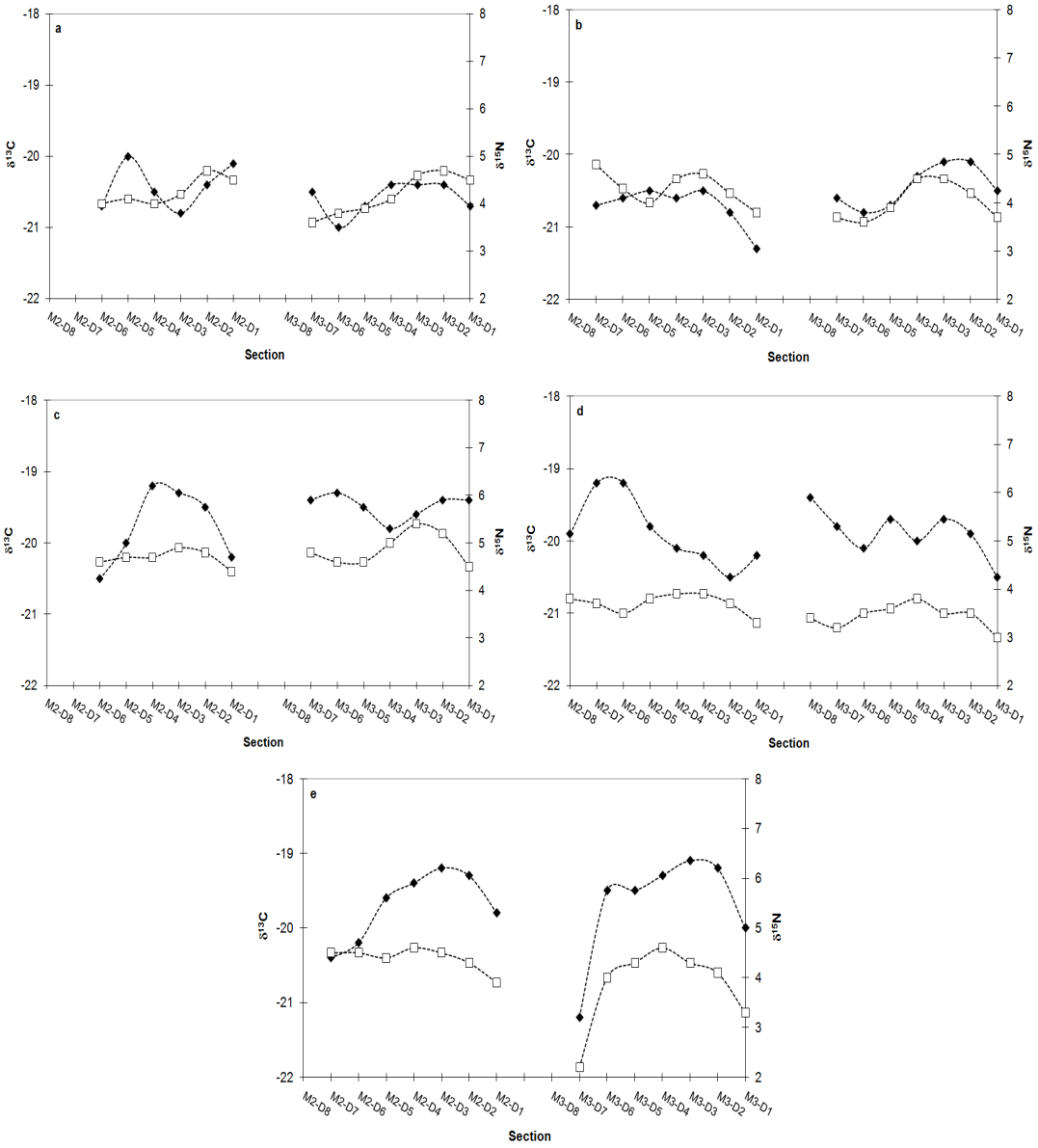


Figure 7.4 $\delta^{13}C$ and $\delta^{15}N$ values from collagen from sequentially sampled dentine from individuals of the Western Arctic caribou herd, Alaska.

(a= WACH-2.210, b= WACH-2000, c= WACH-0.120, d= WACH-2.230, e= WACH-153.180). Solid diamonds = carbon, open squares = nitrogen.

Isotope analysis of sequentially-sampled dentinal collagen revealed variations in the carbon and nitrogen isotope ratio throughout tooth formation of both the second and third molars (Figure 7.4). Dentine growth in these two teeth may represent approximately 8 or 9 months in each case, with little isotopic overlap expected

between the two teeth given that the crown of the third molar only commences growth when root formation is completing in the second.

Carbon isotope values vary by as much as 1.3‰ within a single tooth. Corresponding $\delta^{15}N$ values can vary by more than 2.5‰ within individual teeth. In some instances intra-tooth trends in $\delta^{13}C$ and $\delta^{15}N$ appear to co-vary and in some individuals these changes appear to follow a reoccurring pattern (such as in Fig. 8.4a, b, e). These variations are well above the variation expected from analytical error (<0.2‰), and such changes are due to changes in the isotopic composition of the diet. As described above, such dietary changes in a herbivore such as caribou could be due to a change in the composition of the diet (i.e. in the types of plant foods consumed), a change in the isotopic composition of the plants themselves (due to local seasonal, climatic or ecosystem-level changes) or a change in location of the animal. In the case of nitrogen, a change in diet (i.e. in the protein composition, quality or scarcity of food), is also thought to induce a physiological response in the animal (Caloin 2004; Sponheimer et al. 2003b), enriching growing tissues in ^{15}N. Seasonal dietary and physiological changes are known to occur in many caribou populations, including the Western Arctic herd. This has been demonstrated both through observational feeding ecology studies, and in previous isotope studies of both rumen contents (McLeman 2006) and blood (Ben-David et al. 2001) of caribou. Carbon and nitrogen variations between collagen taken from two adjacent portions of root dentine have also previously been identified and have been attributed to the seasonally-varied quantity of lichen in the diet and also to the physiological responses of the animals to a low-protein diet and seasonal semi-starvation in winter (Drucker et al. 2001).

Unlike the $\delta^{13}C$ variations demonstrated in the sequentially-sampled enamel, isotopic changes in the dentine (expressing isotopic changes in the diet) are subject to temporal delays due to metabolic processes. This metabolic pool effect – due to the process of protein breakdown and synthesis, the incorporation of material from old

tissues and stored metabolites – has been well-characterised. A period where tissues are synthesised including old and new isotopic inputs, precedes the reaching of an equilibrium point where the new diet is fully expressed in tissues. This period may be between 8 and 12 weeks, or more, depending on the tissue in question. A reduction in the protein quantity of the diet, and the physiological effect of body tissues wasting, may also influence and complicate this process. Therefore, changes in the isotopic inputs of these caribou will not be reflected immediately in growing tissues. Given that dietary changes, along with changes in location and (potentially) also physiology, are known to occur seasonally, equilibrium points are unlikely to be reached before another input change occurs. This may complicate interpretations of these dietary changes from dentinal collagen, serving to homogenise isotopic signals and dampen 'end-point' signals.

7.3 Leaf River caribou, Québec/Labrador, Canada

The results of the isotopic measurements of enamel ($\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr/^{86}Sr$) from the three individuals of the Leaf River caribou herd included in this study are summarised in Table A.4. Intra-tooth strontium, oxygen and carbon (enamel) data from this herd are shown in Figs. 7.5, 7.6 and 7.7 respectively. The results of the isotopic measurements of dentine ($\delta^{13}C$ and $\delta^{15}N$) from the same individuals are summarised in Table A.5 and shown in Fig. 7.8 (carbon) and Fig. 7.9 (nitrogen). Data from the stable isotope analysis of bone ($\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$) from all ten individuals from this herd are shown in Table A.6, and discussed below in Section 7.5 with the bone collagen samples from the other caribou herds.

The total isotopic range for all intra-tooth data from this herd was 0.7259-0.7377 ($^{87}Sr/^{86}Sr$), 12.9‰-16.7‰ ($\delta^{18}O_{V\text{-}SMOW}$) and -13.0‰ to -10.9‰ ($\delta^{13}C_{V\text{-}PDB}$) for enamel, and -21.4‰ to -18.9‰ ($\delta^{13}C$) and 2.7‰-6.1‰ ($\delta^{15}N$) for dentinal collagen. Strontium concentrations range from 24ppm to 196ppm, with a mean of 129ppm.

Whole bone collagen was analysed from 10 individuals in this herd, and data ranged from 7.2‰-8.3‰ ($\delta^{34}S$), -20.1‰ to -19.6‰ ($\delta^{13}C$) and 2.6‰-4.0‰ ($\delta^{15}N$).

7.3.1 Strontium

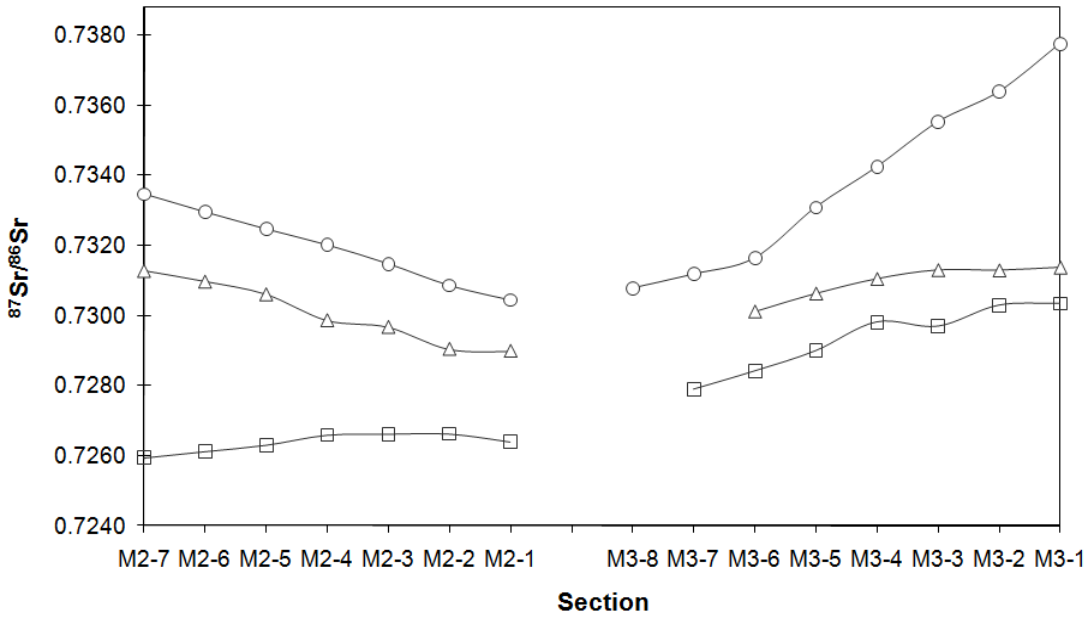


Figure 7.5 Plot of all strontium isotope data ($^{87}Sr/^{86}Sr$) from intra-tooth sections from M2 and M3 enamel of each of the three animals analysed from the Leaf River caribou herd, Canada.
All samples were female (triangle = AFR-1, square = AFR-6, circle = AFR-10).

The high strontium isotope values displayed in these three individuals are consistent with life on the extremely old geologies in this part of Canada. The ancient Archean and Paleoproterozoic rocks in this area are very radiogenic and this is reflected in the high $^{87}Sr/^{86}Sr$ values measured in the enamel of these caribou (*Rangifer tarandus caribou*). There is a similar overall trend in the intra-tooth strontium isotopic values of the three individuals sampled from the Leaf River caribou herd (Figure 7.5). These fluctuate from more elevated values at point M2-7, to lower values at point M2-1 and a return to more elevated values at point M3-1, during the first year of life. This variation broadly agrees with the herd's known pattern of movement, with some of the oldest Archaen and Meso-Archean geologies found at the north of the range incorporated into portions of the calving ground, and more of the younger Neo-Archean geologies found in the south, in the migratory and winter ranges. The

similar overall trend demonstrated between individuals is most likely indicative of the high level of philopatry, stability and fidelity of migratory behaviour in this herd as a whole. However, despite similar patterns, there is a large variation in absolute values exhibited. For example, the total amount of inter-individual variation at point M2-7 is 0.0076 (mean=0.7302, 1σ=0.0039). Other portions of the teeth also display such large amounts of variation (e.g. at points M3-2 and M3-1). These portions of teeth correspond with periods of time spent on the more variable geologies of the calving ground/summer range, perhaps reflecting natural geological variation in the area and the spatial distribution of this huge herd. A lower amount of inter-individual variations is displayed when the strontium isotope values are the lowest, formed during the periods in the south on the less radiogenic (and less variable) winter range. For example, at point M2-1 the variation between individuals is 0.0040 (mean=0.7286, 1σ=0.0020).

7.3.2 Oxygen

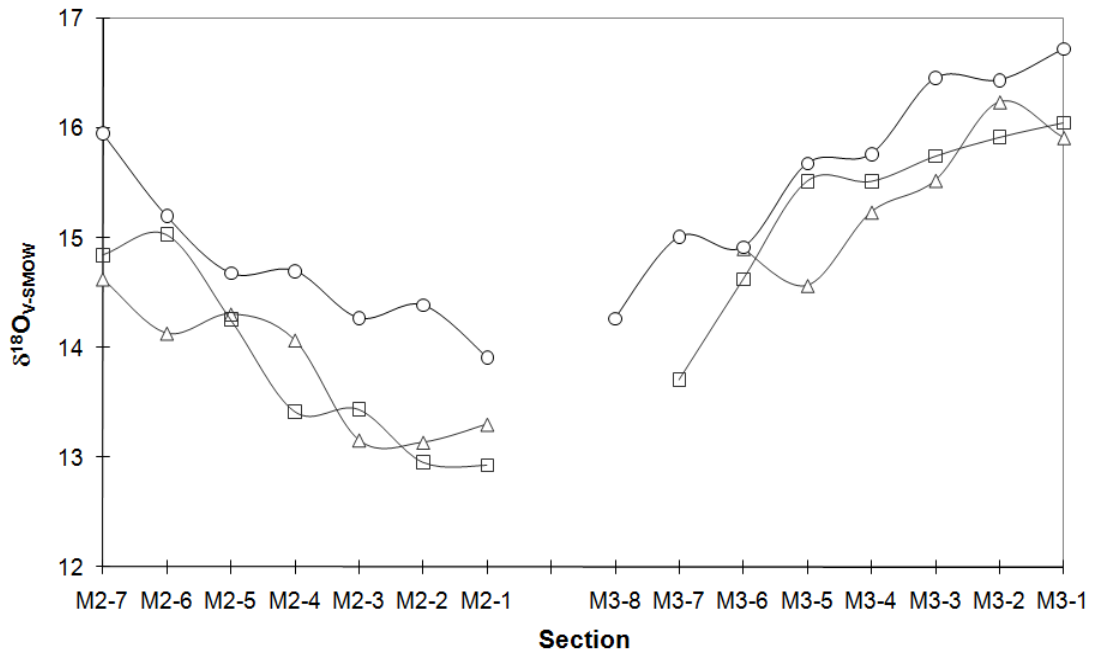


Figure 7.6 Plot of all oxygen isotope data ($\delta^{18}O_{V\text{-}SMOW}$) from intra-tooth sections from M2 and M3 enamel of each of the three animals analysed from the Leaf River caribou herd, Canada.
Triangle = AFR-1, square = AFR-6, circle = AFR-10.

Oxygen values for the three individuals sampled from the Leaf River herd display very similar trends in $\delta^{18}O$ values through time, from higher values, to lower ones, before a return to higher values (Figure 7.6). These values vary from 14.4‰±0.2 (1σ) at point M2-5 to 13.4‰±0.5 (1σ) at point M2-1, to 15.5%±0.3 (1σ) at point M3-4 to 16.2‰±0.4 (1σ) at point M3-1. The inter-individual homogeneity is indicative of shared water sources throughout the enamel formation/the first year of life. These animals were all killed at the same time and were all prime age individuals and may even represent the same birth cohort.

The intra-tooth fluctuations in oxygen isotope ratio are the product of seasonal variations during tooth enamel formation. Interpolated data from this area of Quebec and the Ungava Peninsula indicated substantial seasonal oxygen isotope variation, with winter values at the southern end of the range more than 9‰ lower than summer values at the northern extent of the range. These seasonal variations, even taking the change of location into account, are extreme. This is reflected in the intra-tooth variation. Here, despite the north-south migration, extensive seasonal extremes are still experienced by the caribou and this is apparent in the intra-tooth oxygen isotope data.

7.3.3 Carbon (carbonate)

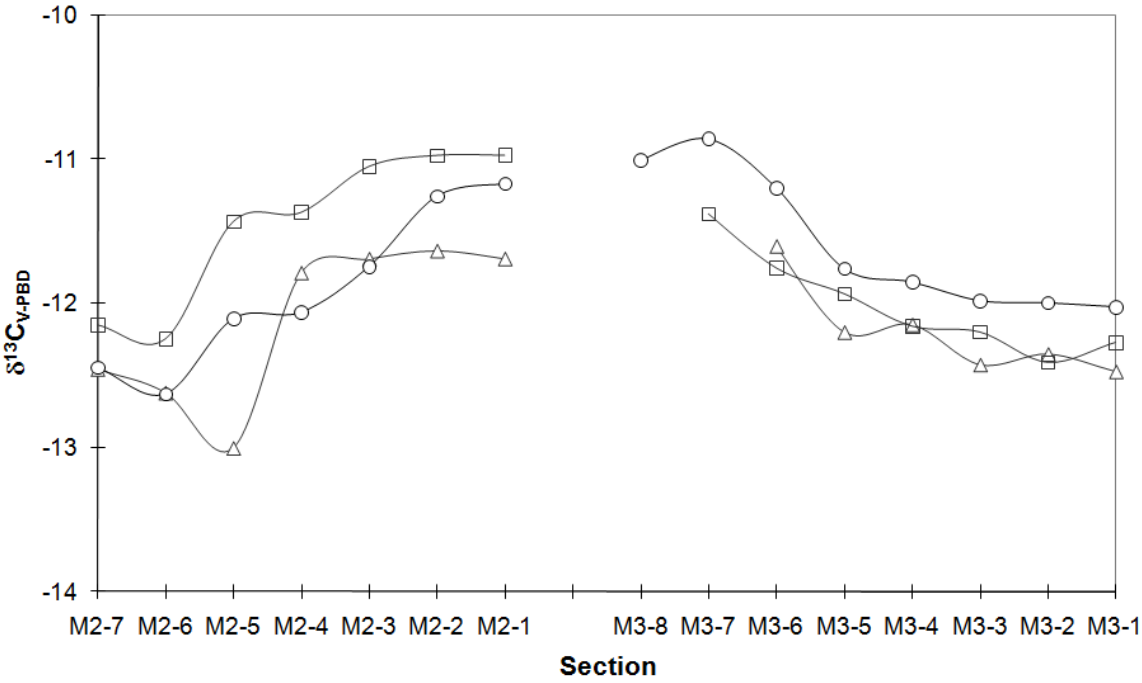


Figure 7.7 Plot of all carbon isotope data ($\delta 13C_{V\text{-}PDB}$) from intra-tooth sections from M2 and M3 enamel of each of the three animals analysed from the Leaf River caribou herd, Canada.
Triangle = AFR-1, square = AFR-6, circle = AFR-10.

The intra-tooth carbon isotope data from sequentially-sampled enamel from the three individuals of this herd display a similar overall trend – from lower $\delta^{13}C$ values, to higher ones, before a return to lower values (Figure 7.7). As with the Western Arctic herd, this coincides with seasonal changes in oxygen isotope values. The prevalence of this trend in both herds, appears to confirm an overall seasonal influence – either due to natural variability in plant tissues throughout the year or seasonal dietary variations (i.e. winter lichen consumption). The similar patterns observed in this herd and the Western Arctic herd allows us to disregard the theory of this shift being the product of geographical baseline shifts as these would be unlikely to follow exactly the same trend in Alaska and Western Canada. Data from the George River herd (discussed below), which do not undertake a clear north-south migration, also indicate that this effect is not likely to be the result of a geographical/latitudinal baseline shift in plant values.

7.3.4 Carbon and nitrogen (dentinal collagen)

As with the Western Arctic herd, there are clear variations in intra-tooth dentinal carbon and nitrogen isotope values. These may correlate with the winter consumption of low-protein, ^{13}C-enriched lichen and the wasting of body tissue during the winter months. In the Leaf River individuals, fluctuations in carbon and nitrogen appear to co-vary and there is a high degree of homogeneity. This is likely the product of similar foraging histories in contemporary individuals. Again, the complications of the metabolic lag during protein cycling and tissue synthesis (described above in Chapter 7.2.4) must be considered when interpreting these data. However, the clear fluctuations and repeat patterns appear to isotopically confirm known seasonal dietary shifts (Figures 7.8 and 7.9). This indicates the potential for this approach to recognise seasonal foraging patterns in archaeological species.

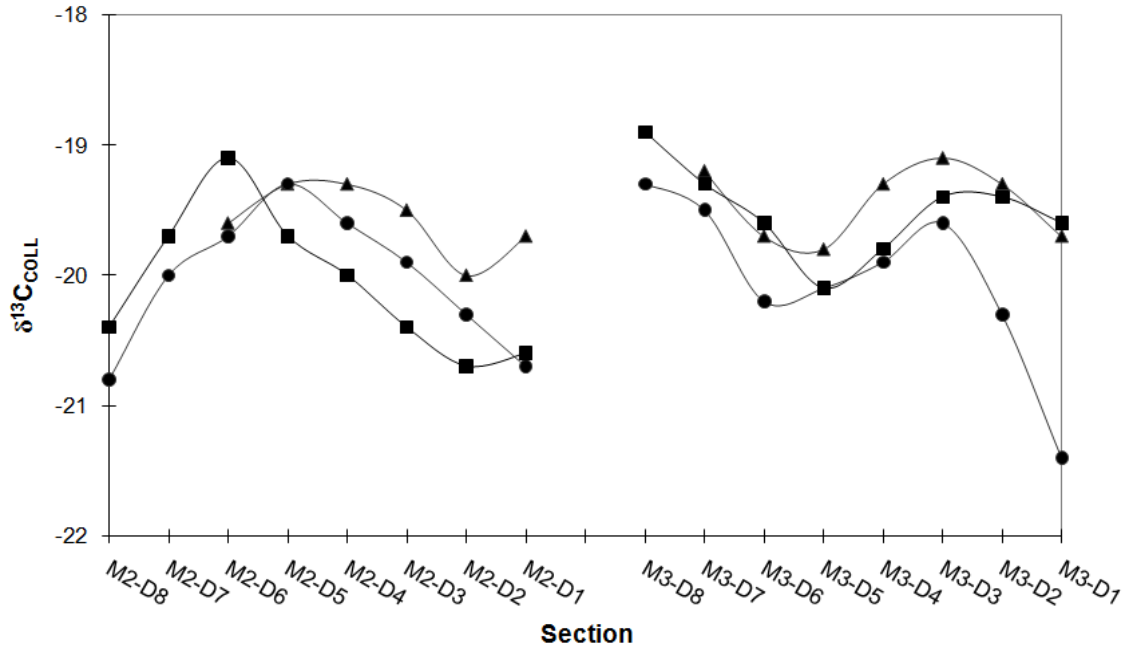


Figure 7.9 Carbon isotope values ($\delta^{13}C$) values from collagen from sequentially sampled dentine from individuals of the Leaf River caribou herd, Canada.

Triangle = AFR-1, square = AFR-6, circle = AFR-10.

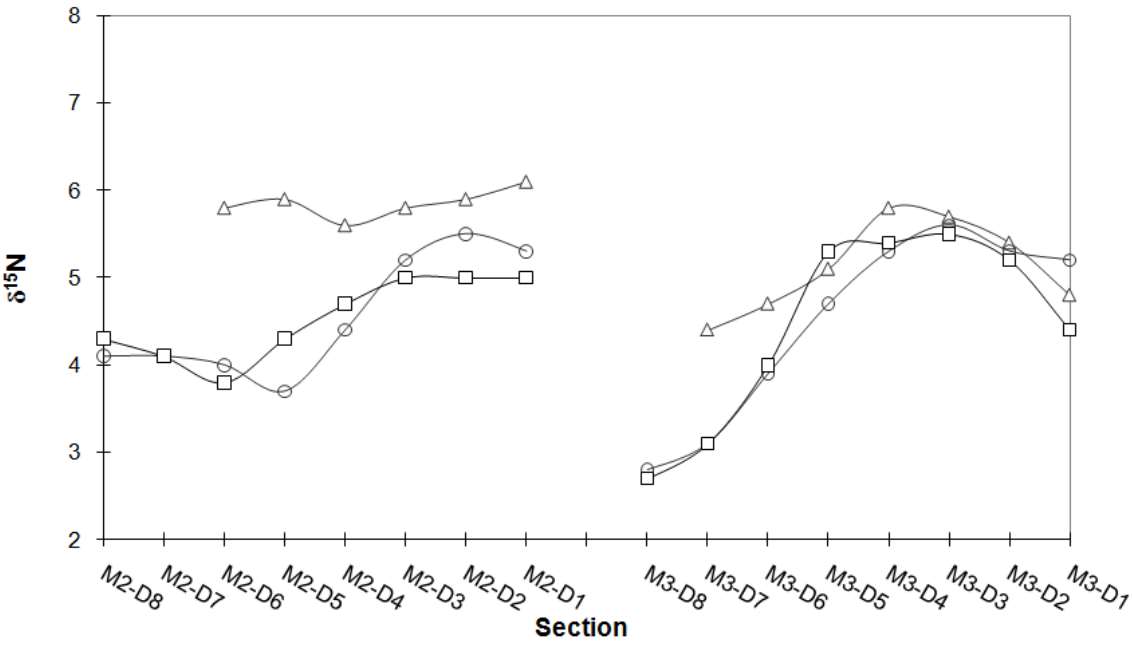


Figure 7.8 Nitrogen isotope values ($\delta^{15}N$) values from collagen from sequentially sampled dentine from individuals of the Leaf River caribou herd, Canada.

Triangle = AFR-1, square = AFR-6, circle = AFR-10.

7.4 George River caribou, Québec/Labrador, Canada

The results of the isotopic measurements of enamel ($\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr/^{86}Sr$) from the three individuals of the George River caribou herd included in this study are summarised in Table A.7. These data are also shown in Figures 7.10 (strontium), 7.11 (oxygen) and 7.12 (carbon). The results of the isotopic measurements of dentine ($\delta^{13}C$ and $\delta^{15}N$) from the same individuals are summarised in Table A.8, and shown in Fig.7.13 and Fig.7.14 respectively. Data from the stable isotope analysis of bone ($\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$) from all ten individuals from this herd are shown in Table A.9 and discussed in Chapter 7.5.

The total isotopic range for all intra-tooth data from this herd was 0.7178-0.7328 ($^{87}Sr/^{86}Sr$), 10.5‰-17.3‰ ($\delta^{18}O_{V\text{-}SMOW}$) and -12.9‰ to -9.8‰ ($\delta^{13}C_{V\text{-}PDB}$) for enamel, and -20.8‰ to -19.0‰ ($\delta^{13}C$) and 2.2‰-6.0‰ ($\delta^{15}N$) for dentinal collagen. Strontium concentrations range from 73ppm to 273ppm, with a mean of 193ppm. Whole bone collagen was analysed from 10 individuals in this herd, and data ranged from 6.0‰-8.0‰ ($\delta^{34}S$), -20.5‰ to -19.6‰ ($\delta^{13}C$) and 2.5‰-3.2‰ ($\delta^{15}N$).

7.4.1 Strontium

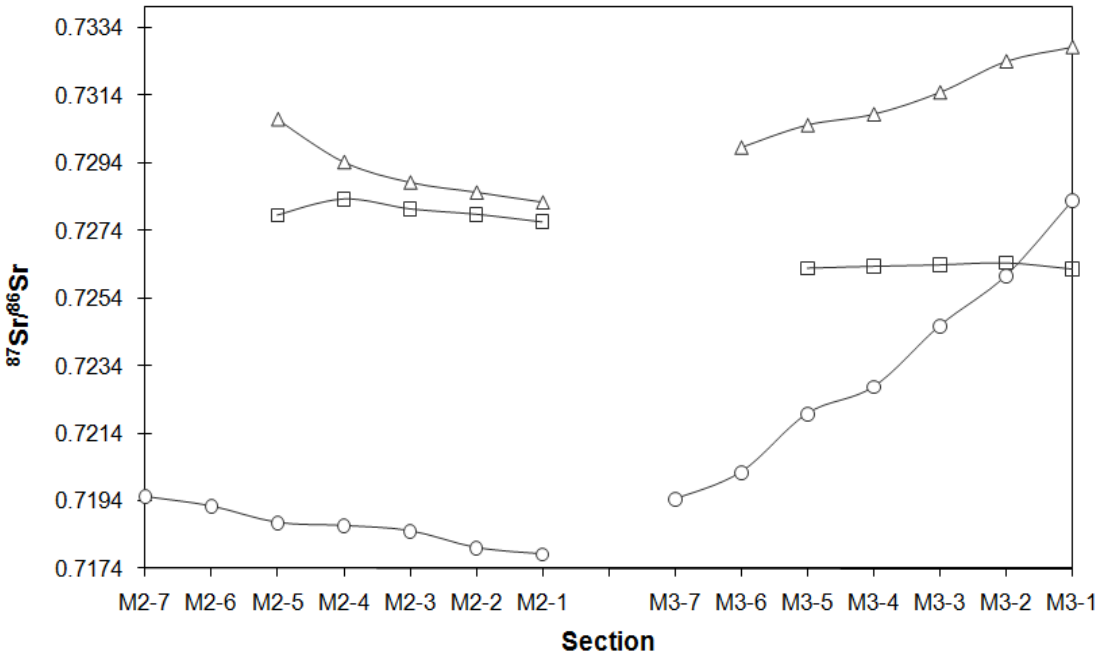


Figure 7.10 Plot of all strontium isotope data ($^{87}Sr/^{86}Sr$) from intra-tooth sections from M2 and M3 enamel of each of the three animals analysed from the George River caribou herd, Canada.

All samples were female (triangle = GR-3, square = GR-8, circle = GR-16).

There is a large amount of variation within the teeth of these individuals and between these individuals, both in terms of absolute values and overall trend (Figure 7.10). The high strontium isotope values largely reflect the very old, radiogenic rocks in the area, with lower values reflecting the inclusion of some younger rocks at the far west of the range. Unlike the Western Arctic and the Leaf River herds, there is little similarity between individuals. The relative instability of migratory behaviour in this population could account for this heterogeneity. Furthermore, given that isotope strontium isotope ratios are geologically- (and therefore spatially-) dependent, this variation may also be due to the varied geology of this large area of more than 900,000km^2 (Schmelzer and Otto 2003).

7.4.2 Oxygen

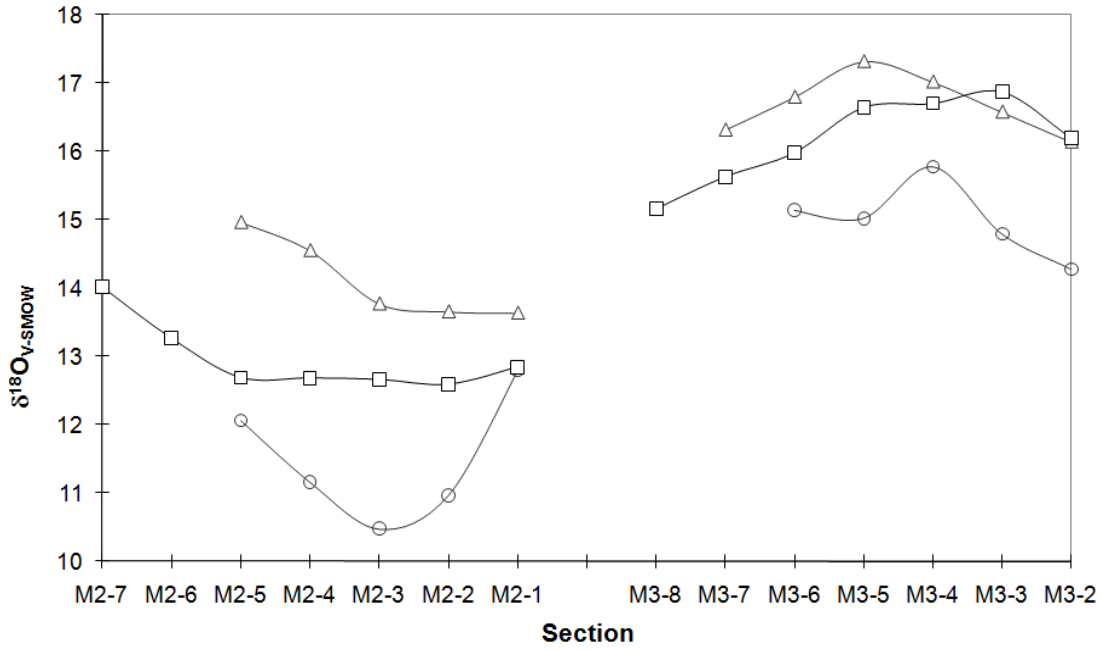


Figure 7.11 Plot of all oxygen isotope data ($\delta^{18}O_{V\text{-}SMOW}$) from intra-tooth sections from M2 and M3 enamel of each of the three animals analysed from the George River caribou herd, Canada.
Triangle = GR-3, square = GR-8, circle = GR-16.

As with the Western Arctic herd, and the Leaf River herd, intra-tooth variations in oxygen isotope composition are clear throughout tooth formation, reflecting the season of formation. As with the other herds, the same broad trend between all individuals is evident (Figure 7.11). However, a higher amount of inter-individual heterogeneity can be observed in this herd compared to the Leaf River herd, possibly reflecting the different water sources or the large geographical spaces between members of the herd. Given that all individuals were roughly the same age and killed at the same time, this is unlikely to reflect extensive intra-annual fluctuations but is more likely due to the more erratic and unstable behaviour of this herd in recent years, and the consuming of local waters from different portions of the large range.

7.4.3 Carbon (carbonate)

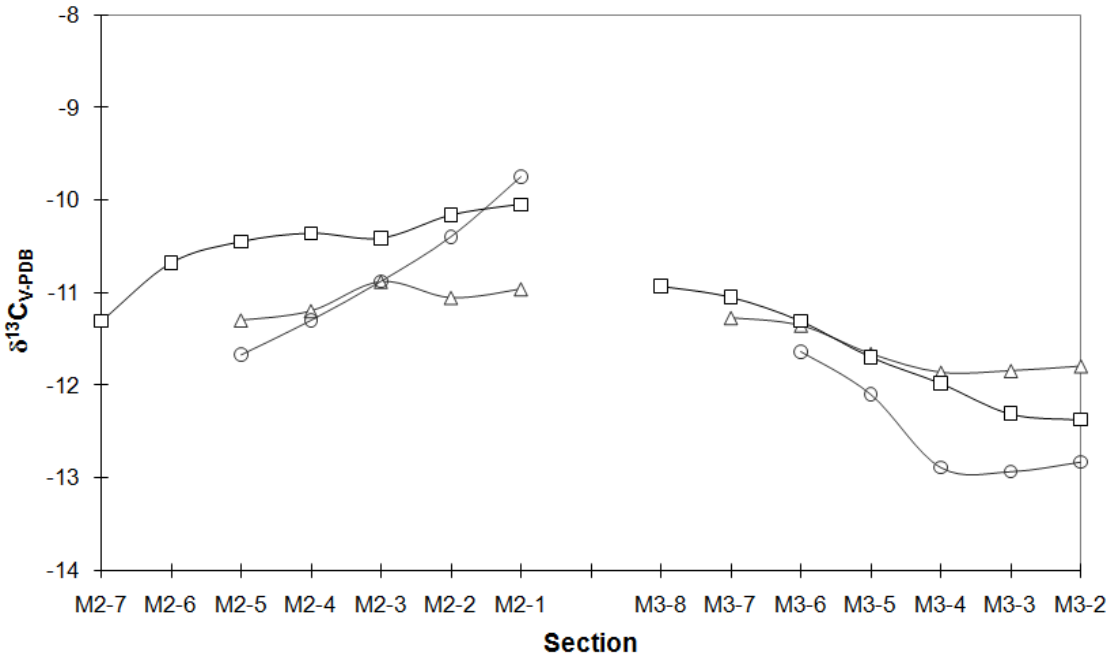


Figure 7.12 Plot of all carbon isotope data ($\delta^{13}C_{V\text{-}PDB}$) from intra-tooth sections from M2 and M3 enamel of each of the three animals analysed from the George River caribou herd, Canada.

Triangle = GR-3, square = GR-8, circle = GR-16.

The carbonate data from the three individuals demonstrates the same trend seen amongst individuals from the other herds, from lower $\delta^{13}C$ values, to higher ones, to lower values (Figure 7.12). As with the other herds, this correlates with changes in oxygen isotope values during tooth formation and appears to be seasonal. Given the evidence (both documentary and isotopic) for the varied biogeography of individuals in this herd, this homogeneity must be due to similar isotopic inputs and not the product of spatial proximity/geographical influences. Therefore, this intra-annual variation in ^{13}C-enrichment is either due to natural intra-annual variations in all plant life or due to the seasonal consumption of isotopically different plant foods.

7.4.4 *Carbon and nitrogen (dentinal collagen)*

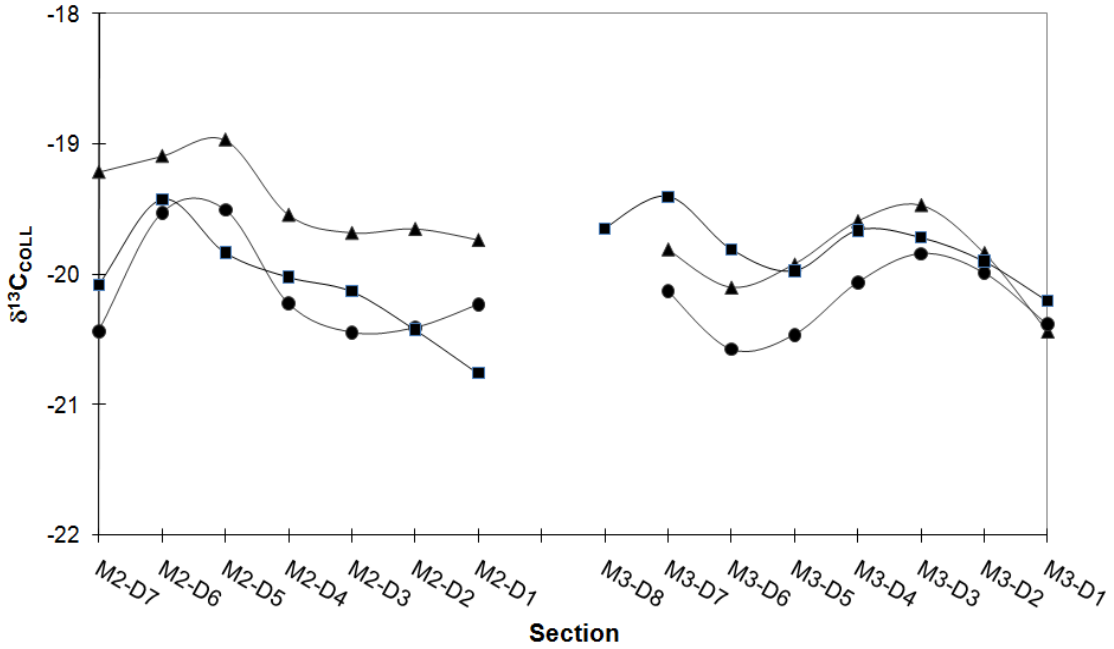


Figure 7.13 Carbon isotope values ($\delta^{13}C$) values from collagen from sequentially sampled dentine from individuals of the George River caribou herd, Canada.

Triangle = GR-3, square = GR8, circle = GR-16.

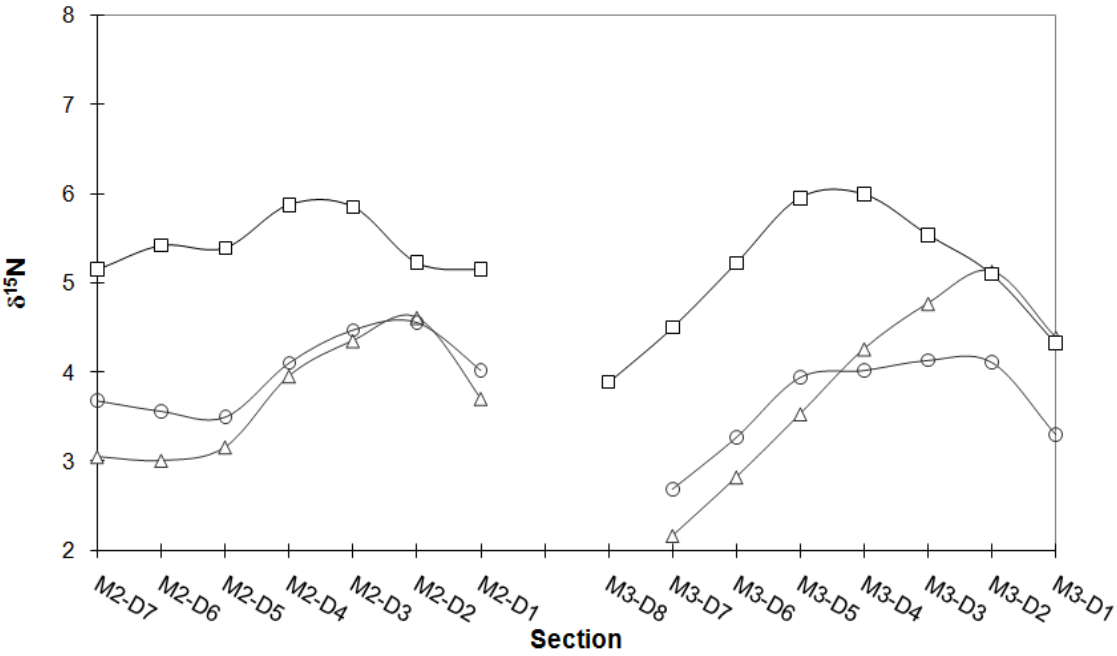


Figure 7.14 Nitrogen isotope values ($\delta^{15}N$) values from collagen from sequentially sampled dentine from individuals of the George River caribou herd, Canada.

Triangle = GR-3, square = GR-8, circle = GR-16.

As with the Leaf River herd, there are intra-tooth variations in the carbon and nitrogen isotopic composition of dentinal collagen amongst members of the George River caribou (Figure 7.13 and 7.14 respectively). Variations of as much as ~3‰ in $\delta^{15}N$ and ~1.5‰ in $\delta^{13}C$ can be observed in individual teeth. As with the carbonate carbon isotope values, the nitrogen and carbon isotope profiles amongst all three individuals demonstrate the same overall trend. Given the low fidelity to migratory route in this herd, confirmed by documentary evidence and by strontium isotope analysis, it seems unlikely that this variation is due to geographical/baseline variations. As with the Leaf River herd and the Western Arctic herd, this is most likely due to shared dietary history (i.e. the seasonal consumption of low-protein, ^{13}C-enriched lichens) or landscape-level changes in isotope chemistry of all plants. Relatively large carbon and nitrogen fluctuations were also observed in the other herds (from Alaska and Canada), and seem to confirm the isotopic-identification of seasonal foraging habits.

7.5 *Rangifer*: whole bone collagen (carbon, nitrogen and sulphur)

In addition to the dental tissues, whole bone was also sampled from the same three caribou herds (for data see Tables A.3, A.6 and A.9 in Appendix). These included a total of ten individuals from the Leaf River and George River herds, and five individuals from the Western Arctic herd. Bulk bone collagen was extracted and $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ values were determined (Figures 7.15 and 7.16).

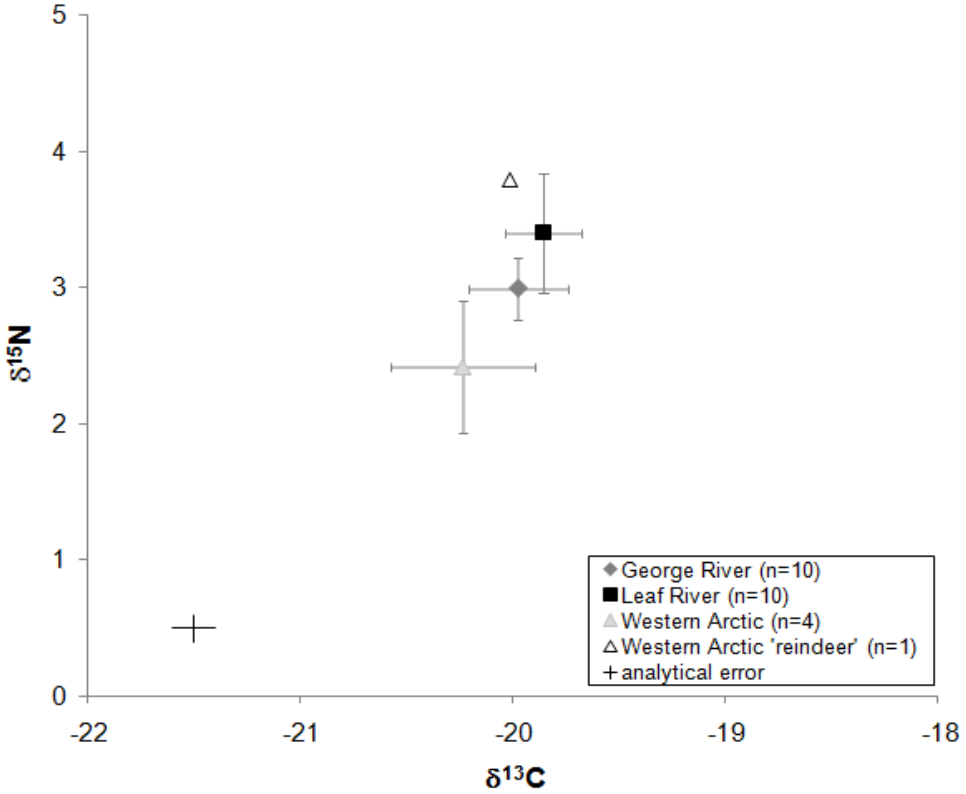


Figure 7.15 Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope data from bone collagen from the George River, Leaf River and Western Arctic herds. Analytical error (1σ) is ±0.1‰ for carbon and nitrogen.

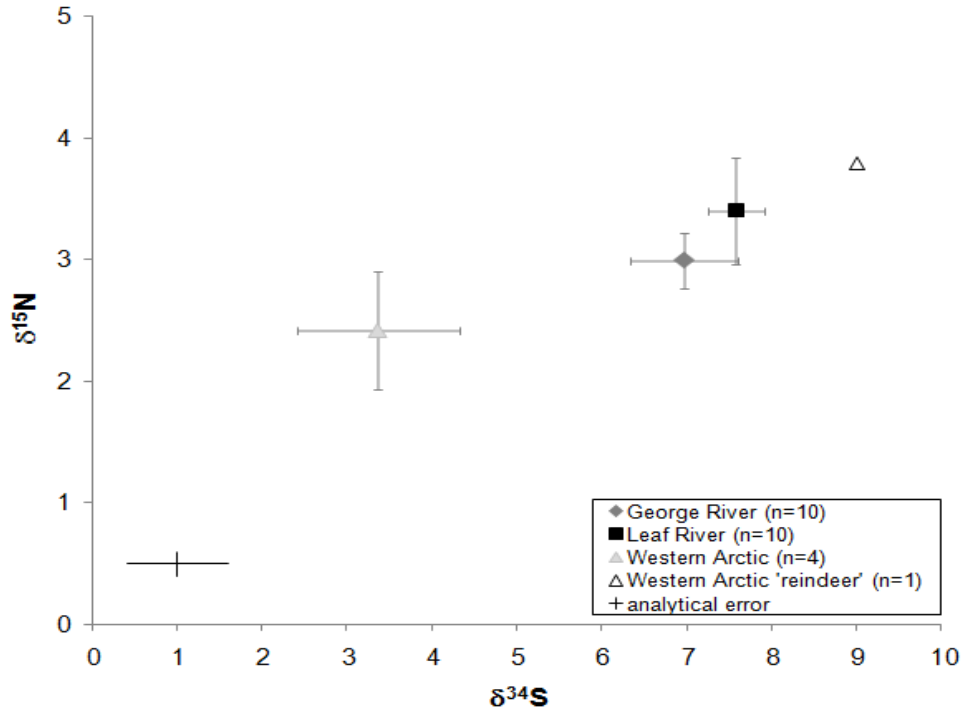


Figure 7.16 Nitrogen ($\delta^{15}N$) and sulphur ($\delta^{34}S$) isotope data from bone collagen from the George River, Leaf River and Western Arctic herds. Analytical error (1σ) is 0.1‰ for nitrogen and 0.6‰ for sulphur.

Carbon and nitrogen isotope analysis can be used to infer dietary, physiological and environmental information. Sulphur isotope ratios in biological tissues reflect local soil, plant and atmospheric values, providing environmental, geological, and thus geographical, information. Unlike the enamel and permanent dentine, bone is remodelled during life and reflects a number of years of averaged isotopic inputs.

The Leaf River and George River caribou herds display little intra-herd variation in carbon, nitrogen and sulphur isotope ratios (Figures 7.15 and 7.16); this not only reflects shared isotopic inputs but is also a likely product of their contemporaneity. All individuals from the Leaf River and George River were approximately the same age and died at the same time. Despite differences in the intra-tooth strontium data displayed in the George River herd (indicating different migration patterns/spatial histories), sulphur data is highly homogenous. This is not surprising given that sulphur isotope ratios will indicate the averaged total environmental sulphur isotope inputs, reflecting all areas of the range occupied at different points during the year. The slightly larger variation in $\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$ displayed amongst the Western Arctic caribou may reflect the fact that these individuals lived and died up to ten years apart from one another – which is also clear from the intra-tooth light isotope data. The previously-identified outlier, individual WACH-0.120, is shown separately from the rest of the Western Arctic herd. This likely semi-domesticated reindeer was first indicated through the strontium and oxygen isotope analysis. The $\delta^{15}N$ value is ~1.5‰ higher than the herd mean, also indicating an outlier. Furthermore, the $\delta^{34}S$ value for this individual is 9.0‰, 5.6‰ higher than other members of the herd. This is consistent with the geological (i.e. geographical) differences indicated by the intra-tooth strontium isotope analysis.

Although all caribou groups analysed are C_3 terrestrial herbivores, mean carbon and nitrogen isotope data for the three herds demonstrates clear grouping (Figure 7.15). Mean carbon values are -19.9‰ (Leaf River), -20.0‰ (George River) and-20.2‰

(Western Arctic). However, differences between these values are only marginally above the mean analytical error (1σ, ±0.1‰). Therefore carbon isotope value of bulk bone collagen is not useful in characterising different reindeer herds, including those that are geographically proximal (i.e. the George River and Leaf River herds) or distant (i.e. the Western Arctic herd compared to the Ungava Peninsula herds).

Mean nitrogen isotope values are 3.4‰ (Leaf River), 3.0‰ (George River) and 2.4‰ (Western Arctic). The lower values displayed the Western Arctic compared to the other two groups most likely reflect the baseline isotopic differences between two geographically-distant northern C_3 environments (eastern Canada and north-west Alaska). Such baseline shifts can be expected over such large distances and likely reflect differences in temperature or water availability (Heaton et al. 1986; Schwarcz et al. 1999). A large difference is also clear in the $\delta^{34}S$ values of the Western Arctic herd compared to the Canadian herds (Figure 7.16). The mean sulphur isotope value was 3.4‰ for the Western Arctic herd, compared to 7.0‰ and 7.6‰ for the George River and Leaf River herds respectively. These differences are consistent with the entirely different geologies in these geographically-distant areas of North America.

There are also differences in mean $\delta^{15}N$ and $\delta^{34}S$ between the Leaf River and George River herds, and distinct grouping is evident (Figure 7.16). Although small these differences are statistically significant, indicated by independent-samples t-tests. Bone collagen from the George River herd are significantly depleted in ^{15}N over those from the Leaf River herd (mean difference = -0.41‰, t=-2.65, df = 18, p=0.02). There is also significant depletion in ^{34}S (mean difference = -0.61‰, t=-2.71, df=18, p=0.02). Assumptions of equal variance in population distributions were met in all tests (Levene's Test for Equality of Variances; $p \geq 0.05$). No significant differences were observable in the $\delta^{13}C$ values. Despite their temporal and spatial proximity, this seems to indicate the potential for these bulk isotopic methods to identify and characterise herds in the archaeological record, even in purely C_3 environments.

However, although differences are statistically significant, a cautious approach must be used when interpreting these data. The mean differences are, certainly in the case of sulphur, only slightly higher than the analytical error. It is therefore suggested that differences, although statistically significant, are not large enough to confidently isotopically characterise the different herds in this case.

7.6 Henry Mountains bison, Utah, USA

The results of the isotopic measurements of enamel ($\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr/^{86}Sr$) from a single bison from the Henry Mountains bison herd, Utah, are show in Table A.10. Sequential strontium and oxygen isotope data is also shown in Figure 7.17. Corresponding sequential carbon and oxygen isotope data is shown in Figure 7.18.

The results of the isotopic measurements of dentine ($\delta^{13}C$ and $\delta^{15}N$) from this animal are summarised below in Table A.11. These data are shown also shown in Figure 7.19.

The total isotopic range for intra-tooth data from this individual is 0.7086-0.7087 ($^{87}Sr/^{86}Sr$), 23.0‰-25.7‰ ($\delta^{18}O_{V\text{-}SMOW}$) and -9.3‰ to -6.6‰ ($\delta^{13}C_{V\text{-}PDB}$) for enamel and -18.2.3‰ to -16.7‰ ($\delta^{13}C$) and 5.0‰-5.9‰ ($\delta^{15}N$) for dentinal collagen.

7.6.1 Strontium and Oxygen

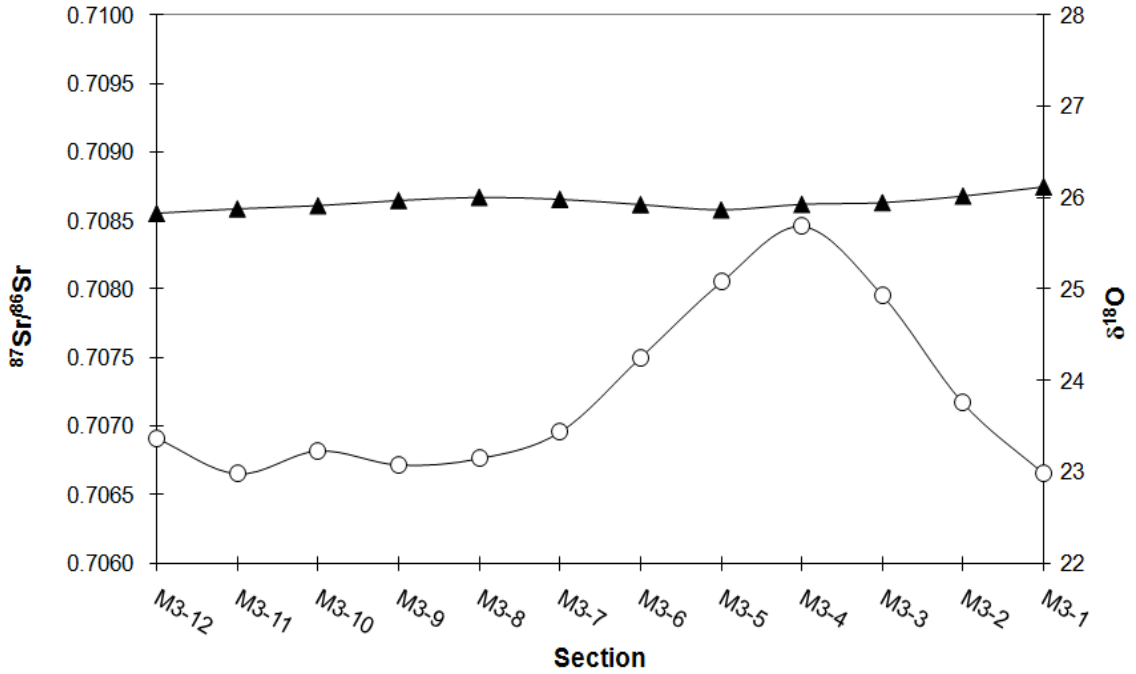


Figure 7.17 Plot of intra-tooth strontium ($^{87}Sr/^{86}Sr$) and oxygen isotope ($\delta^{18}O_{V\text{-}SMOW}$) data from the Henry Mountains bison.

Solid triangles = strontium, open circles = oxygen.

The crown enamel of the bison M3 molar should represent around 11 months of growth (Gadbury et al. 2000). Therefore, although in wear, intra-tooth data from this molar should reveal any seasonal variations in strontium isotope values. This herd occupies a very small range (~1214km^2) of comparatively homogenous geology. This herd spends the majority of their lives on the relatively young mid-late Tertiary igneous foothills and peaks of the Henry Mountains. This is reflected in the low (less radiogenic) strontium isotope values in the dental enamel, which display little variation during formation (Figure 7.17). This confirms a lack of movement between this geology and the neighbouring older, Cretaceous sedimentary geologies, which would be expected to have higher strontium values. The remains of this particular individual were found at a high altitude (>2800m) on the slopes of Mount Ellen. This may indicate that this individual spent the majority of its life at high altitudes on

these less radiogenic upland areas, both during tooth formation and potentially until death.

In contrast to the strontium data, there is a large amount of variation in intra-tooth oxygen in this individual (Figure 7.17). Values for $\delta^{18}O$ range from 23.0‰ to 25.7‰ and seem to demonstrate a full seasonal peak and most of a seasonal trough. This can be expected, given that this tooth should represent around 11 months of growth, with a little lost to wear. The values displayed in this tooth are similar to those determined in this herd previously, the mean for bulk enamel carbonates was determined as 20.7‰ (Hoppe 2006a). Locally-sampled river water had a value of -13.8±0.7‰; the variation observed in this tooth, however, clearly demonstrate intake of water from seasonal, isotopically distinct sources. These values can be compared to theoretical carbonate values calculated from the measured water value and interpolated water isotope data using Hoppe's model (Hoppe 2006a). Using the measured water value (-13.8‰), a carbonate oxygen isotope value of 20.4‰ can be calculated (Hoppe 2006a: 413-414; equations 4-6). The least negative interpolated 'summer' water value (-9.1‰) determined a carbonate value of 23.7‰. Although following the same trend (and displaying the same amount of variation), measured intra-tooth carbonate oxygen isotope values are universally higher than these calculated values. This could be due to inter-annual variation, which has been observed to influence mean annual oxygen isotope values by up to 3‰ (Hoppe 2006a). This apparent shift may also be due to local climatic and environmental influences such as relative humidity, ^{18}O-enrichment in leaves or ^{18}O-enrichment in surface water.

7.6.2 Carbon (carbonate)

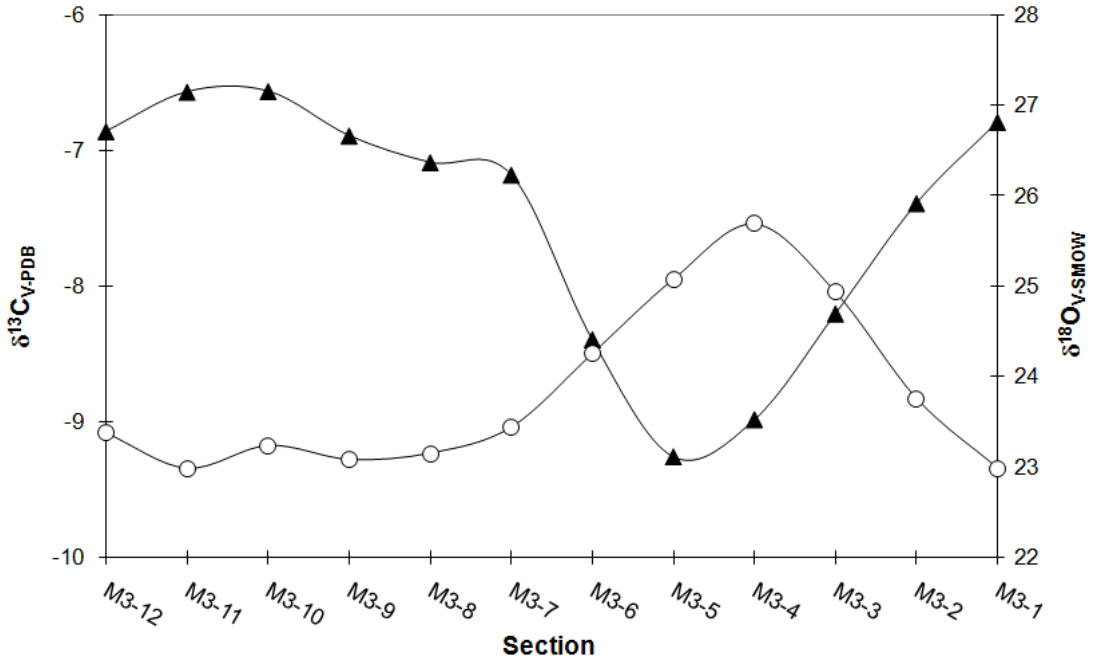


Figure 7.18 Plot of intra-tooth carbon ($\delta^{13}C_{V\text{-}PDB}$) and oxygen isotope ($\delta^{18}O_{V\text{-}SMOW}$) data from enamel from FS-768, the Henry Mountains bison. Solid trianges = carbon, open circles =oxygen.

Intra-tooth bioapatite carbon values range from -6.6‰ to -9.0‰ (Figure 7.18) and these values are consistent with the inclusion of both C_3 and C_4 plant foods in the diet. Previously studies of bison grazing in the park have indicated the inclusion of both types of graze in the annual bison diet. Intra-tooth carbon isotope ratios of bioapatite during tooth formation are also apparent. These fluctuations correlate with oxygen isotope variations and appear to be seasonal. The most negative carbon values in bioapatite correspond with the highest 'summer' oxygen values, and the enrichment of ^{13}C corresponds with the cool-season depletion of ^{18}O. This seasonally varied diet – with the inclusion of more C_3 grasses during the summer months (normally spent at higher altitudes) – has also been indicated by studies of the seasonal composition of bison faeces in the Henry Mountains Wilderness (van Vuren and Bray 1983; van Vuren 1984). Unfortunately, given that only one individual was available for analysis, an assessment of the prevalence of this seasonal dietary behaviour across the herd as a whole is not possible. However, similar trends

have been observed in intra-tooth enamel oxygen and carbon isotope samples in other modern free-roaming bison herds living in mixed C_3/C_4 environments (Gadbury et al. 2000).

7.6.3 Carbon and Nitrogen (dentinal collagen)

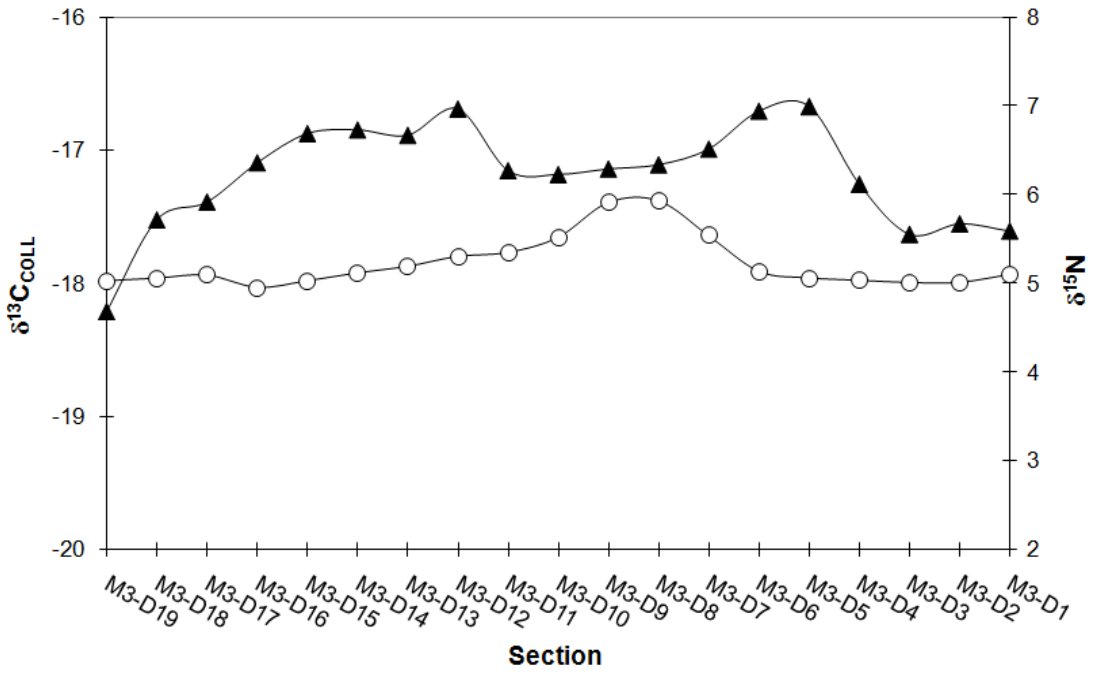


Figure 7.19 Plot of carbon ($\delta^{13}C$) and nitrogen isotope ($\delta^{15}N$) data from sequentially-sampled dentine from FS-768, the Henry Mountains bison.

Solid triangles = carbon, open circles = nitrogen.

Intra-tooth variations in both carbon and nitrogen can be observed in collagen extracted from sequentially-sampled dentine (Figure 7.19). Carbon isotope values range from -18.2.3‰ to -16.7‰, and nitrogen isotope values vary by less than 1‰ (from 5.0‰ to 5.9‰). Three troughs in carbon isotope values (more negative values) can be noted throughout tooth formation, which may correspond with the summer periods in which larger proportions of C_3 grasses are included in the diet. The period from first crown formation to final root formation in the M_3 molars of cattle and bison can be up to 28 months. Although hypsodontic molariform teeth will go into wear before root formation is complete, the period of time expected to be presented

in a large, relatively unworn tooth would still include a number of seasons and years. There is no clear pattern apparent in the intra-tooth nitrogen values aside from a single small peak, which corresponds to a dip in the carbon isotope values in the same portion of the tooth (section M3-D11 to M3-D6). The cause of this is uncertain, and could be a response to different protein contents of C_3 and C_4 plants, producing differential ^{15}N-enrichment in resultant tissues. C_4 plant foods are often low in digestible protein compared to C_3 plants and can produce isotopic enrichments in body tissues due to protein recycling (Richards et al. 2003a). However, given that nitrogen isotope variation is low (~0.9‰) and there is no clear intra-annual trend, care should be taken not to over-interpret this data.

7.7 Wind Cave bison, South Dakota, USA

The results of the isotopic measurements of enamel ($\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr/^{86}Sr$) from the Wind Cave bison, South Dakota, are shown in A.12. Strontium and oxygen data from WCNPB-2 and WCNPB-3 are shown in Figures 7.20 and 7.21 respectively. Sequential carbon (carbonate) data from both individuals are shown in Figure 7.22.

The results of the isotopic measurements of dentine ($\delta^{13}C$ and $\delta^{15}N$) from these animals are summarised in Table A.13. These data are also shown in Figure 7.23 (carbon) and 7.24 (nitrogen).

The total isotopic range for intra-tooth data from these individuals is 0.7128-0.7143 ($^{87}Sr/^{86}Sr$), 19.1‰-23.4‰ ($\delta^{18}O_{V\text{-}SMOW}$) and -10.1‰ to -7.9‰ ($\delta^{13}C_{V\text{-}PDB}$) for enamel and -19.2 to -17.4‰ ($\delta^{13}C$) and 4.1-5.1‰ ($\delta^{15}N$) for dentinal collagen.

7.7.1 Strontium and oxygen

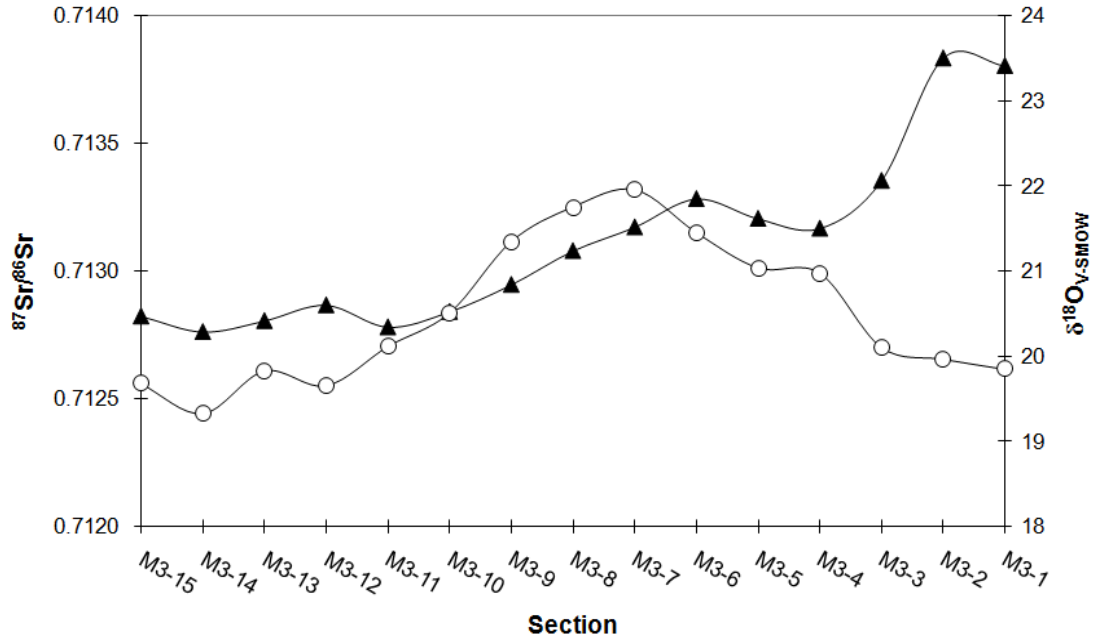


Figure 7.20 Plot of intra-tooth strontium ($^{87}Sr/^{86}Sr$) and oxygen isotope ($\delta^{18}O_{V\text{-}SMOW}$) data from WCNPB-3.

Solid triangles = strontium, open circles = oxygen.

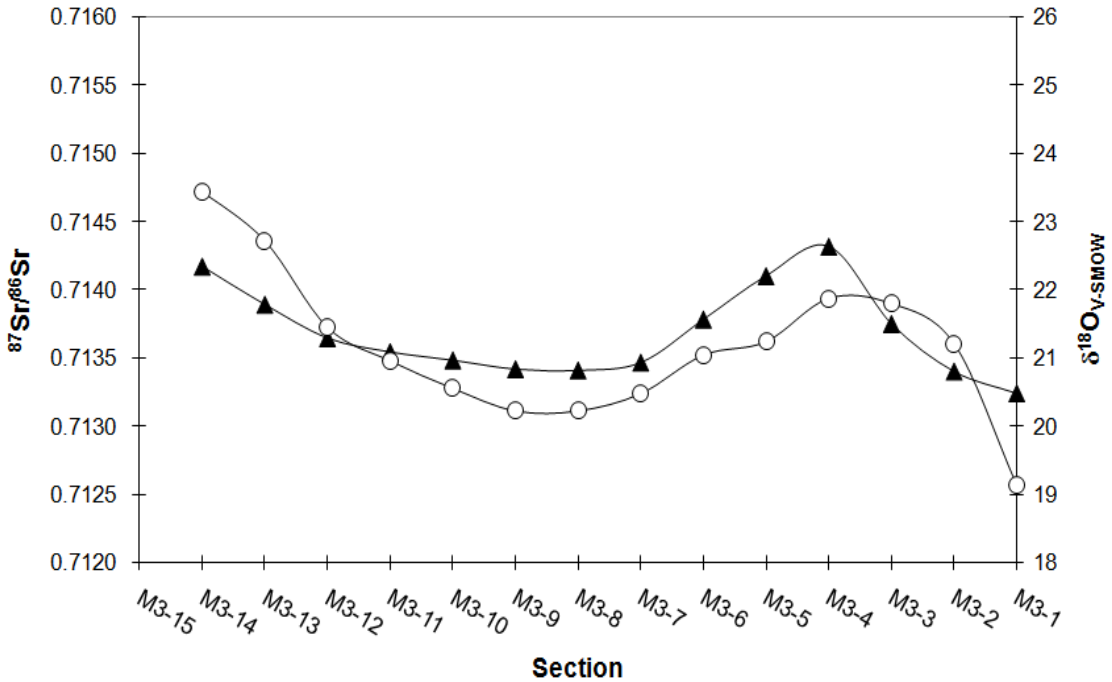


Figure 7.21 Plot of intra-tooth strontium ($^{87}Sr/^{86}Sr$) and oxygen isotope ($\delta^{18}O_{V\text{-}SMOW}$) data from WCNPB-2.

Solid triangles = strontium, open circles = oxygen.

There are clear fluctuations in strontium and oxygen isotope ratio throughout the formation of the M3 of each of these animals (Figures 7.20 and 7.21). Seasonal peaks in oxygen isotope ratio appear to confirm the timing of tooth formation and the periods of growth represented in these teeth (around 1 year, excluding loss to wear). The values displayed in these teeth also correspond well with the local environmental background. The total range of oxygen isotope values (19.1‰ to 23.4‰) match bulk-sampled enamel $\delta^{18}O_{V\text{-}SMOW}$ values from a previous study (21.3‰±0.7‰, 1σ, n=8) and mean local water values (-16.2±0.2‰) (Hoppe 2006a: 409). The range of oxygen isotope values is similar in both individuals. Individual WCNPB-2 demonstrates a clear seasonal peak in oxygen isotope values (rising from 20.1‰ at point M3-11, to 22.0‰ at point M3-7, before returning to 20.1‰ at point M3-3). The other individual, WCNPB-3, also displays a similar range of data, although incorporates a slightly longer period of time and is slightly shifted on the x-axis compared to WCNPB-3. Differences in total amount of time represented in the teeth (as indicated by the additional half peak in the oxygen isotope profile of WCNPB-3) is most likely due to differences in wear between the individuals (reflected in the fact that fewer sections could be taken from individual WCNPB-2). The slightly different isotope values and small shift on the x-axis likely reflects small inter-annual changes in the oxygen isotope composition of precipitation/drinking water and the fact that these individuals are unlikely to have been exactly the same age.

The intra-tooth oxygen isotope values can be compared to theoretical carbonate values calculated from the measured water value and interpolated water isotope data using Hoppe's model (Hoppe 2006a: 413-414; equations 4-6) Using the measured water value (-16.2‰), a carbonate oxygen isotope value of 18.7‰ can be calculated. The least negative interpolated 'summer' water value (-9.6‰) determined a carbonate value of 23.3‰. Both these values correspond well with the values displayed in the teeth. The lowest interpolate environmental values – corresponding

with higher altitudes (and the cooler seasons) do not relate to values seen in the teeth and probably indicate a lack of altitudinal ranging by these individuals in this area.

Variations in the strontium isotope ratios throughout enamel formation vary slightly between individuals. In WCNPB-3, strontium variation appears to occur in a repeated pattern, which also coincides with oxygen isotope ratios. This indicates the movement between the different geological areas of the park. Although there is no evidence for seasonal migration or clear seasonal use of space in this herd, individuals can roam freely within the park boundaries, an area which includes younger and older lithologies. In this individual, the movement between these areas appears to be seasonal. However, a member of the same herd – WCNPB-2 – does not show a similar trend. Although strontium values do vary throughout enamel growth in this individual (and have a similar range of values as WCNPB-3), the same 'seasonal' pattern is not observed. However, there is clear movement between the different geological terrains of the park. The similar distributions of values and different overall trends observed in these two individuals isotopically confirm the lack of cohesive, seasonally-directed movements in this bison herd.

7.7.2 Carbon (carbonate)

The intra-tooth carbon isotope values observed in these individuals range from -10.1‰ to -7.9‰ are consistent with a mixed C_3/C_4 diet throughout tooth formation (Figure 7.22). This is consistent with bulk bone collagen data and bulk sampled enamel carbon isotope data from previous studies, which also indicated mixed feeding (Hoppe et al. 2006; Tieszen et al. 1988). Despite intra-tooth variations, there is no clear seasonal dietary shift. This comes in contrast to a previous study which identified a dominance of C_4 graze in the summer diet from the stable isotope analysis of bison faecal material at the park (Tieszen et al. 1988). These inconsistencies likely indicate the lack of clear seasonal niche feeding habits in this herd or lack of seasonal feeding restraints in this area.

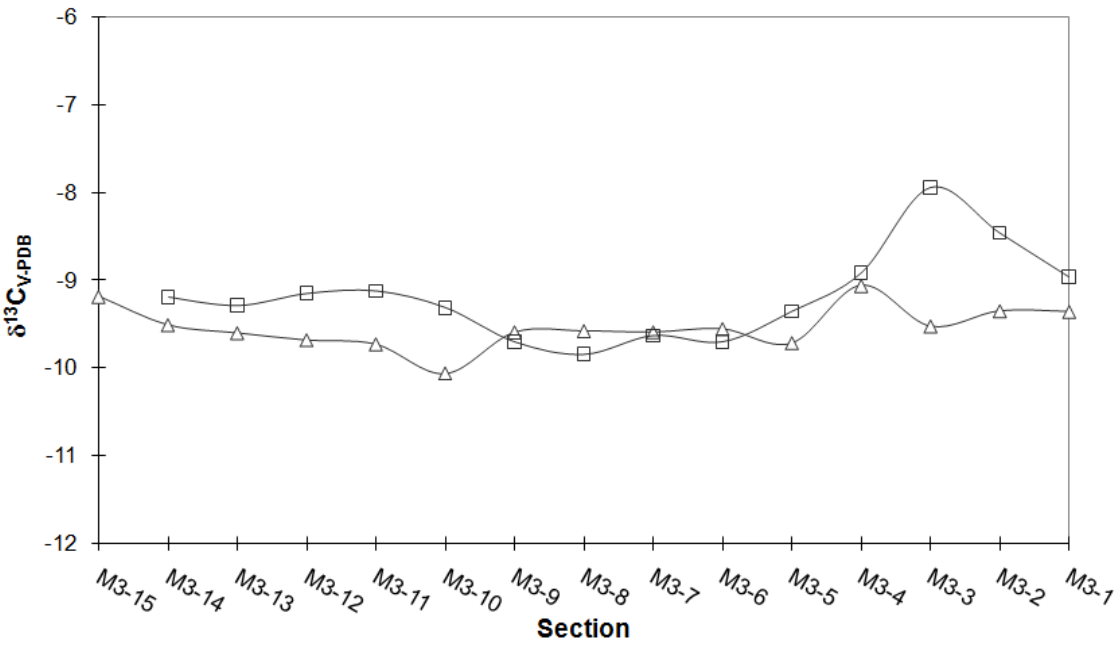


Figure 7.22 Plot of all carbon isotope data ($\delta^{13}C_{V\text{-}PDB}$) from intra-tooth enamel sections from the Wind Cave National Park bison.

Triangle = WCNPB-2, square = WCNPB-3.

7.7.3 Carbon and nitrogen (dentine collagen)

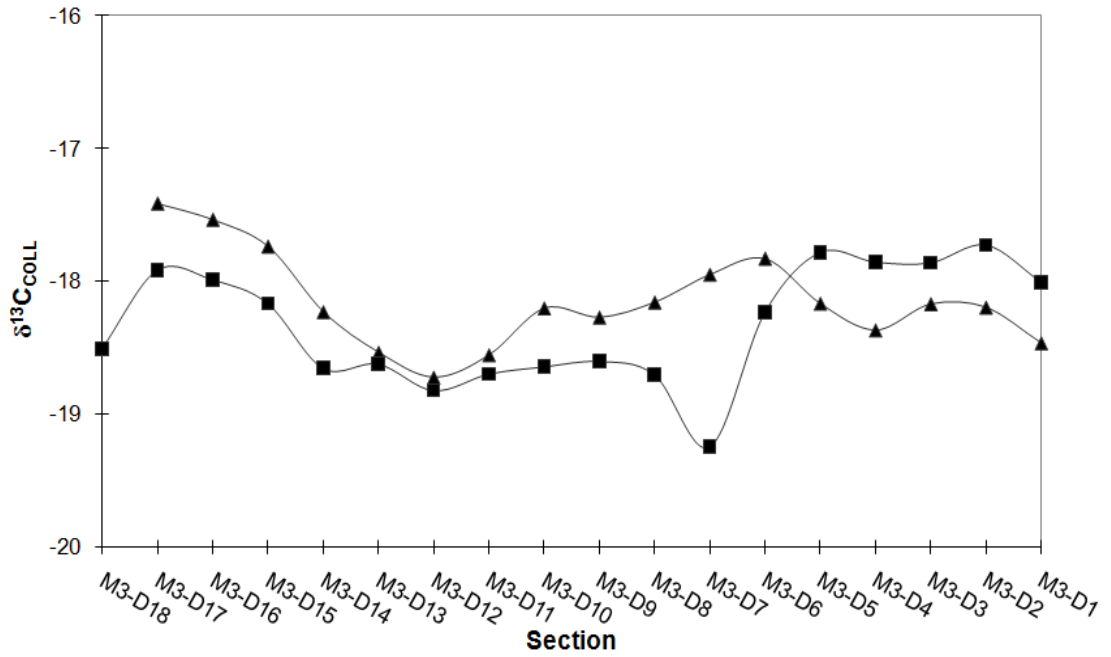


Figure 7.23 Carbon isotope values ($\delta^{13}C$) values from collagen from sequentially sampled dentine from individuals of the Wind Cave National Park bison.

Triangle = WCNPB-2, square = WCNPB-3.

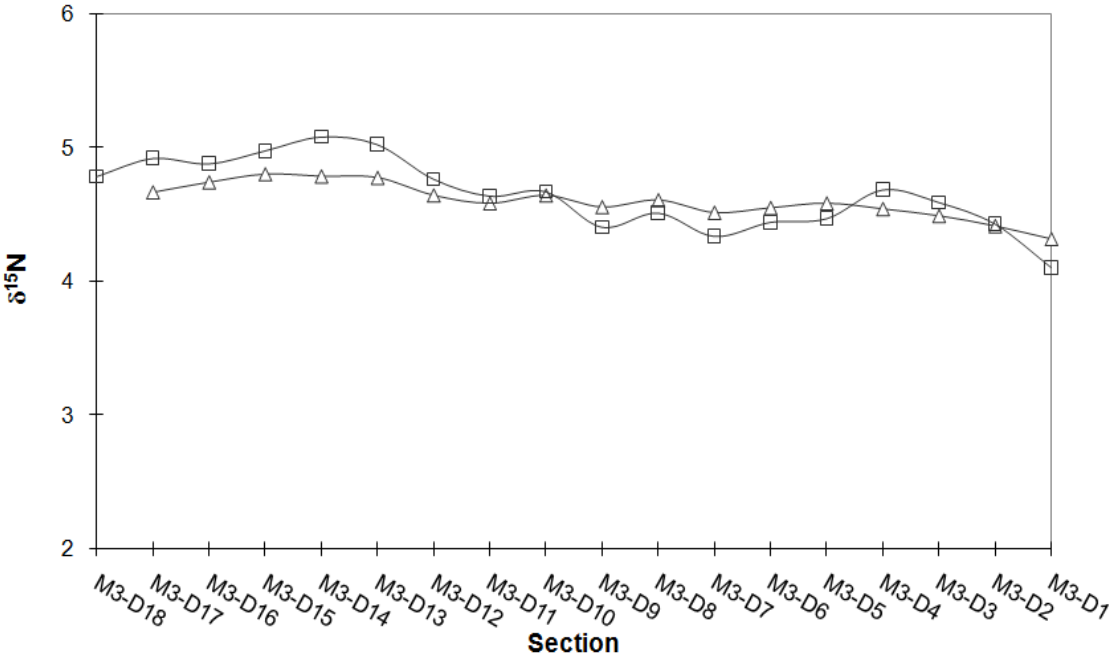


Figure 7.24 Nitrogen isotope values ($\delta^{15}N$) values from collagen from sequentially sampled dentine from individuals of the Wind Cave National Park bison.

Triangle = WCNPB-2, square = WCNPB-3.

Collagen from these two individuals show similar trends throughout tooth formation (Figures 7.23 and 7.24). As described above, total dentine growth in these M3 bison teeth could represent a period of up to 28 months. The addition of root growth makes this a far longer period than the time represented in the enamel of the same tooth. Intra-tooth carbon isotope values vary by ~1.5‰ in both individuals, and demonstrate the varying C_3/C_4 composition of the diet during this time. Although there is a general fluctuating trend, variations do not appear directed or seasonal – especially when compared to the clear, aligned profiles displayed in many of the caribou herds.

There is very little variation in the intra-tooth nitrogen isotope values of these individuals. A total variation of ~1‰ is similar to that displayed in the Henry Mountains bison, and no clear repeating seasonal patterns are apparent. This suggests consumption of an isotopically homogenous diet and that there were no severe reductions in dietary protein during the formation of this tooth.

7.8 Wichita Mountains bison, Utah, USA

The results of the isotopic measurements of enamel ($\delta^{13}C$, $\delta^{18}O$ and $^{87}Sr/^{86}Sr$) from the Wichita Mountains bison, Oklahoma are shown in Table A.14. Sequential strontium and oxygen isotope data are also shown in Figure 7.25 and 7.26 respectively. Corresponding sequential carbon isotope data are shown in Figure 7.27.

The results of the isotopic measurements of dentine ($\delta^{13}C$ and $\delta^{15}N$) from these animals are summarised in Table A.15. These data are also shown in Figure 7.28 and 7.29 respectively.

The total isotopic range for intra-tooth data from these individuals is 0.7106-0.7108 ($^{87}Sr/^{86}Sr$), 26.8‰-30.8‰ ($\delta^{18}O_{V\text{-}SMOW}$) and -5.0‰ to -2.6‰ ($\delta^{13}C_{V\text{-}PDB}$) for enamel and -14.1 to -11.6‰ ($\delta^{13}C$) and 3.1-4.5‰ ($\delta^{15}N$) for dentinal collagen.

In addition to the intra-tooth data from individuals WMB-11 and WMB-12, whole bone collagen was also analysed from a total of five individuals from this herd (WMB-11,-12, -13, -14, -15). Whole bone collagen data ranged from 3.0‰-4.7‰ ($\delta^{34}S$), -13.0 to -11.7‰ ($\delta^{13}C$) and 2.3‰-3.4‰ ($\delta^{15}N$) and can be found in the Appendix (A.16).

7.8.1 Strontium

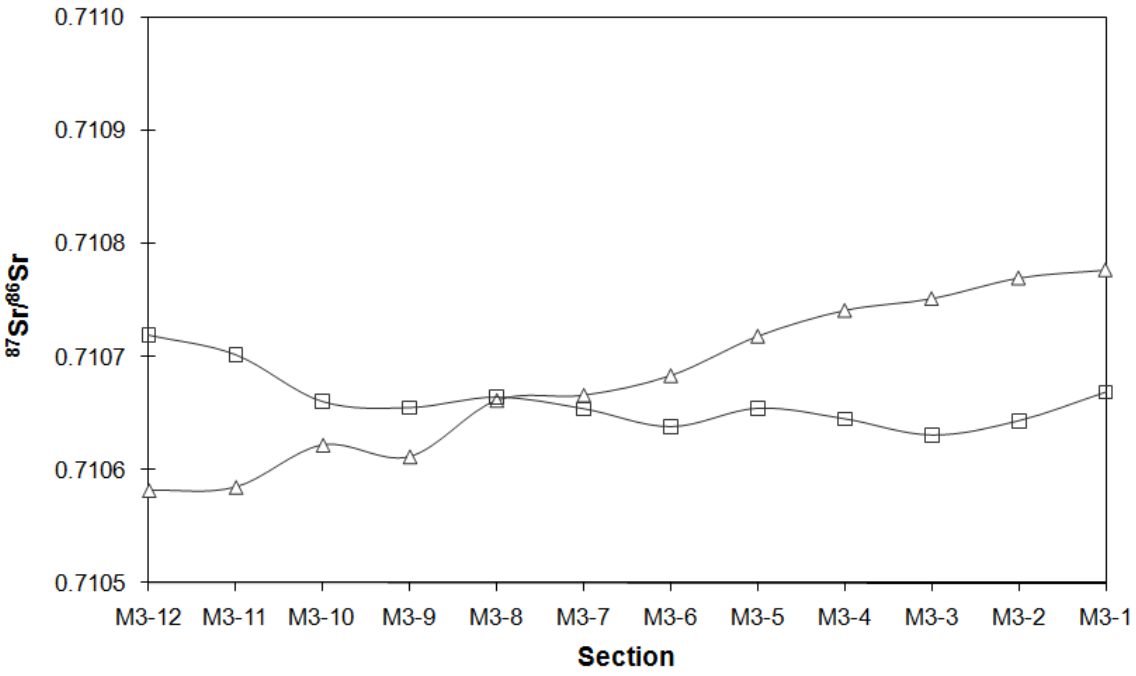


Figure 7.25 Intra-tooth strontium ($^{87}Sr/^{86}Sr$) isotope data from enamel from the Wichita Mountains bison.

Triangles = WMB-11, squares = WMB-12.

Variability in intra-tooth strontium in these two individuals is low (Figure 7.25) and mean values are the same for both individuals (WMB-11 = 0.7107±0.0001, 1σ; WMB-12 = 0.7107±0.00005, 1σ). This is consistent with living on a relatively

homogenous lithology throughout tooth formation, given that the individuals in this herd to do undertake long-distance, seasonal movements in this park (a 240km^2 area bounded by a 2.6m high big game fence).

7.8.2 Oxygen

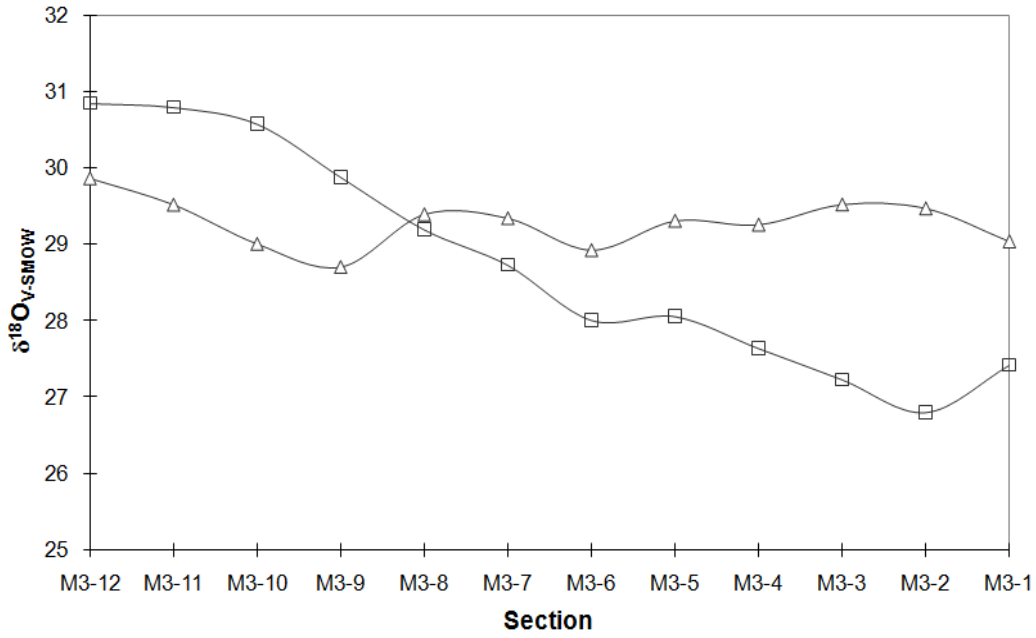


Figure 7.26 Intra-tooth oxygen ($\delta^{18}O_{V\text{-}SMOW}$) isotope data from enamel from the Wichita Mountains bison.

Triangles = WMB-11, squares = WMB-12.

Intra-tooth oxygen isotope values ($\delta^{18}O_{V\text{-}SMOW}$) are enriched in ^{18}O compared to many other herds measured, reflecting the enriched local waters (-3.5±0.7‰; Hoppe 2006a: 409). This value calculates a hypothetical enamel carbonate value of ~28‰ (Hoppe 2006a: 413-414; equations 4-6), similar to the measured values. In one individual, WMB-12, there is variation throughout tooth formation, displaying a general trend from higher to lower values (Figure 7.26). These values are greater than local river water values. The other individual, WMB-11, demonstrates very little intra-tooth variation, indicating an isotopically homogenous source of water during enamel formation. Both this, and the enriched values displayed in the other tooth,

are likely due to the consumption of water from the park's numerous artificially ponds and lakes (Walter Munsterman, personal communication). Although filled by meteoric water, these pools (especially larger ones) are likely to display less variation than seasonal precipitation and are likely to also become enriched in ^{18}O during warmer periods due to the surficial evaporation of lighter water. These factors probably account for the lack of seasonal variation displayed in these individuals, and the higher values shown in one individual.

7.8.3 Carbon (carbonate)

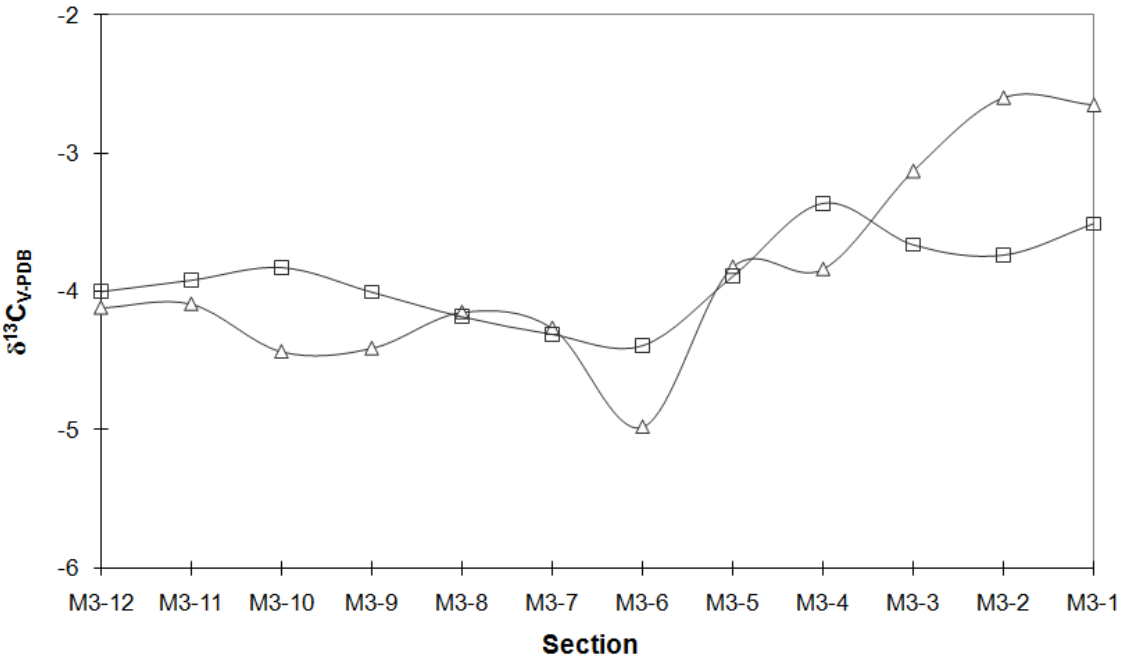


Figure 7.27 Intra-tooth carbon ($\delta^{13}C_{V\text{-}PDB}$) isotope data from enamel from the Wichita Mountains Triangles = WMB-11, squares = WMB-12.

Intra-tooth carbon isotope values measured in enamel carbonates ($\delta^{13}C_{V\text{-}PDB}$) range from -5.0‰ to -2.6‰ (Figure 7.27), indicating the dominance of C_4 grasses in this ecosystem and in the diet of these bison. The values in these two individuals are slightly more negative that those determined in a previous study of bulk enamel carbonates, which had a mean value of -1.9±0.7‰ (1σ, *n*=9) (Hoppe et al. 2006: Figure DR1 (online supplement)). This indicates that the diets of individuals in this

study – WMB-11 and WMB-12 – included a slightly larger percentage of C_3 forbs at Wichita, at least during this year of enamel formation (during M3 crown formation and mineralisation). Although there is no clear seasonal pattern, there are intra-tooth fluctuations, indicating that the proportion of C_3 plants in the diet may fluctuate slightly throughout the year, most likely responding to the availability and phenology of growth.

7.8.4 Carbon and nitrogen (dentine collagen)

Dentinal collagen carbon and nitrogen isotope values show variations throughout the formation of the third molars in individuals WMB-11 and WMB-12 (Figures 7.28 and 7.29).

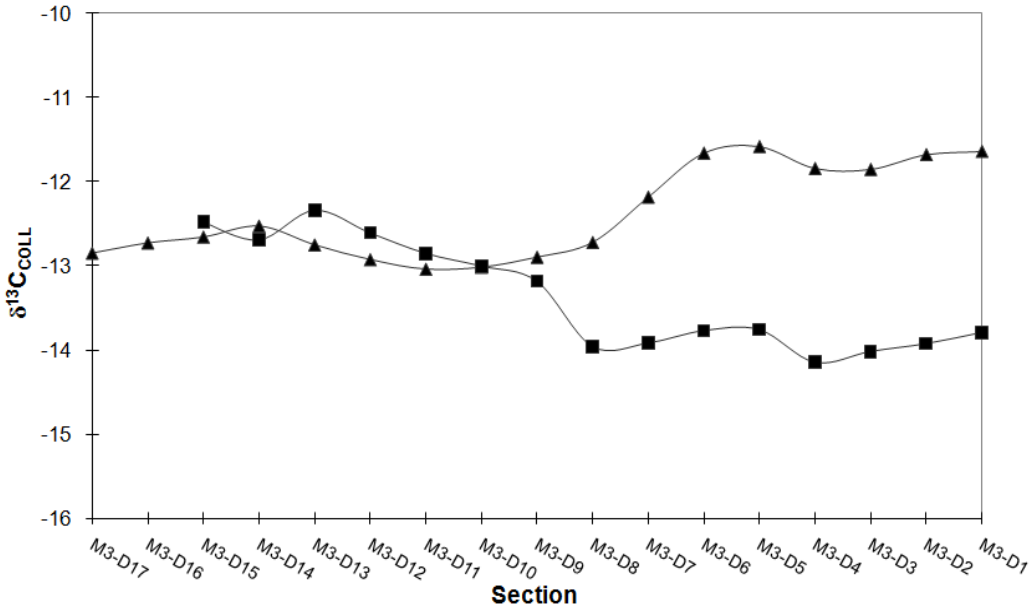


Figure 7.28 Carbon isotope ($\delta^{13}C$) values of collagen from the sequentially sampled dentine from Wichita Mountains bison herd.

Triangle = WMB-11, square = WMB-12.

Carbon values range from -14.1‰ to -11.6‰ ($\delta^{13}C_{COLL}$), deviating by as much as ~1.5‰ in individual teeth. These values are consistent with a diet dominated by C_4 grasses and variations within the teeth may indicate the varying proportion of C_3 plant foods also consumed. The long periods of time represented in the formation of

dentine in these teeth allows the creation of an isotope profile spanning a number of years – given the additional period of root growth, this is longer than that that can be reconstructed from the intra-tooth analysis of carbon in enamel from the same tooth. Intra-tooth variations in individual WMB-11 display no clear pattern, aside from a general trend to less negative values through time (as the proportion of C_3 plant foods in the diet is slightly decreased). WMB-12 demonstrates the opposite trend, from less negative to more negative values through time. Neither individual displays a clear seasonal trend through time.

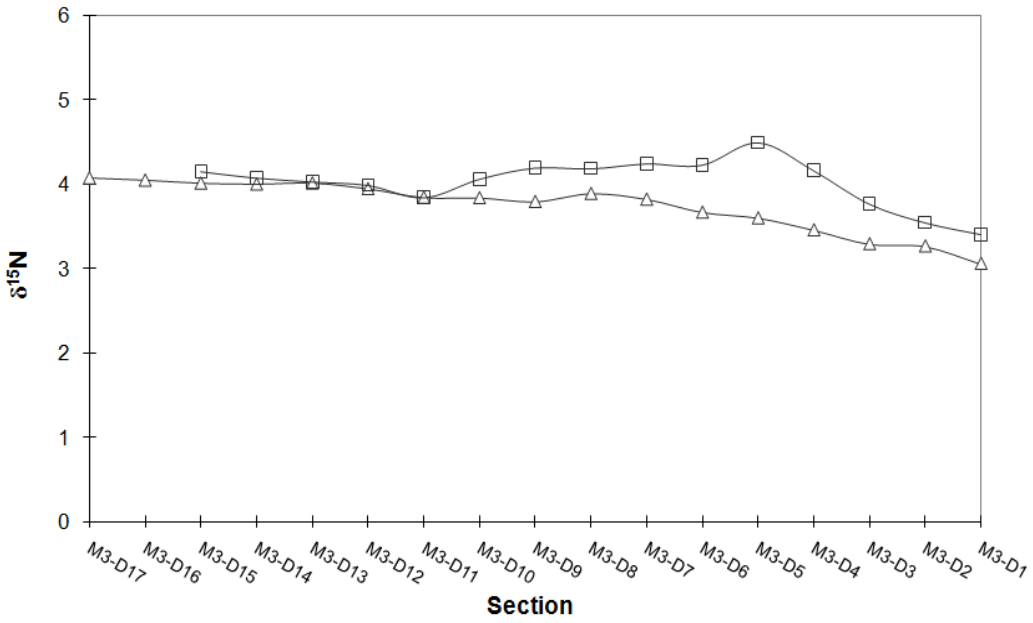


Figure 7.29 Nitrogen isotope ($\delta^{15}N$) values of collagen from the sequentially-sampled dentine from Wichita Mountains bison herd.

Triangle = WMB-11, square = WMB-12.

There is very little variation in $\delta^{15}N$ throughout the two teeth (less than 1.5‰ in total). This is similar to that displayed in bison from the Henry Mountains and Wind Cave herds. Although absolute values shown in individuals from these herds are slightly different (likely due to the natural baseline differences between Utah, Oklahoma and South Dakota), the lack of intra-tooth variation is similar. This suggests the consumption of an isotopically homogenous diet (in terms of nitrogen)

and that there were no severe reductions in dietary protein during the formation of these teeth.

7.8.5 Whole bone collagen (carbon, nitrogen and sulphur)

Collagen was extracted from five individuals from the Wichita Mountains herd, and analysed for carbon, nitrogen and sulphur isotope ratios. When compared to the C_3 feeding caribou also sampled in this study, it is clear that this group are mainly C_4 grazers (see Figure 7.30). There is a slightly larger amount of variation carbon values than seen in the caribou herds, likely reflecting the fact that these individuals live in a mixed C_3/C_4 environment or that this herd demonstrates a less cohesive herding and seasonal behaviour compared to the caribou.

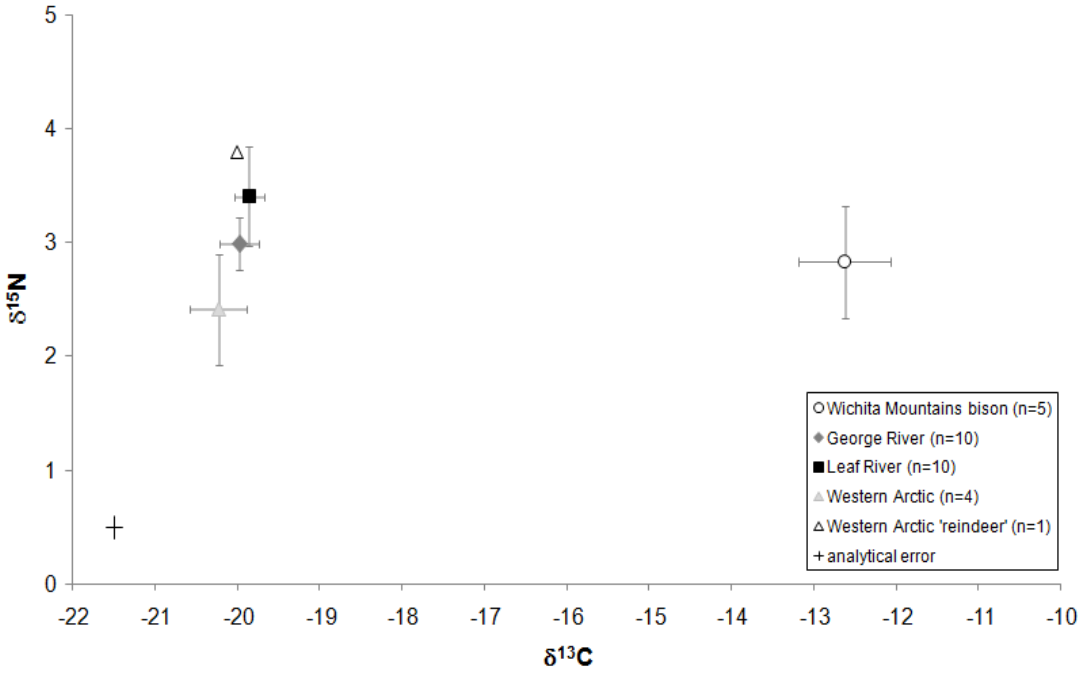


Figure 7.30 Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope data from bone collagen from the George River, Leaf River, Western Arctic and Wichita Mountains herds. Analytical error (1σ) is ±0.1‰ for carbon and nitrogen.

The range of sulphur values measured in members of the Wichita Mountains herd are similar to those demonstrated in the Western Arctic caribou herd (Figure 7.31).

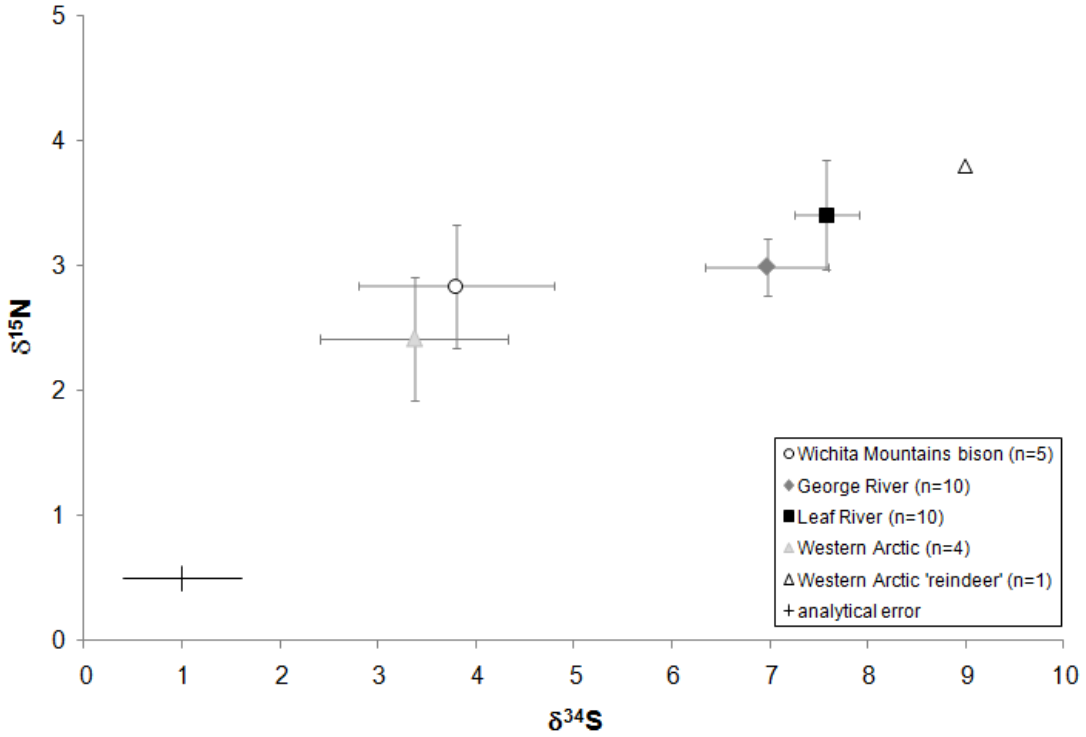


Figure 7.31 Nitrogen and sulphur isotope data from bone collagen from the George River, Leaf River, Western Arctic and Wichita Mountains herds. Analytical error (1σ) is ±0.1‰ for nitrogen and ±0.6‰ for sulphur.

Although in very different portions of North America, the underlying sedimentary and igneous geologies are similar, as are the mean strontium isotope values displayed in these two herds. The strontium mean value for the Western Arctic herd is 0.7106±0.0008 (1σ, all sequential-samples, not including individual WACH-0.120) and the corresponding value for the Wichita Mountains is 0.7107±0.00005 (1σ). Mean $\delta^{34}S$ values from bone collagen from the sample individuals are 3.4‰±0.96 (1σ) and 3.8‰±0.77 (1σ) for the Western Arctic caribou and the Wichita Mountains bison respectively. The values obtained from the Canadian herds are much higher (and also similar to one-another), relating to the far older geologies of Québec, Labrador and the Ungava Peninsula. This clearly indicates the potential for sulphur

isotope data, as well as strontium isotope data, to identify the geological (and possibly geographical) origin of archaeological fauna.

7.9 Discussion

The stable isotope data from modern *Rangifer tarandus* spp. and *Bison bison* explored above have implications for the application of these methods to archaeological or palaeoecological materials. The analysis of these isotope data within the context of the environmental, dietary and mobility histories of these herds permits an assessment of these isotopic methods and sampling techniques. This work will now be discussed with specific reference to the aims highlighted in Chapter 1. The discussion is separated into the reconstruction of migratory behaviour, dietary behaviour and herding behaviour as a whole.

7.9.1 Movements and migrations

The results of the modern studies have promising implications for the reconstruction of seasonal movements in archaeological faunal samples. Data from modern migratory caribou indicate that intra-tooth strontium analysis could be used to elucidate migratory behaviour from archaeological teeth, allowing the reconstruction of movements during a fixed period of an animal's life (i.e. during molariform tooth crown formation). Intra-tooth strontium isotope profiles from two of the migratory caribou herds under analysis (the Western Arctic and the Leaf River herd) clearly demonstrate seasonal migratory behaviour – with repetitive fluctuating patterns of strontium isotope variation throughout tooth formation. Here, not only was intra-tooth strontium isotope variation large in these individuals (indicating the traversing of geological boundaries throughout enamel formation and mineralisation), but the fluctuation in values indicate the regular use of defined areas of the range. In the caribou these largely co-vary with oxygen isotope values, placing the movement in a seasonal context. Where available, comparison of intra-tooth strontium values with

local environmental $^{87}Sr/^{86}Sr$ values within the ranges (i.e. with the Western Arctic herd) also indicate a clear relationship between geological values and those expressed 'seasonally' in the teeth. It must be noted where geology was extremely varied and herding behaviour was inconsistent, intra-tooth strontium isotope data was also inconsistent and did not reveal cohesive or defined migratory behaviour (such as in the George River herd). However, although the migratory signals identified in other herds could not be identified in this herd, intra-tooth strontium isotope variation was still high, indicating the movement across areas of considerably different geology.

In contrast to the migratory caribou herds, the bison generally displayed little intra-tooth variation in strontium isotope ratios and, aside from one individual (WCNPB-3), no repetitive strontium isotope signals were clear which would indicate seasonal use of specific areas. This indicates the potential for such methods to identify migrants and non-migrants in archaeological contexts. Future studies should incorporate modern migratory and non-migratory species from the same geographical areas (such as caribou and non-migratory muskoxen from northern Canada). The comparison of taxa of both types from the same locale would permit a better characterisation of this effect. Where local baselines were comparable, the total amount of strontium isotope variation displayed within a tooth could therefore be utilised to estimate the home-range of different species at the same site. This could be a useful archaeological tool in the estimation of seasonally-available prey and also have wider applications, such as the estimate of human landscape use and the extents of home-ranges, either through the use of animal proxy data or the direct measurement of human intra-tooth strontium isotope ratios. WCNPB-3 provides a cautionary tale; where no known long-distance or defined seasonal migration is known, this individual displays regular strontium isotope fluctuations suggesting the regular seasonal movement of this animal between two geologically defined areas.

The dual application of strontium and oxygen isotope analysis has permitted the 'anchoring' of strontium isotope data within a seasonal context, for both the migratory and non-migratory groups. The oxygen isotope profiles have also served to confirm what is known about the timing of tooth enamel formation in the species under analysis, as seasonal fluctuations give an external indicator of the periodicity of variations in other isotope systems (such as strontium or carbon). Oxygen isotope profiles established for the Western Arctic herd also hint at the potential for this approach to identify long-distance, thermostressed migratory behaviour. This herd are found at the most northern latitudinal extremes included in this study (63 to 71°N), with most of their range lying within the Arctic Circle. Despite the extremes in latitude, seasonal temperature and the seasonal oxygen isotope values of precipitation, a lower degree of oxygen isotope intra-tooth variation was measured in this herd compared to the other caribou and most of the bison. It is suggested that this might be due to the act of migration itself at such environmental or northern extremes, and also due to the causes of migratory behaviour (due to thermostress rather than forage availability or insect/predation harassment). Where a high (and regularly fluctuating) strontium variation and low amount of oxygen isotope variation is determined in archaeological teeth, this could suggest long-distance, climatically-driven migrations. Greater amounts of intra-tooth variation were displayed in the Leaf River and George River herds, which are found further south and – despite having larger total herd ranges – do not make such an extensive north-south migration. Intra-tooth oxygen isotope profiles in the non-migratory animals are generally high and – despite being at generally more southern latitudes – indicate clear seasonal fluctuations. Where herds are utilising artificial water sources (i.e. the Wichita Mountains herd), enrichment in ^{18}O and lack of seasonal variation is evident.

7.9.2 Seasonal diets and feeding niches

The stable isotope analysis of sequentially-sampled enamel and dentine in modern animals also has implications for the reconstruction of dietary as well as migratory behaviours in archaeological species. Carbon and nitrogen isotope data in the modern caribou herds demonstrate clear intra-tooth variations, in both enamel (carbon) and dentine (carbon and nitrogen). Previously published preliminary studies have demonstrated the potential for these methods to identify the regular seasonal consumption of lichen which is enriched in ^{13}C compared to other C_3 terrestrial plants (Drucker et al. 2001). The data obtained from the Western Arctic, Leaf River and George River herds confirm that the seasonal consumption of lichen can be tracked through carbon isotope analysis of sequentially-sampled dental tissues. This highlights the potential for this niche feeding behaviour to be investigated in archaeological *Rangifer*. In all three caribou herds and all individuals, the highest carbon isotope values correspond to the most negative oxygen isotope values, confirming lichen feeding is occurring during the cooler season (i.e. winter). Variations were also revealed in the $\delta^{13}C$ ratios of sequentially-sampled dentine, often co-varying with intra-tooth $\delta^{15}N$ values. The variation in this isotope system for the caribou is far higher than for any of the bison analysed, indicating this variability is not simply the product of natural seasonal variability in plant foods within ecosystems. The prevalence of these patterns in all caribou herds also indicates that these patterns are not the result of a baseline shift as caribou move between different parts of the range on their seasonal migrations as these are unlikely to follow the same trends in geographically-distant portions of Alaska and Canada involved in the study. Instead it is suggested that these pronounced intra-dentinal differences in $\delta^{15}N$ are due to a strongly seasonally varied protein intake and the physiological effects of body tissue wasting during periods of semi-starvation in winter, as caribou are forced to recycle their own body proteins due to the poor protein diet of lichen during the winter months (Drucker et al. 2001; Soveri et al. 1992). Members of the same caribou

herd and different caribou herds show similar trends in carbon and nitrogen variation throughout tooth formation, indicating a cohesive group and taxa-specific feeding behaviour or physiology, resulting in these patterns. However, the seasonal sampling and nitrogen isotope analysis of flora from these areas would be necessary to confirm if these variations are induced by changes in dietary input (i.e. seasonal dietary changes, or seasonal fluctuations in the isotope values of plant foods) or are due to physiological responses within the animals themselves.

In contrast to the defined and repeating carbon and nitrogen isotope variations observed in intra-tooth samples from caribou, the similar analysis of bison dental tissues did not reveal the same patterns. All bison herds sampled originate from areas with varying proportions of C_3 and C_4 plants. This was evident in the carbon isotope values of their teeth, and also of bulk bone collagen sampled from members of the Wichita Mountains herd. Due to differences in photosynthetic pathway, these plants have very different carbon isotope values, leading to distinct isotope values in their feeders. Any regular seasonal dominance of either type of plant should be apparent through the carbon isotope analysis of sequentially-sampled dental tissues. However, generally such trends are not seen amongst the bison. Although values do vary, there is no clear seasonal pattern and little evidence of shared trends within herds. This confirms the lack of any defined seasonally-dependent niche feeding behaviour. In one individual, the Henry Mountains bison (FS-768), intra-tooth enamel carbon isotope values corresponding with oxygen indicated a seasonal feeding behaviour. Two carbon isotope 'peaks' were also indentified in the intra-tooth dentinal collagen samples from the same individual. The Henry Mountains herd are known to undertake seasonal altitudinal ranging. The higher areas are dominated by C_3 scrub and C_4 grasses dominate the valleys, which likely accounts for this seasonal variation in carbon isotope values. The bison, unlike the caribou, display little intra-tooth nitrogen variation. This may further support the contention that the variations seen in the caribou are the result of strong seasonal variations in the amount of protein in

the dietary/internal dietary cycling, as opposed to being solely the product of naturally-occurring intra-annual fluctuations in the nitrogen isotope values of terrestrial plants.

7.9.3 Characterising herds and identifying populations

Intra-tooth isotope analysis permits the reconstruction of time-series isotopic information, creating isotopic histories of individual animals. However, the analysis of multiple individuals from the same modern herds allows an assessment of intra-herd variability. The establishing of a normal amount of variation within a herd (both in terms of intra-tooth and bulk isotopic data) is an important consideration for archaeological case studies, where interpretations based on isotopic data must be relevant on a group/herd level. Furthermore, this can allow the discerning of individuals displaying the expected amount of normal variation from those from other herds, with different migratory habits or feeding behaviours.

The majority of caribou individuals show a high degree of homogeny within their own herds – both in terms of trends and absolute values – across most isotope systems. Strontium isotopes show the largest amount of inter-individual variation. Although many of the migratory individuals show the same overall trends within their herds (e.g. the Western Arctic and the Leaf River herds), absolute values vary considerably – much more than the non-migratory individuals. This is most likely a product of the large size of these herds, the size of their ranges and the varied lithologies these large areas can incorporate. In spite of this, there is a large amount of agreement in intra-tooth oxygen isotope data in this herd, despite spatial differences that are visible in the strontium isotope data. These isotope systems provide different scales of information. These herds are very large (up to 650,000 members) and individuals within the same herd can spend much of their lives tens or even hundreds of kilometres apart from one another, moving considerable distances

daily as they feed. On these scales there may only be small variations in the oxygen isotope values of precipitation but potentially large variations in the strontium isotope ratios of underlying geology, soils and plants. This effect is most apparent in the George River herd, where inter-individual variation in strontium is high but oxygen isotope profiles are more similar.

Carbon and nitrogen intra-tooth isotope profiles in the caribou also generally show a high degree of intra-herd homogeneity, in terms of absolute value, seasonal variations and overall trends. There are also clear similarities between the different herds, despite their geographical differences. These similarities, along with the often repeating intra-tooth isotope fluctuations, are interpreted as evidence for the highly seasonal dietary behaviour of the caribou, their likely consumption of large quantities of lichen in winter and the associated physiological implications of a low-protein diet. It is suggested that because these seasonal changes are so pronounced, and shared amongst different populations of this taxon, carbon and nitrogen isotope values and trends are similar within and between groups. Where such cohesive taxon-specific niche feeding behaviours exist this should be evidenced using stable isotope analysis. The same trend is not apparent amongst the modern bison herds where feeding behaviours, as well as movements, are more idiosyncratic.

The bone collagen data from the caribou herds and the Wichita Mountains bison herd, demonstrate statistically significant differences between one another. This isotopic clustering ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) separates all the herds from one another; the bison herd is clearly separated from the caribou herds, and the caribou herds are statistically different from one another ($\delta^{15}N$ and $\delta^{34}S$). Aside from identifying the C_4 feeding group, carbon isotope analysis alone was not sufficient to separate the different herds of C_3 feeding caribou. This suggests, in the case of *Rangifer*, carbon isotope analysis could not be utilised to identify the origin of archaeofaunal accumulations, such as identifying single events or repeated-use mass kill sites.

However, these methods might be useful in identification of the feeding niche of caribou and the prevalence of lichen feeding in prehistory. Lichen is indigestible to other modern herbivore species and is not the favoured graze of caribou and reindeer. However, where grasses and forbs are not available, *Rangifer* have gut flora able to tolerate and digest lichen species, rendering them uniquely adapted to life in the northern tundras and taigas. The antiquity of this adaptation is not known and could potentially be investigated in the archaeological record using stable isotope analysis. Unfortunately no other herbivore species were available from areas proximal to the caribou ranges for comparative purposes. Given the ^{13}C-enrichment in lichen and the seasonal ^{13}C-enrichment noted in dental tissues, it is suggested that higher $\delta^{13}C$ values would be observable in the bulk bone collagen of caribou compared to other herbivore species in the same locale. More modern samples would be required to investigate this.

Mean nitrogen and sulphur values could be used to distinguish the herds, even amongst the geographically proximal Leaf River and George River herds. The sulphur values can be related to the differences in geology and there are similar bulk sulphur values associated with similar strontium isotope values (such as seen in the Wichita Mountains herd and the Western Arctic herd). Furthermore, the outlier identified in the Western Arctic herd confirms that this method can be used to identify potential immigrants to a population. It must be noted that, in the case of the Leaf River and George River herds, the statistically-significant differences equate to small isotopic differences, and these may not be distinguishable in archaeological materials. However, where there are temporal effects or groups with very different total annual ranges/feeding behaviours, nitrogen and sulphur isotope data may be able to identify groups within archaeological assemblages and the origins of archaeofaunal accumulations in exclusively C_3 environments. A larger amount of modern data, from more individuals and wider geographical contexts, are required to better characterise this effect.

7.9.4 Summary and future directions

This study is the first demonstration of intra-tooth strontium and oxygen isotopic ratio variations amongst populations of extant migratory and non-migratory herbivores. These data have allowed an evaluation of the relationship between real-life movements and the isotopic variations measured in dental enamel. Generally these data correlate with geological and local climatic settings and have allowed the identification of trends which have implications for our interpretation of archaeological data. Although there are exceptions, the results largely confirm that these methods can be used to determine migratory behaviour in extinct and ancestral archaeological species. The analysis of multiple individuals within the same populations has allowed an assessment of intra-herd variability and also demonstrated that this can be influenced by the extent of local geological variation but also by the cohesiveness and fidelity of herding behaviour. The dual-application of strontium and oxygen allows the 'anchoring' of strontium data within a seasonal context and, in some cases, may even independently indicate a thermostressed migration in highly seasonal environments. The results also confirm that bulk bone collagen sulphur isotope analysis could be utilised to trace the geographical origins of individuals within and between populations within archaeological assemblages.

Carbon and nitrogen isotope analysis of sequentially sampled dentine has allowed investigation of seasonal dietary variations. The analysis of two different species with different seasonal feeding habits has allowed an assessment of the isotopic visibility of such behaviours. The pronounced bi-annual diet shift of wild caribou is clear in the isotope chemistry of their dental tissues, indicating that the incidence of winter lichen consumption could be investigated in archaeological populations using these methods. The more idiosyncratic diet choices of the nomadic bison are also evident in the lack of regular intra-tooth fluctuations in $\delta^{13}C$ or $\delta^{15}N$.

Although offering promising results, there is a clear need for more work, incorporating a greater number of modern individuals and archaeological materials. The comparing of data from modern migratory and non-migratory fauna from the same area would lead to a much better understanding of many of the effects discussed above. The addition of more species, and individuals from wider geological and climatic zones, would also be useful. Future work should also incorporate an added focus on the sequential-sampling methods themselves, potentially incorporating laser ablation or micro-drilling techniques in order to assess the resolution achievable. This purpose of this study has been the characterisation of migratory behaviour and seasonal dietary changes in wild populations, in order to assess the use of sequential-sampling methods and multi-isotopic analysis to archaeological materials. Given the fact that wild populations were used and that these originated from very vast areas, the precise relationship between absolute isotopic inputs and the isotopic signatures of tissues was beyond the scope of this study. More controlled feeding studies, field studies and isotopic baseline surveys, will help to better understand the influence of mineralisation phasing, physiology and natural feeding behaviour on the isotopic signatures detected in teeth.

Finally, the application of these techniques to pertinent and carefully selected archaeological pilot studies, will allow a further assessment of these techniques, their suitability to ancient materials and archaeological problems, and the types of information such methods can help to discern. In the following chapter, these techniques will be applied to fauna from the Middle Palaeolithic site of Jonzac (or Chez Pinaud), Charente-Maritime, France.

CHAPTER EIGHT ARCHAEOLOGICAL CASE STUDY: THE MIDDLE PALAEOLITHIC SITE OF JONZAC

8.1 The site

8.1.1 Introduction

The site of Jonzac (also known as Chez Pinaud) is located in Charente-Maritime in southwest France, approximately 80km north of Bordeaux and 110km southeast of La Rochelle (Figure 8.1). The site is a collapsed rock shelter in a small river valley, the Seugne, a tributary of the Charente River. The site is now an open-air site, situated against a low, limestone cliff.

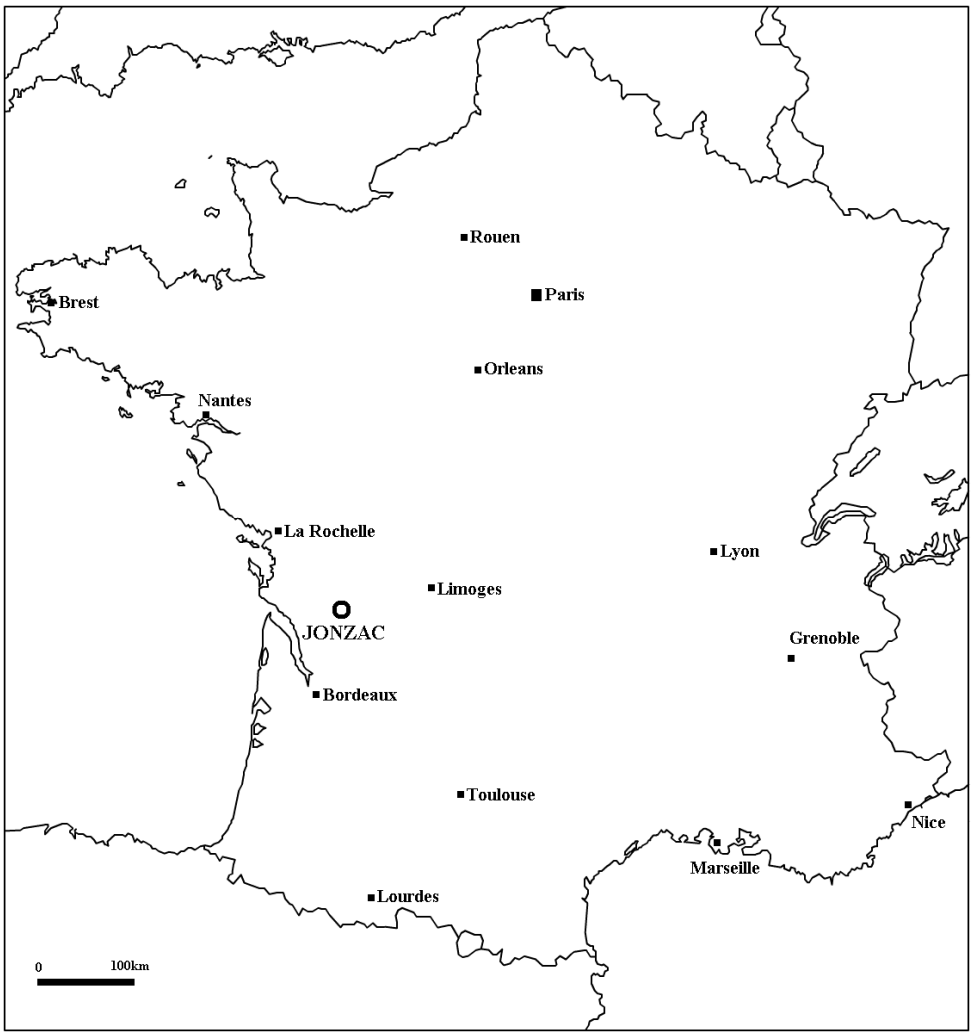


Figure 8.1 The location of Jonzac (Chez Pinaud), Charente-Maritime, France.

The site was discovered in the 1990s and has been excavated during two campaigns – the first led by Jean Airvaux (1998-1999) and the second as a larger scale collaboration (2004-2007) between the Max Planck Institute of Evolutionary Anthropology, Leipzig (led by Jean-Jacques Hublin) and the Université de Bordeaux I (led by Jacques Jaubert). The first phase of research conducted by Airvaux resulted in a monograph (Airvaux 2004). The latter has involved a multidisciplinary research program including geoarchaeological analysis of sediments, site formation processes, taphonomic studies of the faunal assemblage, raw material studies, use-wear analysis, radiometric dating and stable isotope analysis (Jaubert et al. 2008; Richards et al. 2008c).

8.1.2 Archaeology

The archaeological sequence at Jonzac comprises rich late Middle Palaeolithic and early Upper Palaeolithic assemblages. The stratigraphic sequence includes Aurignacian, Mousterian of Acheulian Tradition (MTA), Dentinculate Mousterian and Quina Mousterian. These are critical industries, which straddle the transition of Neanderthals to anatomically modern humans in Western Europe. The stratigraphic units include a vast number of lithics, anthropogenically-modified bone and even a MTA (Mousterian of Acheulian Tradition) Neanderthal tooth. The oldest deposits at the site incorporate a rich Quina Mousterian industry with a thick, reindeer dominated 'bonebed'. There is also good evidence of a Denticulate Levallois industry, followed by MTA deposits including numerous bifaces. The sequence is topped by Aurignacian deposits but these are dispersed throughout the site and are low in density (Airvaux 2004; Airvaux and Soressi 2005; Jaubert et al. 2008).

It must be noted that the level designations used in this report respond to those used in the most recent excavations (Jaubert et al. 2008), which may differ from those in the original reports (Airvaux 2004; Airvaux and Soressi 2005). The upper portions of

the Middle Palaeolithic sequence are mainly confined to the south-western portions of the site and consist of Denticulate Mousterian (with Levallois technology) of Level 8 (SW-US08) and the MTA layers of 7 (SW-US07) and 6 (SW-US06). Level 5 contains Aurignacian artefacts, although the densities of materials are low (Jaubert et al. 2008). The older, Quina Mousterian deposits are found in south-west and west areas of the site and include SW-09, SW-12, W-US016, W-US018, W-US020 and W-US022.

In addition to lithics, excavations at Jonzac yielded thousands of animal remains (approximately 20,000 from the 2004-2007 excavations alone). The taxonomic composition varies through the sequence, both in occurrence with lithic technology and with broader climatic variations over a period spanning up to 50,000 years (see Figure 8.2).

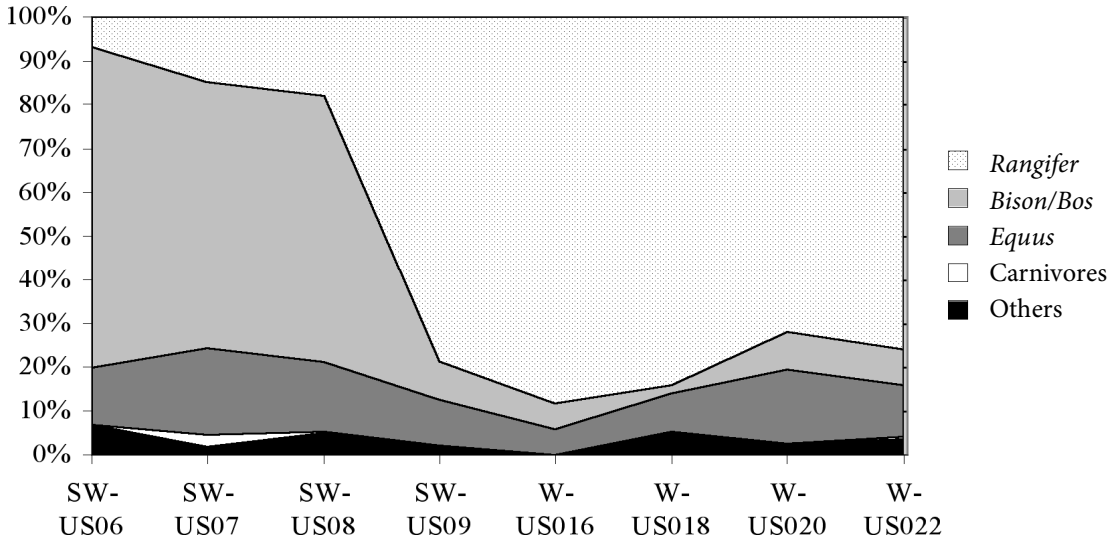


Figure 8.2 Taxonomic composition of different stratigraphic levels excavated and analysed at Jonzac (from Jaubert et al. 2008, Steele et al. 2009, courtesy of the Jonzac Project).

The faunal assemblage present in the upper levels (Level 6, 7 and 8) is dominated by large bovids (*Bison priscus* and/or *Bison primigenius*) but also include some reindeer (*Rangifer tarandus*) and horse (*Equus cabullus*), along with a few examples of an extinct equid (*Equus hydruntinus*), red deer (*Cervus elaphus*) and giant deer (*Megaloceros giganteus).* Faunal remains show evidence of human activity, including

cut-marks, percussion impacts and burning, and carnivore gnawing. The MTA and Denticulate Mousterian animal assemblage is generally poorly preserved, but specimens have yielded collagen suitable for stable isotope analysis (Richards et al. 2008c). The MTA and Denticulate faunas include visible traces of carnivore activity, but this is rare in the Quina Mousterian fauna. The older, Quina Mousterian fauna is well-preserved, coming from a 1-meter thick artefact-dense deposit (the reindeer bone bed) (see Figure 8.3).

Figure 8.3 Close-up of the Level 22 bone bed at Jonzac (photo courtesy of the Jonzac Project).

The large quantity of faunal remains, mostly reindeer, can clearly be seen.

This portion of the site includes *in situ* fauna deposits, with some articulated limb units, and complete hemi-mandibles with multiple teeth; there is minimal evidence of post-depositional disturbance. Skeletal elements indicate that a number of complete or nearly complete reindeer (*Rangifer tarandus*; NISP = 5232; MNI = 18) were introduced to the site for butchering, individuals that had been hunted by Neanderthals and transported to the Jonzac rockshelter (Steele et al. 2009). These deposits also consist of smaller numbers of horse (*Equus* sp.; NISP = 359) and bison (*Bison priscus*; NISP = 361) remains. Stone tool cut marks are frequent on the bones,

indicating disarticulation and meat removal. Appendicular bones were also systematically fractured for marrow extraction (see Figure 8.4).

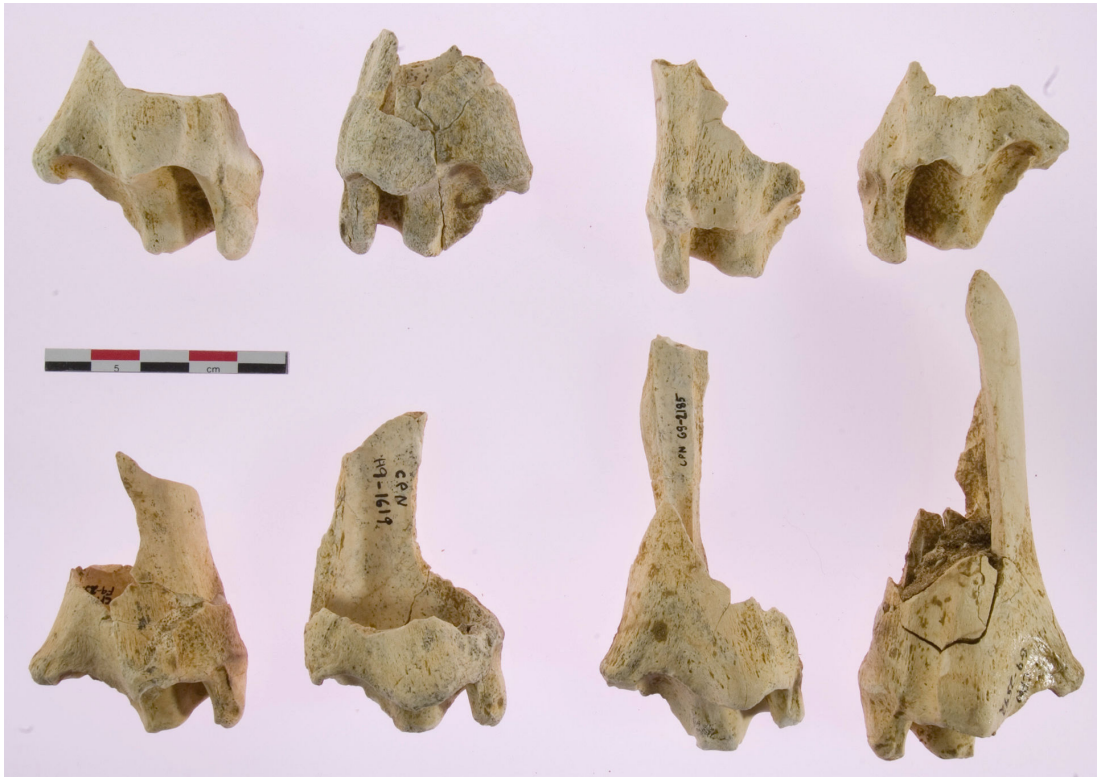


Figure 8.4 Examples of reindeer distal tibiae that were systematically fractured for marrow extraction at Jonzac (photo by S. Lätsch, courtesy of the Jonzac Project).

Prime-age adult individuals (both males and females) are most commonly represented in the Quina Mousterian deposits. Season-of-death information comes from two different sources including tooth eruption and cementochronology. Both types of data indicate Neanderthal hunting of reindeer during the winter and spring, with a probable additional autumn event too (Steele et al. 2009). This may indicate that Neanderthals were intercepting reindeer close to the cave site during their seasonal migrations and Jonzac may have been situated close to the migration route. Site formation and zooarchaeological evidence implies rapid accumulation but from a number of hunting episodes (Steele et al. 2009).

Preliminary thermoluminescence (TL) dates on burnt flints from a number of contexts at the site have been provided by Dr. Daniel Richter, Dept. of Human Evolution, Max Planck Institute of Evolutionary Anthropology and weighted means of dates obtained are summarised below (Table 8.1).

Table 8.1 Summarised TL dates determined from burnt flints from various levels at Jonzac (provided by Daniel Richter, personal communication).

Level	Period	TL date (ka)
E-US05	Aurignacian	37±4
SW-US06	MTA	42±4
SW-US07	Denticulate Mousterian	49±3
SW-US08	Denticulate Mousterian	56±3
SW-US22	Quina Mousterian	73±7

8.1.3 Geological, geochemical and environmental setting

In order to interpret the isotope data gained from the analysis of faunal samples from Jonzac, it is necessary to appreciate the broad geological and environmental setting. An assessment of local geochemical conditions (in terms of the locally bioavailable strontium) is important in determining local and non-local animals and can, in some cases, help to establish likely areas highly-mobile species may have visited during their movements or migrations. The area surrounding the site is dominated by limestones, with the site itself lying on Late Cretaceous (Turonian) limestone deposits (Girard 2009: 147, Figure 1). These deposits consist of both Cretaceous and older Jurassic limestones. The Cretaceous lithologies date to the Late Cretaceous (100 – 70 Ma; Cenomanian, Turonian, Coniacian, Santonian and Campanian) comprising fossiliferous, bioclastic and argillaceous limestones. The Late Jurassic (165 – 150 Ma) deposits consist of chalky, oolitic, fossiliferous reef limestones with argillaceous limestones and marl. These geologies continue eastwards throughout the surrounding region into the Dordogne. Further to the east is the Massif Central. This area is more elevated and consists of Devonian (380 – 350 Ma) granitoids. These are fine and coarse grained granites and granodiorites and are mica-rich. This area of

south-western France also features biotite-rich gneisses, which are metamorphic and display some mixing with the granites (Kelly 2007). In addition to the limestone dominated lowlands and the elevated granitoid regions, there are also areas of Teritary and Quaternary surficial geology, including clays, clay sands, colluvium and alluvium (Kelly 2007).

A recent isotope study at the nearby site of Les Pradelles by Kelly and others (unpublished data from Kelly's Bachelors thesis) has incorporated the sampling of soils and grasses from the range of different geological units in this area (Kelly 2007; Kelly et al. 2008). As part of Kelly's study, top soils, bottom soils and grasses were sampled from a range of sites spread across the limestone, granitoid and clay regions of Charente. Locations were recorded by GPS and samples were mainly collected by roadsides. The influence of these sampling points (and any potential strontium-containing contaminates that could come from petrochemicals, fertilisers, etc) has not been estimated. Samples were taken from a total of 39 sites, including some riverside areas. Labile strontium from the soil and plant samples was then used to determine the biologically available strontium of the area (Kelly 2007; Kelly et al. 2008). Given that the area incorporated into Kelly's study is adjacent to Jonzac and features the same geologies, the strontium isotope analysis of these sediments and plants allows an estimation of the locally bioavailable strontium at the site of Jonzac and on the surrounding geological substrates. Selected data (incorporating top soil and plant values) from Kelly's study are shown in Figure 8.5, exemplifying the range of values demonstrated on each geological type. It is important to note the median values of these samples, as well as the means, as these data might be more representative of the bulk of sampling sites within a particular geological area. Caution should be taken when determining means from environmental data collected in this way (including high or low value outliers, and a limited number of samples to represent the whole area), as they can skew interpretations.

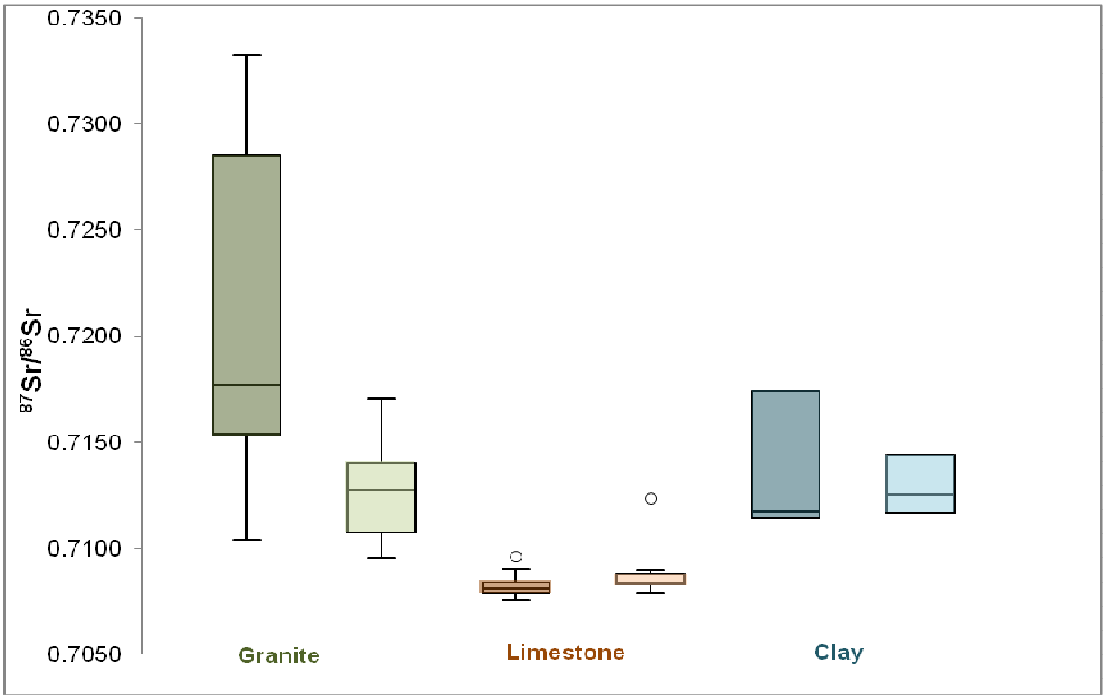


Figure 8.5 Summarised strontium data for the main geological units surrounding Les Pradelles and Jonzac (data based on top-soil and plant data taken from Kelly 2007).
Box plots display the first and third quartile, median, minimum and maximum and identified outliers. Soil values are the darker colours, plant values can be identified with lighter colours in each instance.

8.2 Aims and objectives

Given the density of anthropogenically-modified faunal remains (indicating Neanderthal hunting) and the excellent preservation conditions (including a number of complete tooth rows), the site of Jonzac presents a great opportunity to use isotope analysis to explore the seasonality of animal movements in the Middle Palaeolithic. Bulk isotope analysis may also allow the assessment of local environmental conditions and allow the reconstruction of the ecological niches of these ancestral species. The chronological depth at the site will also allow a comparison of faunal data through time, allowing diachronic assessment of movement patterns, environmental changes and dietary niches as inferred from isotope data.

This study will utilise the isotope analysis of bone and dental tissues from reindeer and bison from Jonzac in order to reconstruct the biogeochemistry of these

herbivores, their feeding ecology and movements. This will be done using the carbon and nitrogen isotope analysis of bulk bone collagen and the strontium isotope analysis of sequentially-sampled enamel. In this study, strontium data obtained from Level 22 fauna (Quina Mousterian) will be compared to material sampled from Level 8 (Denticulate Mousterian). Bulk bone collagen carbon and nitrogen isotope data will be combined with data obtained by Richards and colleagues (2008) during previous isotopic work at Jonzac (MTA and Denticulate levels) and comparisons will be drawn between both different species and different stratigraphic units of Jonzac.

In order to understand $\delta^{13}C$ and $\delta^{15}N$ values from archaeological faunal samples it is essential to establish an isotopic food web whereby the $\delta^{13}C$ and $\delta^{15}N$ ratios of different species at a site can be compared. Establishing these biogeochemical relationships will allow the reconstruction of trophic relationships and resource portioning at the particular site of interest but also help to establish baseline comparisons for top-level feeders such as humans. The investigation of these baselines in different geographical areas and diachronically at the same locations also allows the observation of any shifts that could be related to local environment or to global effects such as climatic change (e.g. Richards and Hedges 2003).

8.2.1 Aims

The aims of this study can be summarised as:

- to explore the potential of using $^{87}Sr/^{86}Sr$ isotope analysis and sequentially-sampled enamel to establish the movements and migrations of Middle Palaeolithic reindeer and bison from Jonzac
- to assess whether intra-tooth variations in strontium isotope composition can indicate local and non-local/migratory species

- to establish when these different species (reindeer and bison) used the area surrounding the site and comment on their seasonal movements
- to ascertain if there is any evidence for change in migratory behaviour in reindeer between the earlier (Quina Mousterian) and later (Denticulate Mousterian) phases of the site
- to comment on the influence that the seasonality of migratory and non-migratory species may have had upon Neanderthal hunters
- to utilise the $\delta^{13}C$ and $\delta^{15}N$ values of bone collagen from multiple species from different stratigraphic units to explore niche partitioning and climatically-induced baseline changes through time

8.2.2 Objectives

The specific objectives of this study are:

- to determine the strontium isotope ratio composition of tooth enamel from a small number of reindeer and bison from the Middle Palaeolithic site of Jonzac
- to determine the isotope ratio composition of bulk bone collagen (carbon and nitrogen) from multiple animal species from a number of stratigraphic units (and time periods) at Jonzac
- to compare strontium isotope intra-tooth variations between reindeer and bison from Level 22 and between reindeer from Level 22 and Level 8
- to compare carbon and nitrogen isotope variations of bone collagen from multiple species through time in order to evaluate any temporal or species-specific trends
- to comment on the seasonal, spatial and temporal aspects of herbivore ecology at Jonzac and the implication for our understanding of Neanderthal behaviour

8.3 Materials

This portion of the project forms a pilot study, utilising the methods explored using modern material in this volume to investigate archaeological faunal samples. Only a small number of samples were selected given the experimental nature of this work and the destructive nature of the sampling method. Once the data from this first application to Palaeolithic material have been assessed, it will then be appropriate to apply this method to more material from this site and to other sites.

Teeth and bone were selected for isotope analysis from a number of stratigraphic units at Jonzac (see Table 8.2 and 8.3 respectively).

Table 8.2 Herbivore molars sampled from Jonzac for strontium isotope analysis.

Square ID	Level	Period	Species	Component
G9-2068	W-US22	Quina Mousterian	*Rangifer tarandus*	M_2R, M_3R
H9-2221	W-US22	Quina Mousterian	*Rangifer tarandus*	M_2R, M_3R
H10-1002	W-US22	Quina Mousterian	*Rangifer tarandus*	M_2R, M_3R
G8-2285	W-US22	Quina Mousterian	*Bison* sp.	M^1 or M^2
F15-557	SW-08	Denticulate Mousterian	*Rangifer tarandus*	M_2L

Teeth were primarily selected from the Quina Mousterian bone bed of Level 22 (W-US22). These deposits are rich with faunal remains, including whole and partial mandibles (with tooth rows; Figure 8.6) and some articulated skeletal components from multiple *Rangifer* individuals. Intra-tooth sampling (and subsequent strontium isotope analysis) was therefore possible from multiple teeth from the same individual allowing the extending of the isotopic profile in each animal. Furthermore, the analysis of multiple individuals is permitted, allowing comparisons within a temporally defined group.

Figure 8.6 Reindeer mandible with complete tooth row from Level 22 at Jonzac (photo courtesy of the Jonzac Project).

The analysis of a single bison molar from Level 22 (the only suitable example available) will allow inter- as well as intraspecies comparisons to be drawn. A single *Rangifer* tooth was also sampled from Level 8 (SW-US08) in order to preliminarily identify any differences in intra-tooth strontium isotope values compared to the earlier Quina Mousterian samples.

Animal bone was also selected for carbon and nitrogen analysis, to complement and add to the existing body of carbon and nitrogen isotope data from the site (Richards et al. 2008c). The data of Richards and colleagues will be included in the subsequent data analysis and discussion of the site in this volume, adding to the new carbon and nitrogen data. This new analysis includes bone from all available units, including the Quina Mousterian fauna, previously not sampled by Richards and colleagues (2008c). This included samples from all stratigraphic units (where available). Other

sampled fauna included horse (*Equus* sp.), bovids (*Bison* sp./*Bos* sp.), beaver (*Castor* sp.) and hyena (*Crocuta* sp.) (see Table 8.3).

Table 8.3 Faunal bone sampled from Jonzac for collagen extraction and carbon and nitrogen isotope analysis during this study.

(* denotes samples that have been identified with a high level of confidence but, due to fragmentation or the loss of non-diagnostic components cannot conclusively be assigned to species). The table does not include the sample list from the previous study (see Richards et al. 2008c).

Square ID	Level	Period	Species
D19-726	SW-US06	MTA	*Equus* sp.
E18-1610	SW-US08	Denticulate	*Crocuta* sp.
D19-1296	SW-US08	Denticulate	*Castor* sp.
E18-404	SW-US08	Denticulate	*Equus* sp.
F12-669	SW-US08	Denticulate	*Equus* sp.
E13-1491	SW-US08	Denticulate	*Equus* sp.
G16-669	SW-US08	Denticulate	*Megaceros* sp.
E13-872	SW-US08	Denticulate	*Bos* sp.
G16-679	SW-US08	Denticulate	*Bos* sp.
E13-974	SW-US08	Denticulate	*Bos* sp.
E16-1327	SW-US08	Denticulate	*Bos* sp.
F15-557	SW-US08	Denticulate	*Rangifer tarandus*
F14-406	SW-US09	Quina Mousterian	*Rangifer tarandus*
F12-549	SW-US09	Quina Mousterian	*Rangifer tarandus*
F16-1144	SW-US09	Quina Mousterian	*Rangifer tarandus*
F16-1143	SW-US09	Quina Mousterian	*Rangifer tarandus**
F12-607	SW-US10	Quina Mousterian	*Rangifer tarandus*
F12-590	SW-US10	Quina Mousterian	*Rangifer tarandus*
F13-823	SW-US10	Quina Mousterian	*Rangifer tarandus*
D17-3	SW-US10	Quina Mousterian	*Rangifer tarandus**
F12-569	SW-US10	Quina Mousterian	*Rangifer tarandus**
F11-166	SW-US12	Quina Mousterian	*Rangifer tarandus*
F11-188	SW-US12	Quina Mousterian	*Rangifer tarandus*
G9-3202	W-US22	Quina Mousterian	*Bison* sp.
H8-2774	W-US22	Quina Mousterian	*Bison* sp.*
G8-2285	W-US22	Quina Mousterian	*Bison* sp./*Bos* sp.
G9-2156	W-US22	Quina Mousterian	*Bison* sp.*
G9-2068	W-US22	Quina Mousterian	*Rangifer tarandus*
G9-2156	W-US22	Quina Mousterian	*Rangifer tarandus*
H10-1002	W-US22	Quina Mousterian	*Rangifer tarandus*
H10-1356	W-US22	Quina Mousterian	*Rangifer tarandus*
H10-1399	W-US22	Quina Mousterian	*Rangifer tarandus*
H9-2221	W-US22	Quina Mousterian	*Rangifer tarandus*

Collagen data will be compared with those already obtained through a previous study (*n*=46; Richards et al. 2008c). These data will be presented alongside those produced from this investigation and will be incorporated into the analysis and discussion of any intraspecific, interspecific and temporal trends.

8.4 Methods

A detailed account of the methods used in the preparation of these samples for isotope analysis can be found in Chapter 6 of this volume. A summary of these methods is also given below, including any modifications made for the archaeological materials.

Isolated teeth, teeth with attached bone and several hemi-mandibles (with complete or partial tooth rows) were selected for analysis. Further bone samples from identified animal bones were also selected. Second and third molars were carefully removed from the hemi-mandibles, using a diamond coated circular drilling disc where necessary. In each instance, where possible, a section of bone was also removed for collagen extraction and isotope analysis (approximately 0.5-1.0g).

8.4.1 Bone collagen

Bone sections were cleaned using air-powder power abrasion in order to remove adhering extraneous materials or trabecular bone. This step to remove an external layer of bone is especially important during the analysis of archaeological materials as contaminants originating from the burial environment could have penetrated the surface of the bone and could influence isotope ratios of extracted collagen (e.g. with soil lipids or humic acids).

Bone samples were then demineralised and collagen was extracted, filtered and analysed as detailed in Chapter 6.4.

8.4.2 Tooth enamel

Teeth were prepared and serial sectioned using the same methodology described in Chapter 6 (this volume) and also described by Britton et al. (2009). After being extracted from the mandibular bones (where necessary), all teeth were mechanically abraded using a tungsten carbide burr (NTI-Kahla, Germany). This was done to remove surficial enamel, which is more likely to be diagenetically altered or contaminated with exogenous strontium from the burial environment. As with the modern samples, intra-tooth sampling was performed using superfine diamond-coated circular drilling discs. All drill-bits were cleaned prior to use and between samples (to avoid powder cross-sample contamination) using a weak nitric acid solution, a water rinse and the ultrasonic bath (see details in 'Methodology', Chapter 6.2).

Using the circular drilling discs, the buccal face of the anterior loph of each tooth was removed. This was selected due to the slightly thicker enamel normally found in this portion of the tooth (Britton et al. 2009). Adhering dentine in the interior of each portion of enamel was removed using a clean tungsten carbide burr. Then, in order to remove further material from the dentine-enamel junction, interior surfaces were additional abraded clean. This was done to ensure all dentine was removed and to ensure only enamel would be analysed. This is important because dentine has a different structure to enamel and forms at different rates. Furthermore, and perhaps most significantly, dentine is less dense and more porous than enamel and is far more susceptible to diagenetic alteration in the burial environment (Budd et al. 2000; Hoppe et al. 2003; Trickett et al. 2003). Therefore the careful removal of all dentine (along with external and internal enamel surfaces) is imperative when preparing archaeological or palaeoecological samples for strontium isotope analysis.

Intact faces of enamel were then marked for horizontal sequential sampling using the diamond-coated disc. This was done at ~1.5mm intervals. Whole enamel faces were ultrasonicated for 10 min and left to dry at room temperature. Sections were cut using the drilling disc, with each section being ultrasonicated in deionised water individually for ~5 min in order to remove any adhering enamel powder. As with the modern samples, sections were given sequential sample number assignments, starting from cemento-enamel junction, in order to plot the data in order of tissue formation.

Enamel samples were then prepared for solution strontium analysis in the clean laboratory facilities and MC-ICP-MS facility at the MPI-EVA. Methods used were similar to those detailed by Deniel and Pin (2001) with modifications outlined in Copeland et al. (2008a). Details of this procedure are also described in full in Chapter 6 'Methodology'.

8.4.3 Isotope ratio measurements

Stable carbon and nitrogen isotope measurements on collagen were performed in duplicate (0.45 – 0.55mg of collagen per sample) on a Delta XP mass spectrometer coupled to a Flash EA 2112 elemental analyzer in the Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. The $\delta^{13}C$ values and $\delta^{15}N$ values are reported relative to the V-PDB standard and AIR standards respectively. Analytical error for the $\delta^{13}C$ and $\delta^{15}N$ measurements was calculated from repeat measurements of internal and international standards and was determined to be ±0.1‰ (1σ) or better. The international standards NBS-22, IAEA-CH6, IAEA-CH7, IAEA-N1 and IAEA-N2 were used to calibrate the reference gas and to assess inter- and intra-run accuracy and precision.

Strontium isotope ratio measurements were determined using a Thermo Fisher Neptune™ plasma ionization multicollector mass spectrometer. $^{87}Sr/^{86}Sr$ measurements were corrected for krypton (Kr) and rubidium (Rb) interferences and normalised for instrumental mass bias. Repeated analysis of an international standard (NIST SRM987) was used for external normalization of all data. The long-term $^{87}Sr/^{86}Sr$ value, determined over a ten-month period, was 0.710273±0.000033 (46ppm, 2σ, *n*=97). The average internal error of any given measurement was 0.000006±0.000004 (8ppm, 2σ, *n*=97) (Copeland et al. 2008a). Reported $^{87}Sr/^{86}Sr$ values were adjusted to the published SRM987 value of 0.710240 (Johnson et al. 1990; Terakado et al. 1988) and strontium concentrations were determined with an accuracy of ±31ppm (Britton et al. 2009; Copeland et al. 2008a).

8.5 Results and Discussion

8.5.1 Results

The results of isotopic measurements are summarised in the Appendix in Tables A.17 and A.18 (intra-tooth enamel $^{87}Sr/^{86}Sr$), Table A.19 (dentine $^{87}Sr/^{86}Sr$) and Table A.20 (whole bone collagen carbon and nitrogen).

8.5.2 Strontium

Sequential strontium data are plotted in Figure 8.7 and as box plots in Figure 8.8. Given the number of individuals in question, no statistical approaches for data analysis have been employed with the analysis of the serial strontium data.

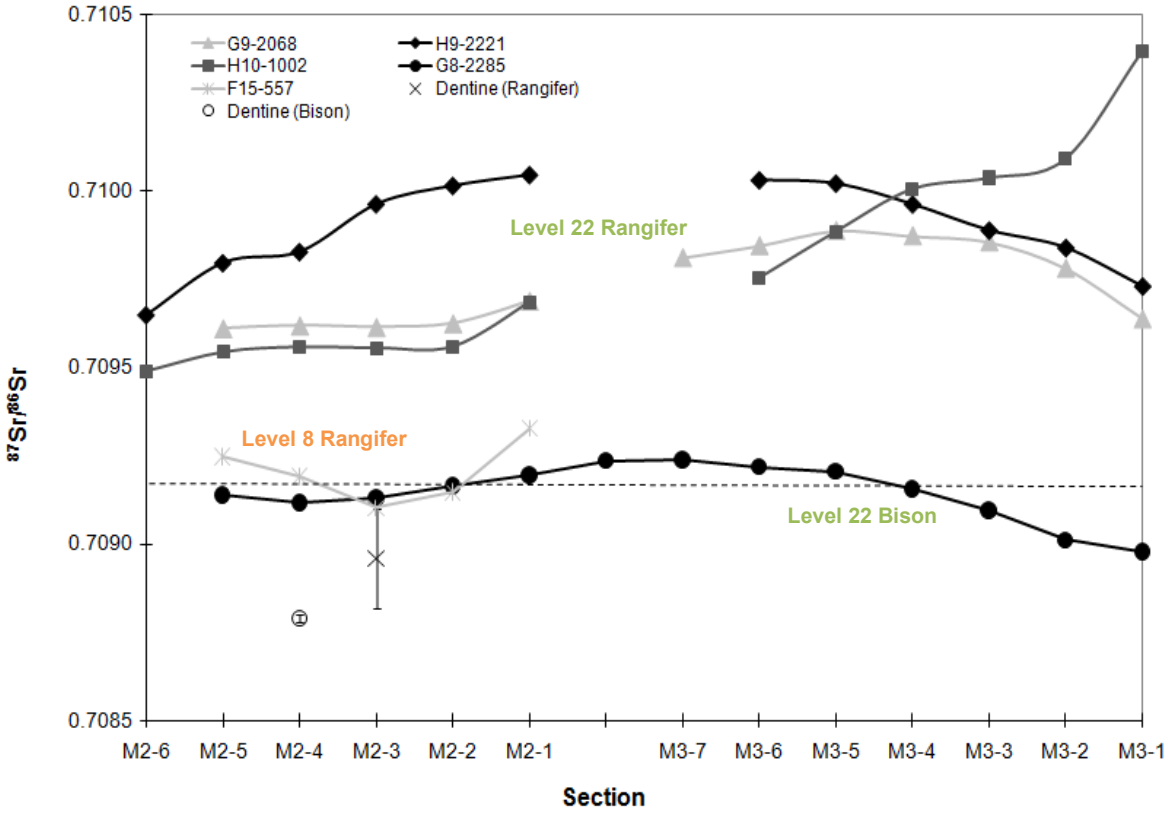


Figure 8.7 Sequential $^{87}Sr/^{86}Sr$ data from *Rangifer* and *Bison/Bos* enamel from Level 22 and the single Rangifer from Level 8.

This graph also incorporates dentine strontium isotope data and the dashed line shows the $^{87}Sr/^{86}Sr$ value of modern rainwater. Analytical error is within the point markers. Level 22 reindeer =G9-2068, H10-1002 and H9-2221, Level 22 bison = G8-2285, Level 8 reindeer = F15-557)

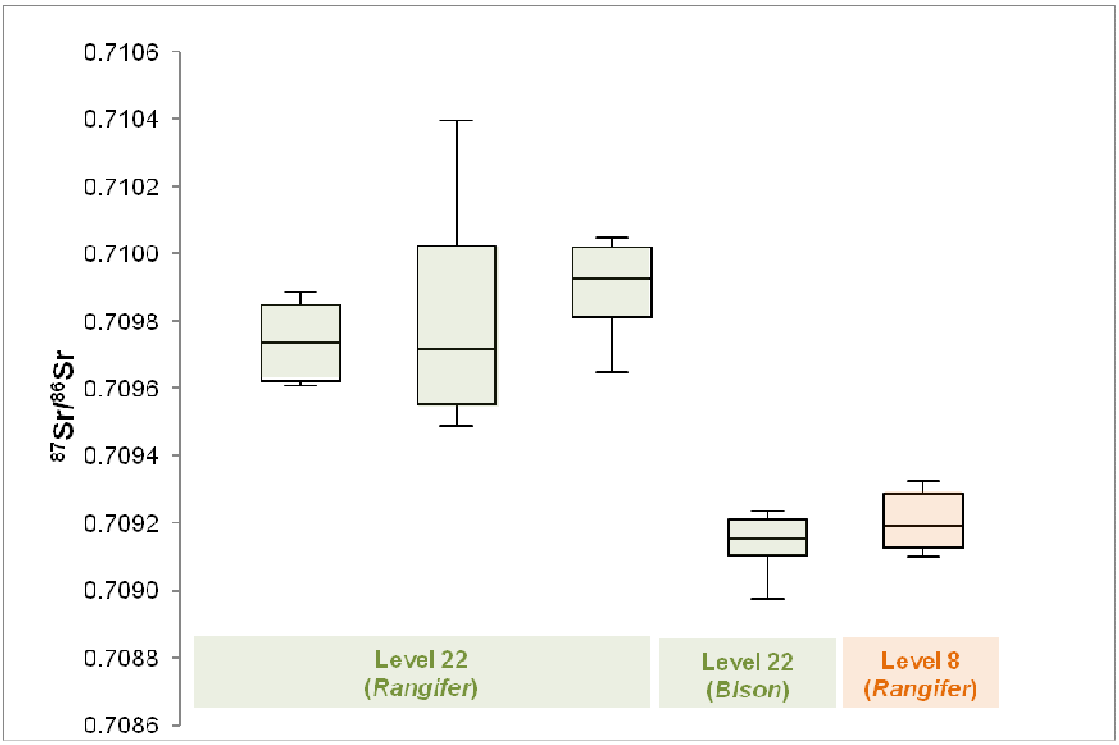


Figure 8.8 Sequential $^{87}Sr/^{86}Sr$ data from *Rangifer* and *Bison/Bos* enamel from Level 22 and the single Rangifer from Level 8.

Box plots display the first and third quartile, median, minimum and maximum and any identified outliers.

The total isotopic range of strontium data from all samples and all animals involved in this study is fairly large (from 0.7090-0.7104). Strontium concentrations in the enamel range from 13 to 166 (±31)ppm with a mean of 75ppm. These values are comparable to those observed in archaeological domestic cattle from England (Evans et al. 2007) and modern Alaskan and Canadian caribou (Britton et al. 2009: 1167 and this study, Chapter 7). The strontium isotope values determined from the Level 22 herbivore dentine are lower than the values measured in the enamel (range = 0.7087-0.7092, mean = 0.7089 ± 0.0001 (1σ)) and strontium concentrations are higher (mean = 100ppm). These data indicate that diagenetic alteration of dentine within the burial environment has occurred moving dentine strontium isotope values towards the strontium isotopic composition of the surrounding limestone soils (0.7089±0.0017; Kelly 2007). This type of diagenetic alteration is expected in dentine

(Budd et al. 2000; Hoppe et al. 2003; Trickett et al. 2003), confirming it as an unsuitable analyte for archaeological strontium isotope studies.

8.5.2.1 Level 22 Rangifer

The three *Rangifer* individuals from Level 22 demonstrate strontium isotope intra-tooth variation in the second, third or fourth decimal place. Given that analytical precision was 0.000006±0.000004 (2σ, *n*=97), this is within the level of interpretation. The total range of enamel $^{87}Sr/^{86}Sr$ isotope data for these individuals is 0.7095-0.7104 with a mean of 0.7098±0.0002 (1σ). These three individuals (G9-2068, H10-1002 and H9-2221) display a strikingly similar overall trend in the first-forming second molar, from lower values in the earliest forming parts of the M2 (0.7096 ± 0.0001(1σ) at point M2-5) to slightly higher values (0.7098 ± 0.0002 (1σ) at point M2-1). There is also agreement between strontium isotope data obtained from the three individuals from the upper and middle crown portions of the third molar and clear continuation from the latter forming parts of the M2 (0.7099 ± 0.0001 (1σ) at point M3-6 and 0.7099 ± 0.0001 (1σ) at point M3-4). Individuals G9-2068 and H9-2221 remain similar (0.7097 ± 0.0001 (1σ) at point M3-1) but H10-1002 differs at this point, rising to 0.7104 at point M3-1. The total amount of time incorporating these isotopic fluctuations is inferred to represent approximately one year of life of these animals (Britton et al. 2009: 1167; Brown and Chapman 1991a, 1991b). The amount of intra-tooth variation and general pattern of strontium isotope variation is consistent with a seasonally migrating animal (Britton et al. 2009). The fluctuating strontium isotope ratios within the enamel demonstrate movement between two different geological terrains. This is the first evidence for seasonal migratory behaviour in Pleistocene reindeer. Furthermore, the close agreement between the different individuals in many portions of their M2 and M3 molars, is similar to patterns observed between members of the same modern herd (Britton et al. 2009).

In fact, intra-group variability within this small sample of late Pleistocene *Rangifer* is as small as, or smaller than, the modern herds investigated in this study.

The inter-individual similarities in major portions of both teeth indicate spatial proximity throughout much of the first year of life, indicating that these individuals shared the same migration routes and may be from the same herd. The degree of similarity in these values could indicate either closely-allied behaviour in contemporary individuals or high fidelity to movement patterns throughout the period of time represented in the human accumulation of these deposits. The reindeer bone bed in this portion of Level 22 is a deep sequence, rich in anthropogenically modified bone but is likely to have been accumulated fairly rapidly, perhaps during a small number of hunting events (Steele et al. 2009). The isotope data here perhaps supports the idea of a rapid accumulation, the product of hunting events in which Neanderthals targeted the same reindeer herd. These data go beyond bulk isotopic sampling techniques which have been employed to identify single or multiple kill events in archaeological contexts (Fenner 2008, 2009), not only identifying a group – the likely product of a single hunting event or closely-timed series of episodes – but also revealing the movement habits of the animals in question.

Given the large volume of remains and butchery evidence at Jonzac (i.e. primary processing), it is unlikely that these materials were transported long-distances from other areas. It is therefore clear that the *Rangifer* found at Jonzac did spend a portion of their annual movement cycle in the area close to the site. However, the strontium isotope values of the Level 22 *Rangifer* are universally higher than the top soil and plant strontium values from a proximal area of similar geology (~0.7089; see Kelly 2007, and Figures 7 and 8 above). The strontium isotopic evidence therefore does not indicate they were a local species and instead geologies other than those found at the site contribute to strontium isotope ratios observed in the dentition. Like modern

caribou, the Jonzac reindeer may have moved quickly through the local area during their annual migrations, with the local area strontium isotope signature becoming 'diluted' by contributions from other geological areas. Given that season-of-death information indicates Neanderthal hunting of reindeer during the winter and spring (with a possible event in the autumn) the different types of evidence are in agreement, pointing to the exploitation of these animals during their annual migrations. It is the seasonal availability of reindeer in the local area that accounts for the abundance of *Rangifer* in the Level 22 assemblage compared to other herbivores.

Despite being higher than values measured in the local limestone soils and plants, strontium isotope ratios determined in the Level 22 reindeer enamel are not as high as those measured in Kelly's study for the clay and granite zones (~0.7129 and ~0.7168 respectively; Kelly 2007). The shape of the intra-tooth strontium isotopic profiles indicates seasonal movement; however, the isotopic data do not confidently tie these animals to any of the proximal geologies. A degree of attenuation can be expected in the intra-tooth isotope values – the likely product of the formation/mineralisation phasing in the teeth, the sampling method and the feeding/ranging behaviour of this animal. A similar effect has been observed in the modern herds (Britton et al. 2009; this study). In this instance, perhaps the mixing of isotopic signals in these individuals is indicative of moving between these areas or through these areas during their migrations. The range size of these animals could have been vast, with the winter and summer portions of their range (while being geographically distinct and producing a specific isotopic signature in the teeth) incorporating a range of geological substrates and producing a mixed signal in the teeth. Although locations of the summer and winter ranges cannot be inferred, using the isotopic data we can deduce that these animals shared similar life histories, were non-local (i.e. they were incorporating non-local strontium throughout much or all of their enamel formation), and engaged in seasonal migratory movements. The

isotopic evidence for the consumption of lichen (see below), winter behaviour demonstrated in modern caribou and isotopically apparent in experimental studies, further supports this seasonal behaviour.

8.5.2.1 Level 22 Bison/Bos

The *Bison/Bos* $^{87}Sr/^{86}Sr$ values range from 0.7090-0.7091 (0.7091±0.0001 (1σ)) throughout the formation of this molar. These values are lower than the contemporary *Rangifer* (discussed above) and a lower amount of intra-tooth variation is displayed in this animal compared to the second or third molars of any of the Level 22 reindeer. Strontium isotope ratios displayed in this individual are also far more similar to the mean local soil and plant values, determined from Kelly's study of a proximal area of similar limestone geology (2007; Kelly et al. 2008). Both these factors indicate that this animal did not undertake significant movements over different geological terrains during molar enamel formation and that local strontium sources made a large contribution to the strontium isotope values found in the tooth. This may indicate that *Bison/Bos* were available in the area throughout the year. This may be true of other species which are also represented in low-densities in the Quina Mousterian deposits at Jonzac, such as horse.

8.5.2.3 Level 8 Rangifer

A single *Rangifer* molar (M2) from Level 8 deposits at Jonzac was also sequentially-sampled and strontium isotope ratios were determined. The range of values measured in this tooth was 0.7091-0.7093 (0.7092±0.0001 (1σ)). Given that this is a single tooth, caution must be taken when interpreting the data. However, it is nevertheless apparent that patterns observed in this Denticulate Mousterian individual are different from those seen in the earlier Quina Mousterian *Rangifer*. The strontium isotope values measured in the Level 8 individual are lower than those from the Level 22 reindeer, and are closer to mean strontium values measured in

local soils and plants (Kelly 2007; see Figures 8.7 and 8.8 above). Furthermore, the range of values and amount of intra-individual variation is lower in this specimen (see Figure 8.10). This pattern persists when the strontium data from only the second molars of the Level 22 *Rangifer* are included (0.7097±0.0002 (1σ) in the Level 22 *Rangifer* M2 and 0.7097±0.0002 (1σ) in the Level 22 *Rangifer* M3). These differences in absolute values and intra-tooth variation between the Quina and Denticulate Mousterian period *Rangifer* may provide the first tentative evidence for changes in reindeer migratory behaviour through time, and may indicate that this species was more 'local' and less vagile during the later, warmer period. This may account for the more even representation of the different herbivore species in this period. However, more individuals would be required in order to validate this hypothesis. This is especially important given that a large level of intra-herd variability has been revealed in some modern caribou herds included in this study (see previous Chapters). This could mean that the differences observed between the Level 22 and Level 8 reindeer are not beyond those expected within a typical herd, especially since behavioural outliers have been noted in modern wild herbivore populations (Hoppe 2006b; Hughes 2003). However, given the low level of intra-group variability displayed in the Level 22 *Rangifer*, this seems unlikely. The level of intra-group variability in the Level 22 *Rangifer* is discussed below (see Chapter 8.5.4 'Discussion').

8.5.3 Carbon and nitrogen (bone collagen)

The results from the analysis of the animal bone collagen from Jonzac are summarised in Table A.19 (see Appendix). Considering the age of the samples, collagen preservation is generally good. A number of samples have %C <30% and %N <11%. Despite this data were considered to be acceptable as all C:N ratios fall between the range of 3.1 and 3.5 (after DeNiro 1985; van Klinken 1999) and the δ-values of these samples fall within the main group of the samples (van Klinken 1999).

Collagen yields are relatively low, including many below 1%. However, these C:N ratios demonstrate that the use of ultrafiltration has aided the purification of the sample and the isolation of the intact collagen fibrils in the >30kDa fraction (Richards et al. 2008c).

Rangifer analysed in this study (*n*=18) have $\delta^{13}C$ values ranging from -19.8‰ to -18.4‰ with a mean of -19.1±0.4‰ (1σ). Corresponding $\delta^{15}N$ values range from 4.3‰ to 8.4‰ with a mean value of 6.5±1.3‰. *Bison/Bos* (*n*=8) have $\delta^{13}C$ values ranging from -20.2‰ to -19.1‰ with a mean of -19.7±0.4‰. Associated $\delta^{15}N$ values range from 4.0‰ to 9.0‰ with a mean of 6.2±1.8‰. *Equus* (*n*=4) have $\delta^{13}C$ values ranging from -20.4‰ to -19.8‰ with a mean of -20.1±0.2‰. $\delta^{15}N$ values for horses ranged from 3.9‰ to 6.1‰ with a mean of 5.0±1.0‰. The single examples of other species have $\delta^{13}C$ and $\delta^{15}N$ values of -20.0‰ and 4.7‰ (*Megaceros*), -21.4‰ and 6.2‰ (*Castor*), and -18.48‰ and 8.2‰ (*Crocuta*). Mean isotope data for the different species (all levels) is presented in Figure 8.9.

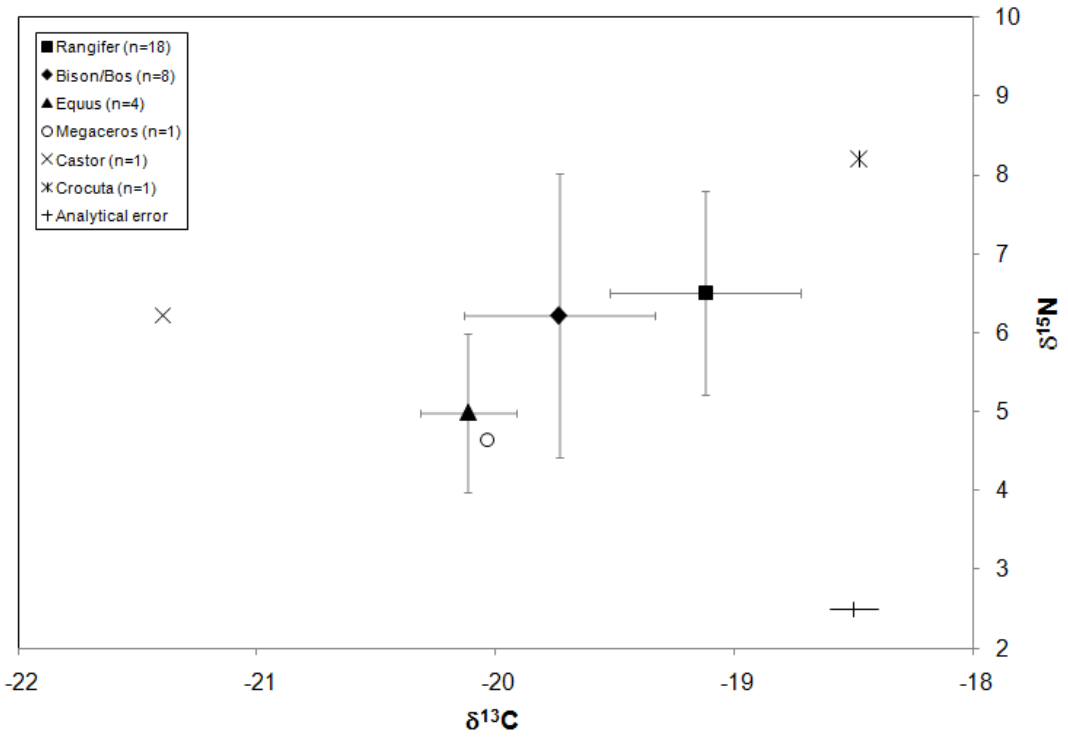


Figure 8.9 Mean carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratio data for Jonzac faunal collagen (this study, all levels). Analytical error (1σ) is ±0.1‰ for carbon and nitrogen.

Despite the small number of samples, some initial patterns are apparent in the data. One clear observation is the higher $\delta^{15}N$ measured in the single sample of *Crocuta*, placing this carnivorous species 2-3‰ (i.e. a trophic level) higher than the majority of herbivorous fauna sampled. Another outlier is the single *Castor* sample, displaying $\delta^{13}C$ values at least 1.5‰ more depleted in the heavier isotope compared to any of the other species. Modern beaver species are herbivorous, living in freshwater environments. Their diet consists of herbaceous terrestrial foods, the leaves, twigs and bark of certain tree species, and freshwater plants (Aleksiuk 1970; Doucet and Fryxell 1993; Jenkins and Busher 1979; Northcott 1972). It could be suggested that the comparatively more negative $\delta^{13}C$ values observed in the *Castor* collagen could be consistent with the consumption of woody plant foods. ^{13}C depletion has been noted in forested environments, where CO_2, organic decomposition and light intensity influence carbon isotope availability to understory trees and shrubs – the so-called 'canopy effect' (Medina and Minchin 1980; van der Merwe and Medina 1991). However, it is suggested that this effect – seen in modern rainforests – is not a likely scenario in glacial northern Europe. Instead it is suggested that the more negative $\delta^{13}C$ values indicate the consumption of aquatic plant foods, which tend to be depleted in the heavier isotope (Cloern et al. 2002). The slightly elevated $\delta^{15}N$ values are also consistent with the consumption of freshwater plants (Cloern et al. 2002), which has been observed in modern moose (Maccracken et al. 1993). Generally the range of carbon values from the other species is small and the values observed in *Equus*, *Megaceros* and *Bison/Bos* are typical of purely C_3 terrestrial grazers/browsers. *Rangifer* individuals demonstrate slightly less negative values than the other ungulates. This could be related to the consumption of lichen by this species (Ben-David et al. 2001; Drucker et al. 2001) and is discussed in more depth below. The ungulates display a range of nitrogen values (spanning over 4‰). This, along with the carbon isotope ratios exhibited by these species, can be placed in a better interpretative context when added to the previously published Jonzac faunal data

(Richards et al. 2008c) and arranged stratigraphically (i.e. temporally) (see Figure 8.12 and 8.13 and the discussion below).

The $\delta^{13}C$ and $\delta^{15}N$ data for *Rangifer*, *Bison/Bos* and *Equus* from all levels, with averages for all three species, are plotted in Figure 8.10 and Figure 8.11 respectively. Data from Richards et al. (2008c) have been incorporated into these figures, adding an additional 42 data points (*Rangifer* n=12, *Bison/Bos* n=20, *Equus* n=10).

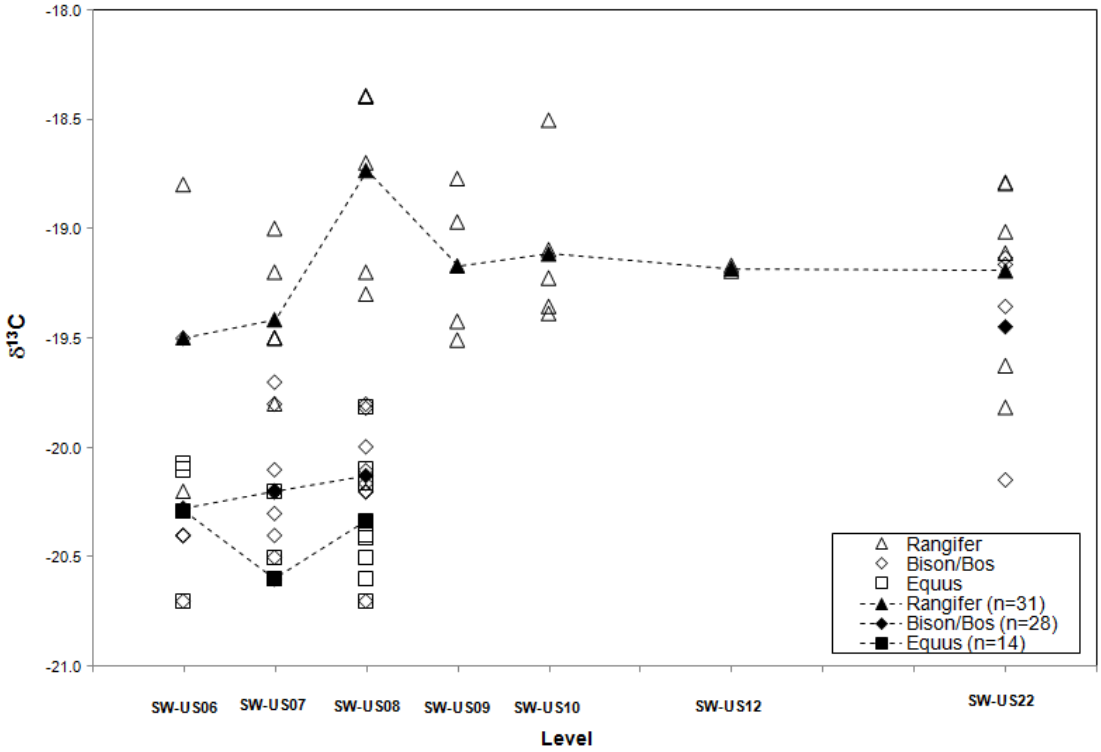


Figure 8.10 $\delta^{13}C$ data for *Rangifer*, *Bison/Bos* and *Equus* from all levels, incorporating data from this study and data taken from Richards et al. (2008c).

Mean values are shown in the block symbols. Analytical error was ~0.1‰ or better (1σ).

The $\delta^{13}C$ values show little variation within species between the different levels. This correlates with the previous findings from Jonzac (Richards et al. 2008c). Furthermore, these findings also agree with other data from the European late Pleistocene, which also demonstrate little temporal variation in herbivore bone collagen (Richards and Hedges 2003). However, data from this study (and when combined with that of Richards and colleagues (2008c)), demonstrate clear

interspecies variation – specifically consistently less negative $\delta^{13}C$ values in *Rangifer* compared to *Bison/Bos* and *Equus* (see Figures 8.10 and 8.11), with a mean $\delta^{13}C$ value of -19.2‰ for *Rangifer* (n=31), -20.1‰ from *Bison/Bos* (n=28), and -20.4‰ (n=14) for *Equus* (data combined from this study and Richards'). Although this difference of ~1‰ is fairly small, *Rangifer* values are consistently less negative across all contexts, confirming this is a real pattern. Mann-Whitney U tests confirm the $\delta^{13}C$ reindeer data is significantly different from the bison (p<0.001) and the horse (p<0.001). A pairwise comparison on the horse and bison is not significant at the 0.01 level, and only just significant at the 0.05 level (p=0.05).

Higher proportions of ^{13}C have been previously observed in *Rangifer* from other late Pleistocene European sites (Bocherens 2003; Fizet et al. 1995). This has been related to the seasonal consumption of forage such as lichens and mushrooms, which are enriched in ^{13}C compared to other C_3 plants (Ben-David et al. 2001; Maguas and Brugnoli 1996; Park and Epstein 1960). These seasonal dietary shifts and the influence of winter foraging on the tissue isotope chemistry of *Rangifer* has been demonstrated by the preliminary studies of modern caribou dentine (Drucker et al. 2001) and blood (Ben-David et al. 2001). This conjecture is also strongly supported by the extensive data set produced by the current study of modern Alaskan and Canadian caribou (see Chapter 7). The Jonzac *Rangifer* bone collagen carbon isotope data provide insight into the feeding ecology of this species, demonstrating the conservation of niche behaviours over many thousands of years and confirming that, in this species, resource portioning within an ecosystem can be discerned using carbon isotope ratios even in purely-C_3 terrestrial environments. The consumption of lichen (and the necessary gut microflora required to do this) is clearly a biological adaptation with a long history in genus *Rangifer*, and is not a more recent adaptation to life in the northern circumpolar barrenlands and taigas. The occurrence of this behaviour and adaptation in the past clearly warrants further investigation. Intra-

tooth dentinal collagen and/or sequentially-sample enamel carbonate carbon isotope analysis could potentially reveal whether or not this behaviour was seasonal, as with the modern caribou herds.

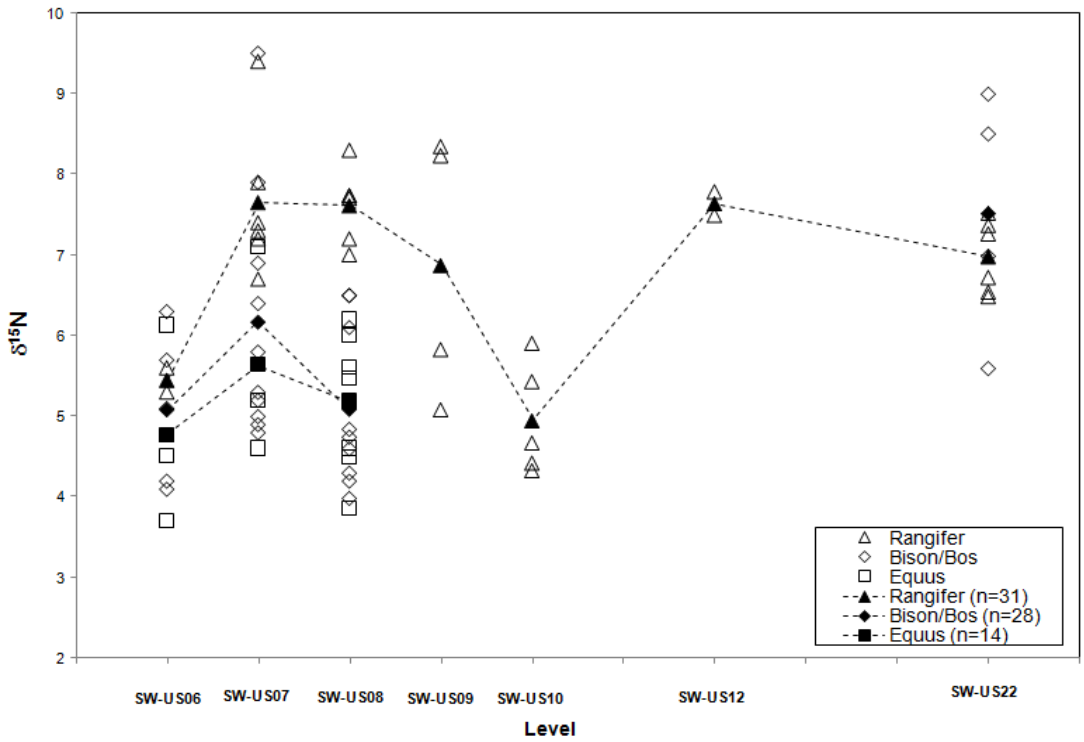


Figure 8.11 $\delta^{15}N$ data for *Rangifer*, *Bison/Bos* and *Equus* from all levels, incorporating data from this study and data taken from Richards et al. (2008c).

Mean values are shown in the block symbols. Analytical error was ~0.1‰ (1σ) or better.

The corresponding mean nitrogen isotope values at different levels also demonstrate ^{15}N-enrichment in *Rangifer* compared to the two other main herbivore species found at the site. Mean $\delta^{15}N$ for *Rangifer* is 6.8 (n=31), compared to 5.8 (n=28) and 5.2 (n=14) in *Bison/Bos* and *Equus* respectively. On average, *Rangifer* $\delta^{15}N$ values are ~1.3 higher than the other two herbivore species. Pairwise comparisons using the Mann-Whitney U test indicate significant differences between the reindeer and bison (p=0.003), and the horse (p<0.001). There is no significant difference between the $\delta^{15}N$ of the horse and bison at the 0.05 level (p=0.238). As with the observed trend in $\delta^{13}C$, these higher $\delta^{15}N$ could correspond to certain foods present in the diet of the reindeer and not included in the diet of other contemporary herbivores which have

higher $\delta^{15}N$ values, such as mushrooms (Ben-David et al. 2001). Other winter foods, such as lichens, are also poor in protein and may cause the recycling of body protein during winter (Drucker et al. 2001). This produces urea enriched in ^{14}N and tissues with higher $\delta^{15}N$ values. The relationship between dietary protein content and excreted nitrogen has been demonstrated by a number of controlled feeding experiments (e.g. Sponheimer et al. 2003a). It is therefore possible that the higher amounts of ^{15}N found in the bone collagen of these late Pleistocene *Rangifer* (compared to other Jonzac herbivores) are the product of regular periods of prolonged low-protein intake or semi-starvation brought about by the low-quality of winter forage, its scarcity, or both. Higher $\delta^{15}N$ values are then expected in remaining tissues (Caloin 2004; Macko et al. 1986; Macko et al. 1987). These data indicate that, like modern caribou, late Pleistocene reindeer suffered (potentially seasonal) periods of physiological stress, due to the low quality or low availability of their forage. As bone remodels slowly over time, with periods of malnutrition resulting in halted growth and possible protein re-absorption, it would be likely that bulk bone collagen values could become permanently enriched in ^{15}N.

Unlike the $\delta^{13}C$ values, there is considerable variation in $\delta^{15}N$ in all species throughout different periods studied at Jonzac. Such $\delta^{15}N$ values have been noted in herbivore species at other sites during the Pleistocene and Holocene and may be linked to environmental change (Richards and Hedges 2003; Stevens and Hedges 2004; Stevens et al. 2008). The mean $\delta^{15}N$ values for *Rangifer*, *Bison/Bos* and *Equus* are all higher in Level 7 than Level 6, *Rangifer* values remain high in Level 8, whereas *Equus* and *Bison/Bos* $\delta^{15}N$ values are reduced. Changes in the 'baseline' $\delta^{15}N$ (as indicated by the typical C_3 grazers, horse and bison/aurochs), may be correlated with environmental shifts that could have occurred during this period. Higher $\delta^{15}N$ in soils and plants have been linked to water-availability in soils, with aridity, salinity and freezing-conditions (fixing available water in ice) contributing to higher

proportions of ^{15}N in soils and plants (e.g. Heaton et al. 1986; Schwarcz et al. 1999; van Groenigen and van Kessel 2002). The $\delta^{15}N$ for all three species are far more similar to each other in Level 6 than any other level, possibly indicating similar feeding behaviours in what may have been a slightly warmer and moister period (Richards et al. 2008c). The $\delta^{15}N$ of *Rangifer* bone collagen remains is much higher than that of *Equus* or *Bison* for the preceding period (Levels 7 and 8) and may indicate more specialised feeding behaviour in less clement environmental conditions. Alternatively, these data could indicate the greater occurrence of physiological stress in *Rangifer* populations at this time. The $\delta^{15}N$ of *Rangifer* is much lower in Level 10, perhaps indicating a shift in baseline $\delta^{15}N$ due to climate or an increase in forage quality and availability. *Rangifer* dominate the assemblage in the later levels (12 and 22) and $\delta^{15}N$ values remain high, indicating consistency in the feeding behaviour or physiological responses of this species for a significant period of time. *Bison/Bos* $\delta^{15}N$ are also high in the earliest phases of this site (Level 22), indicating that baseline $\delta^{15}N$ may have been high due to contemporary environmental conditions. The faunal suite (*Rangifer*-dominated) and dating of these contexts point to a cold, tundra-like environment and the high $\delta^{15}N$ values seen in both species in Level 22 appear to confirm a cooler and more arid period. A larger number of analyses conducted on different species from Levels 9, 10 and 12 are needed in order to complete a picture of temporal isotopic change in herbivore collagen at Jonzac and will help to differentiate between species-specific/niche related trends and those that could be the product of fluctuating climatic conditions.

Another factor that must be considered during the analysis of trends in $\delta^{15}N$ is the influence of migratory behaviour – and therefore feeding from two or more potentially distinct climatic zones – on bulk bone collagen. High $\delta^{15}N$ values are observed in both the 'local' Level 8 *Rangifer* and the migratory, non-local *Rangifer* (as indicated from the strontium isotope data) from Level 22. This may indicate that

migration and feeding from multiple areas may play less of a part in determining bulk bone nitrogen isotope ratios than the niche feeding behaviour of an animal. Conversely the high $\delta^{15}N$ values – similar to those of *Rangifer* - measured in the 'local' Level 22 bison appear to confirm that overall climatic trends play the largest role in determining bulk bone collagen nitrogen isotopic ratios. Significantly the variable migratory behaviours observed through time, combined with climatic variations (as evidenced by the isotopic 'baseline' shifts and differential species abundance) and apparent changes in feeding behaviour/physiology in response to nutritional stress indicate the clear variability of these factors through time. This highlights the importance of faunal isotopic studies in order to understand the complexity of broad-scale ecosystemic and animal behavioural change in archaeological and palaeoecological contexts. It is clear that the dynamism of animal feeding and migratory behaviour (as evidenced by stable isotope analysis) is multi-faceted and the degree to which exhibited values are the product of environmental change (without foraging behaviour modification) or due to changes in feeding/migratory habits in response to climatic change (or other factors) is something which warrants greater investigation. For this, a larger number of samples from multiple herbivore species of different sizes should be incorporated into future studies. Where possible, data should be correlated with other direct palaeoclimatic or dating evidence or aligned with other proxies.

8.5.4 Discussion

Despite limitations of scale, this study has provided insight into the seasonal movements and palaeoecology of late Pleistocene *Rangifer* and *Bison* at the Middle Palaeolithic archaeological site of Jonzac. This study has been the first to unequivocally demonstrate seasonal movements in populations of ancestral European reindeer, a behaviour that has hitherto been assumed on the basis of modern species. The data presented here provide direct evidence that this species –

like many modern Alaskan and Canadian caribou populations – undertook seasonal migrations, at least during this cool and arid climatic phase in southwest France.

These data are the result of the first practical application of methods developed and tested on modern caribou and bison samples in this study. The three Level 22 reindeer analysed demonstrated a high degree of intra-group fidelity, which is perhaps surprising given that (as an archaeological context) the precise nature and timing of deposition of these faunal remains cannot be known. This low-level of intra-group intra-tooth variability demonstrates that these individuals shared similar migration routes and life-histories – at least during the period of second and third molar formation (i.e. during the first year of their lives). This low level of intra-individual variation is striking and – disregarding the unlikely instance these individuals are from exactly the same birth cohort – perhaps exemplifies that herd behaviour (both inter-individual and inter-annual) was more stable in the late Pleistocene than in many modern herds. This may be due to the lack of interferences of modern infra-structure, range disruption, herd management and humanly-induced climatic/environmental changes that have been demonstrated to influence migration habits in modern herbivore species (e.g. Dahle et al. 2008; Joly et al. 2002; Joly et al. 2003; Serneels and Lambin 2001).

The low-level of intra-group variability observed in the Level 22 *Rangifer* leads to two interpretative scenarios – that (a) the specimens originate from the same large herd, hunted over a number of small chronologically-proximal episodes, or (b) that migratory behaviour in the Quina Mousterian reindeer population at Jonzac was relatively stable throughout the formation of the deposits. Given the richness of the faunal deposits and other evidence for a rapid accumulation of these deposits, the former explanation may be more likely. This complements season-of-death data at the site and implies the *Rangifer* remains are the result of intensive seasonal exploitation of this species during their annual migration. The strontium isotope

values obtained from these individuals implies that they spent large portions of their lives on non-local geologies, which may also support the conjecture that Jonzac was situated somewhere along the migration route of these seasonally-moving animals. This may explain the selection of this site by Quina Neanderthals, who may have returned to the site each year over a number of years, exploiting the seasonally-abundant and predictable resources. This seasonally-restricted use is also indicated by the low density of remains from other species in the Level 22 deposits, with species such as *Bison/Bos* likely to be local species available all year round (as inferred by the strontium isotope data).

These strontium data also give tentative evidence for a shift in migratory behaviour in *Rangifer* at Jonzac through time. The later Level 8 reindeer demonstrates both a decrease in intra-tooth variability in strontium isotope ratios, and universally lower values compared to the Level 22 population, exhibiting more 'local' strontium isotope values. Given the similar trends in intra-group intra-tooth values in the Level 22 reindeer, it seems unlikely that data from this individual represents the expected range of values from the Jonzac reindeer as a whole. The evidence instead suggests that this individual undertook movements that encompassed more of the local lithology and therefore may have had a restricted herd range compared to the earlier Level 22 reindeer. The increased local availability of this species throughout the year, along with horse, bovids and other herbivore species, probably explains the more even representation of these species in the Level 8 deposits compared to the earlier contexts. Furthermore, without a long-distance seasonal migration it is unlikely that the local environment could have supported the vast numbers of animals seen in modern migratory caribou. Populations of modern sedentary (or short-distance-migratory) woodland and barren-ground caribou are normally smaller than their long-distance-migratory counterparts by several orders of magnitude. For example, the sedentary Red Wine Mountains caribou herd occupy a herd range of approximately 25,000km^2 in central Labrador and had a population of ~150 animals

in 1997 (Schaefer et al. 1999). By contrast, the migratory George River herd (Labrador and northern Québec) has a total herd range of around 700,000km^2 and was estimated to have a population of between 600,000 and 800,000 in 1996 (Schaefer et al. 2000).

Unfortunately, the lack of an M3 in the Level 8 individual means that the seasonality of any movements evidenced by the intra-tooth strontium isotope variation in the M2 cannot be estimated (as the period of growth in each molar is only ~6months). The strontium isotope evidence suggests a more local home range for this animal but whether this individual was exhibiting true (albeit short distance) migratory or home ranging (non-migratory) behaviour is not known. The variations observed between the Quina and Denticulate Mousterian reindeer certainly warrant more investigation and highlight the potential of this method to reveal changes in the migratory behaviour of prey species through time. These approaches could therefore be used to correlate broad-scale climatic shifts in archaeological contexts (e.g. over the Pleistocene/Holocene boundary) with changes in the behaviours of species such as reindeer. This could help gain a better understanding of the impact of climatic change on wildlife populations and also help to understand and define the ecological phenomena of animal dispersals and migrations. Furthermore, such temporal data could also have archaeological implications and help in the interpretation of variations through time within lithic assemblages. Where the organisation of the human landscape is dependent on the niche geography of their prey, understanding what are predictable and unpredictable seasonal resources can influence our understanding of the 'seasonal rounds' of human groups and the preparations (i.e. material culture) made to process the resources encountered.

The carbon and nitrogen isotope data obtained from the analysis of bulk bone collagen from the Jonzac fauna have allowed an examination of climatically-induced baseline changes through time. These data have also given evidence of resource

portioning within this ecosystem, differential feeding behaviours in certain species and even identified what may be some species-specific physiological influences upon body tissue isotope chemistry. Perhaps, as expected, variations in $\delta^{13}C$ values in herbivore collagen through time do not exhibit any significant trends. However, differences in mean bone collagen $\delta^{15}N$ are large between the contexts, reaching more than 3‰. It is suggested that that these variations correlate with changes in local climate and aridity. This trend is especially clear in the reindeer (which are represented in each of the contexts under investigation) and seem to indicate a fluctuating local environment, from potentially cold and arid conditions in Level 22 (TL age 73±7 ka), to moister and warmer conditions in Level 12 (currently no date), before a return to more arid conditions in Level 8 and 7 (TL 55.7±3.2 ka and 49.2±2.8 ka respectively). The lower $\delta^{15}N$ values in the latest phases of the site analysed (Level 6; TL 42±4 ka) indicate a possible return to moister, warmer conditions (Richards et al. 2008c: 182).

In addition to the inferences concerning climatic conditions, the $\delta^{13}C$ and $\delta^{15}N$ data also provide evidence for the different feeding habits employed by *Rangifer* and their physiology. The $\delta^{13}C$ exhibited in the reindeer sampled from all levels are universally higher than those observed in other species. This has been attributed to the seasonal consumption of lichen, a phenomenon seen in modern caribou and known to influence $\delta^{13}C$ of body tissues. $\delta^{15}N$ values are also higher for reindeer in the majority of instances. This can perhaps be linked to the periods of semi-starvation and body wasting the late Pleistocene *Rangifer* may also have undergone on their low-quality winter forage, like modern caribou. Interestingly, nitrogen values of some *Bison/Bos* individuals are also high in some contexts – especially those where colder and more arid conditions are inferred (Levels 7, 8 and 22). This may be a product of natural variation or might indicate that this species suffered some nutritional stress.

8.6 Summary

This study is the first demonstration of the use of isotope analysis to elucidate movements in European late Pleistocene herbivore species. Strontium isotope analysis and the sequential-sampling of enamel has allowed the identification of migratory and non-migratory species at the Middle Palaeolithic site of Jonzac. The analysis of multiple *Rangifer* individuals from the Quina Mousterian bone bed at Jonzac has revealed clear similarities in the seasonality and route of migration. The inter-individual variability within this group is very low, suggesting consistent migration routes at this time and/or the contemporaneity of these individuals, their birth, death and deposition. When combined with seasonality data from Jonzac, it is probable that Neanderthal hunters intensively exploited the reindeer as the herds passed through the area, the rockshelter of Jonzac being located on or near their migration routes. Additional analysis of a single Denticulate Mousterian individual has indicated the potential of this method to reconstructing changes in movement patterns of the same species through time. However, more samples from more individuals would be required to draw conclusions about changes in *Rangifer* migratory behaviour through time at Jonzac. Unfortunately this is beyond the scope of the current preliminary study.

The carbon and nitrogen isotope analysis of bulk bone collagen from the same species in multiple contexts of the same site facilitated the reconstruction of the palaeoclimatic history of the site and also helped to reveal niche feeding behaviours and physiologies of certain species. The analysis of the faunal samples in this study has complemented and built on the existing publish data for the most recent phases of this site (Richards et al. 2008c). The combined data set, now with 79 $\delta^{13}C$ and $\delta^{15}N$ measurements and 53 $^{87}Sr/^{86}Sr$ data points, emphasises the importance of sampling multiple individuals from multiple species when bulk sampling (where possible) and also the validity and importance of detailed individual intra-tissue sampling. The use

of different analytes and isotope systems – methods previously explored on modern experimental samples – have provided complementary data, allowing the reconstruction of the temporal, spatial and feeding palaeoecology of herbivore species at Jonzac. Although small, this preliminary archaeological case study has demonstrated the great potential of the use of multiple isotope methods in the reconstruction of the biogeochemical landscapes of the past and the impact such studies can have in our understanding of hominid site-selection and predation behaviour.

CHAPTER NINE CONCLUSIONS

9.1 Introduction

Through the use of modern wild herbivores, this study has demonstrated the potential for intra-tooth sampling and multi-isotope analysis to reconstruct seasonal movements and dietary habits in archaeologically-important prey species. The stable isotope data, from both bulk and sequentially-sampled tissues, was interpreted within the context of the known behavioural, environmental and climatic parameters of the modern herds, allowing an assessment of the methods. Multiple individuals were analysed, from the two different species, from geographically-distant herds, from proximal herds, and from within the same herd. This permitted the characterisation of intra-herd variability and inter-group differences. The results from the modern *Rangifer* and *Bison* indicate seasonal biogeography and feeding habits that could also be identified in archaeological samples, and also highlight important considerations and possible constraints.

The second stage of this study employed intra-tooth sampling, bulk bone collagen sampling, and multi-isotope analysis to investigate herbivore ecology at the Middle Palaeolithic site of Jonzac. This archaeological case study utilised methods developed from the analysis of modern materials, allowing interpretations of results to made within a framework of reference data. The innovative application is the first demonstration of bi-annual migration and niche feeding behaviour in Pleistocene *Rangifer*. The application of these techniques at Jonzac has also identified biogeographical differences between taxa (i.e. the Quina Mousterian reindeer and bison) and within the same species through time.

With reference to the original aims and objectives (see Chapter 1), the main findings of this research can be summarised in the following points:

- Strontium and oxygen isotope analysis of intra-tooth enamel samples in North American herbivores of known movement histories has demonstrated that these methods can successfully identify patterns of seasonal movements in both migratory and non-migratory fauna.
- Carbon and nitrogen data from sequentially-sampled dentine have been shown to correlate with seasonal dietary changes in wild fauna, particularly in wild caribou, where the seasonal consumption of lichen was isotopically identified in several herds.
- Isotope data from multiple individuals within the modern same herds has indicated the level of intra-herd homogeneity, demonstrating these methods are relevant on a herd level, as well as on an individual level.
- Comparison of different herds has demonstrated that there can be statistically significant differences between groups, even within purely C_3 environments.
- Intra-tooth strontium isotope analysis of Middle Palaeolithic reindeer from the Neanderthal site of Jonzac has revealed the first evidence of seasonal migration in Pleistocene *Rangifer* and indicated possible intraspecific changes through time. Analysis of a single bison suggests that this taxa was non-migratory.
- Bulk bone data from the Jonzac fauna indicate that carbon and nitrogen isotope ratios can be used to reconstruct the feeding and niche ecology of archaeological animals.
- When combined with the archaeological and zooarchaeological evidence from Jonzac, the isotope data indicate that Neanderthals may have employed seasonal strategies of interception hunting in this area of southwest France.

The main conclusions of this study, its potential limitations, implications and future work, are discussed more fully in the following sections.

9.2 Migrants and nomads

The use of two different modern species helped to identify intra-tooth strontium isotope trends that can be expected both in seasonally migratory animals and in nomadic herbivores. Although absolute strontium isotope ratios vary with geological substrate, the data suggest that both total intra-tooth strontium variation and the repeating pattern of values through enamel development can be used to determine seasonal migratory behaviour. In general, the seasonally-migrating modern caribou showed large amounts of intra-tooth strontium isotope variation whereas the non-migratory/nomadic bison showed little intra-tooth variation. Where intra-tooth strontium variation was noted in the bison, the same 'targeted' fluctuating trends seen in the bi-annually migratory caribou was rarely displayed. These same patterns were identified in the Palaeolithic fauna, permitting the identification of local and non-local/migratory species exploited by Neanderthals at the site of Jonzac. However, data from the George River caribou herd indicate that inconsistent herd behaviours or highly variable geologies could potentially complicate the interpretation of strontium isotope data.

9.3 Multi-isotope approaches

Multiple isotope analyses have been applied to both the modern and archaeological fauna in this study, allowing complementary types of data to form a more complete synthesis of spatial and feeding ecology in herbivores. The innovative dual-application of oxygen and strontium isotope analysis to modern sequentially-sampled enamel allowed the placing of strontium data within a seasonal context. At moderate or northern latitudes, where there are seasonal temperature variations and differences in the oxygen isotope composition of water, intra-tooth oxygen isotope analysis can be used to establishing the periodicity of variations in other isotope systems. In modern caribou, this has allowed the isotopic-identification of seasonal migrations (Sr) and the winter consumption of ^{13}C-enriched lichen. The dual-

analysis of nitrogen and carbon isotope ratios in the collagen of sequentially-sampled dentine in modern caribou also suggests seasonal feeding behaviours and physiological effects (where sufficiently pronounced) can also be characterised.

The data suggests that intra-tooth oxygen profiles can be used to complement strontium data in the identification of migrants from non-migrants at a site. Data from the Western Arctic caribou herd suggested that long-distance migratory behaviour in areas of seasonal extremes may serve to attenuate the intra-tooth oxygen isotope signal. Here, the act of migration itself allows the escaping of climatic extremes at either end of the range, resulting in a lower amount of oxygen isotope variation than seen amongst other herds. This could allow the independent confirmation of thermostress migratory behaviour in archaeological fauna. Where migrations are driven by non-climatic factors, this effect is not likely to be seen, as indicated by other modern data. Additional experimental or field data from modern animals is required to better characterise this effect.

9.4 Niche feeding behaviours

The intra-tooth carbon isotope analysis of both enamel and dentinal collagen in modern wild caribou has clearly demonstrated the potential for these methods to identify lichen consumption in this species. Although intra-tooth carbon isotope analysis was not conducted on the archaeological *Rangifer*, bulk bone collagen analysis reveals consistent enrichment in ^{13}C in this species compared to other herbivores analysed throughout the temporal sequence at Jonzac. This trend has also been observed in other archaeological studies (e.g. Fizet et al. 1995).

All of the modern bison included in this study lived in areas of mixed C_3 and C_4 vegetation, which was reflected in the carbon isotope chemistry of their bones and teeth. For the majority of individuals, no clear seasonal use of these different plant foods could be identified. In one individual, the free-ranging Henry Mountains

bison, a pattern of intra-tooth carbon isotope variations was identified, suggesting the incorporation of more C_3 foods during winter periods in low-land areas. This hints at the potential for this technique to investigate seasonal dietary behaviours in the ancestral North American Plains bison. Unfortunately, the other bison under analysis in this were taken from herds contained within national parks and wildlife refuges, so the prevalence of this seasonal habit in free-roaming herds cannot be estimated.

9.5 Herds and kill events

The analysis of multiple individuals within the herd groups allowed an assessment of the amount of natural intra-herd variability. In spite of large home ranges and many hundreds of thousands of animals in the modern caribou herds, individuals show similar isotope values to other herd members – both in their bulk bone collagen and their intra-tooth isotope values. Where seasonal feeding and migratory behaviours are cohesive, and a high degree of fidelity to these shared habits is displayed, this is reflected in the isotope chemistry of the herd. This was reflected in the low amount of inter-individual heterogeneity displayed in the caribou herds compared to the bison herds. The expected variation between individuals of the same modern population was an important consideration for the subsequent archaeological study. The intra-tooth strontium profiles from the three Quina Mousterian Jonzac reindeer displayed as much as or even more intra-group homogeneity than the modern herds. These similarities indicate shared spatial behaviours, indicating these individuals were killed in short temporal proximity and are possibly even from the same herd group, targeted by Neanderthals in multiple hunting episodes.

Bulk bone collagen stable isotope analysis ($\delta^{13}C$, $\delta^{15}N$ and $\delta^{34}S$) of the different herds demonstrated group clustering. Aside from carbon isotope differences due to the separation between the C_4 and C_3 feeders, these herd differences were most

pronounced in the sulphur isotope ratios. The Western Alaska caribou herd exhibited very different bulk collagen sulphur isotope ratios from the geographically distant and geologically distinct Ungava herds. However, although statistically significant, differences in bulk bone collagen data from the geographically-proximal George River and Leaf River herds are small. This suggests that, in purely C_3 ecosystems, the analysis of bulk bone collagen may not be sufficient to identify herd groups of the same species (and thus single kill events) in the archaeological record. However, a large spread of data points within an archaeological assemblage of the same species (i.e. exceeding the amount of variation shown within the same modern group) may indicate contributions from different groups or multiple kill events through time. More work on geographically proximal herds is required to better understand this.

9.6 Limitations

Although all the aims and objectives of this study were achieved, there are some limitations of the current work. Although the modern data have provided a strong basis for the interpretation of archaeological data, there are a number of limitations with the modern data set. Primarily, these issues centre on the quantity of data. Although a large volume of data was generated, using multi-isotope approaches and from different herds, an increased amount of data would give greater support to the conclusions drawn. Furthermore, although comparisons between the modern caribou and bison herds were useful, data from contemporary proximal herds would have been more valuable (for example, obtaining non-migratory muskoxen from the same areas as the migratory caribou). In addition, the collection of local environmental isotope data (for 'bioavailable' strontium), plant foods (carbon and nitrogen) and drinking water (oxygen) would have greatly increased the resolution of these modern studies. However, meaningful environmental sampling in these vast areas would have been extremely difficult for the purposes of this study and far

beyond the scope of the current project in terms of study scale, timing and finance. Finally, although general information about the movements of the modern herds as a whole could be obtained, subject-specific information was unavailable for the individuals involved in this study. In some instances, for example with the Western Arctic caribou herd, it became evident through the isotope analyses that some individuals had very different life histories from other members of the same group (i.e. were population outliers or immigrants). Although all individuals included in this study from the Western Arctic herd had been radio collared for some portions of their lives, this was not during the crucial phases where tooth formation and enamel mineralisation occurred. Therefore, it was not possible to draw correlations between precise known movements and the isotope data determined from teeth.

The archaeological case study offered new and exciting results, and demonstrated the great potential that these multi-isotope approaches have within the field of archaeology and palaeoecology. However, the clear limitation of this application was size. Ideally, a larger number of individuals would have been included in the Jonzac case study. Although the evidence for seasonal migration in the Pleistocene reindeer is novel and compelling, a greater quantity of data would be required to definitively characterise this behaviour. Most notably, data from single specimens (such as the Level 22 bison and the Level 8 reindeer) currently allows little more than tentative preliminary conclusions concerning intra- and inter- specific differences. However, these data have revealed promising insights and suggest great scope for future research.

9.7 Implications and future directions

This study has been the first application of intra-tooth strontium and oxygen isotope analysis to extant wild fauna of different movement habits and herding behaviours, producing an extensive comparative data set for archaeological studies. These data,

along with intra-tooth and bulk tissue carbon and nitrogen isotope analysis, has allowed an assessment of the relationships between herd behaviours and the isotope chemistry of individual animals. The modern data indicates that these methods can be used to explore migratory and seasonal feeding behaviour in archaeological reindeer, and the new archaeological data in the pilot study presented here confirm this, revealing migratory behaviour and niche feeding behaviours in Late Pleistocene reindeer.

Although this study has identified patterns of migratory and non-migratory behaviour in the herbivore species at Jonzac using strontium isotope analysis, it is not currently feasible to suggest more specific geographical and geological points of origin for these animals. This highlights a clear need for more work on the fundamentals of these isotope techniques within the discipline before studies of this type can produce higher-resolution results. In addition to the generation of more modern experimental and observational data, more baseline studies, characterising the local 'bioavailable' strontium in different areas, are required to better understand the relationship between geological substrates and the values exhibited in the mineralised tissues of animals. Work is also needed to understand the chemistry, phasing and geometry of dental tissue formation and maturation. This will also help to determine the best ways of conducting intra-tooth sampling, which should be done in a way to best preserve and represent intra-tooth isotopic variations that were incorporated during life. Methods such as micro-drilling allow the taking of smaller samples which can limit the amount of isotopic signal homogenising during sampling and, in the case of laser ablation, even allow sampling along individual growth lines with teeth. This could be one approach to limit signal dampening through intra-tooth sampling and aid the determining of isotopic inputs. However, these visible structures within enamel do not represent the phases when the majority of mineral incorporation takes place or the direction of this mineralisation process,

and many questions remain. Controlled feeding studies using strontium isotope tracers or trace elemental spikes may represent one effective way of exploring this.

The results of this study are very promising, although it is clear that a greater deal of work is required before higher-resolution data can be obtained. This will only be obtained through a deeper knowledge of the relationship between 'local' isotope signatures, tooth structure and mineralisation, and tissue isotope chemistry. The results from the modern caribou and bison sampled in this study also iterate the importance of considering the physiology, and the behavioural, feeding and ranging ecology of animal subjects when conducting stable isotope studies. It is, however, also clear from the modern data that multi-isotope analysis and sequential dental sampling is a powerful tool for the reconstruction of animal palaeobiogeography and palaeoecology. It is suggested that these methods could be applied to other archaeological and palaeobiological case studies to investigate the spatial and dietary behaviours of other herbivore species. These techniques could also be applied to archaeological fauna from specific sites and contexts, in order to better interpret anthropogenically-accumulated deposits, such as mass kill sites or sites of repeated/seasonal use. In these contexts, an understanding of the palaeoecology and migratory behaviour of large herbivore species could provide insight into the subsistence choices, hunting strategies and the 'seasonal-rounds' of contemporary human groups, as demonstrated by the pilot study at Jonzac. These techniques may also allow the establishing of relationships between different archaeological sites through the reconstruction of the large scale movements of animals, permitting the connectivity of ancient ecosystems and facilitating a better understanding of the socio-cultural connections across the human landscapes of the past.

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PERSONAL COMMUNICATIONS

Dau, J. 2009. Various telephone and email communications.

Munsterman, W. 20th July 2009. Telephone and email communication.

Richter, D. Jan-Feb 2009. Various verbal and email communications

APPENDIX

***For all carbonate data ($\delta^{13}C_{V\text{-}PDB}$ and $\delta^{18}O_{V\text{-}SMOW}$) colours denote in which laboratory data was measured (Durham = green; Bradford = brown; Iso-Analytical Ltd = blue). Please see discussion in Chapter 6.4.2.**

Table A.1 Intra-tooth $\delta^{13}C_{V\text{-}PDB}$, $\delta^{18}O_{V\text{-}SMOW}$ and $^{87}Sr/^{86}Sr$ values and strontium concentration data (ppm) for enamel from *Rangifer tarandus granti* from the Western Arctic herd, Alaska.

Individual	Sample	$\delta^{13}C_{V\text{-}PDB}$	$\delta^{18}O_{V\text{-}SMOW}$	$^{87}Sr/^{86}Sr$	Sr conc (ppm)
WACH-2.210	M2-6	-11.9	14.3	0.7108	180
♀	M2-5	-11.5	13.8	0.7106	172
	M2-4	-11.5	13.3	0.7103	181
	M2-3	-11.5	13.2	0.7103	187
	M2-2	-11.7	12.9	0.7102	146
	M2-1	-12.0	13.0	0.7103	161
	M3-6	-12.6	15.4	no data	no data
	M3-5	-13.0	15.8	0.7107	176
	M3-4	-13.0	16.0	0.7109	117
	M3-3	-13.1	16.2	0.7112	130
	M3-2	-13.1	16.2	0.7112	137
	M3-1	-12.9	16.2	0.7113	134
WACH-2000	M2-5	-11.9	15.4	0.7108	118
♀	M2-4	-11.5	15.0	0.7105	184
	M2-3	-11.2	15.1	0.7102	187
	M2-2	-11.2	15.0	0.7102	188
	M2-1	-11.7	14.8	0.7101	174
	M3-4	-11.9	16.5	0.7114	185
	M3-3	-12.5	17.1	0.7118	81
	M3-2	-12.9	17.3	0.7119	197
	M3-1	-13.1	17.4	0.7119	164
WACH-0.120	M2-6	-12.0	18.5	0.7092	135
♀	M2-5	-11.8	18.0	0.7092	127
	M2-4	-11.1	17.5	0.7092	79
	M2-3	-10.7	16.7	0.7091	83
	M2-2	-10.8	16.7	0.7091	68
	M2-1	-10.5	16.4	0.7091	78
	M3-6	-10.0	16.1	0.7090	111
	M3-5	-10.2	16.2	0.7090	119
	M3-4	-10.6	17.1	0.7090	102
	M3-3	-10.9	17.7	0.7091	110
	M3-2	-11.4	18.5	0.7090	99
	M3-1	-11.6	18.2	0.7091	138
WACH-2.230	M2-6	-10.4	14.4	0.7105	91
♂	M2-5	-9.8	14.0	0.7106	72
	M2-4	-9.5	13.9	0.7098	73

	M2-3	-9.3	13.7	0.7093	92
	M2-2	-9.4	13.7	0.7090	197
	M2-1	-9.9	13.6	0.7091	95
	M3-7	-10.9	15.4	0.7094	72
	M3-6	-11.3	15.6	0.7097	111
	M3-5	-11.6	15.6	0.7101	91
	M3-4	-11.6	16.0	0.7102	78
	M3-3	-11.7	15.7	0.7106	81
	M3-2	-11.7	15.7	0.7106	73
	M3-1	-11.7	15.8	0.7105	81
WACH-153.180	M2-5	-12.4	14.0	0.7110	130
♂	M2-4	-12.1	13.9	0.7107	111
	M2-3	-11.7	13.0	0.7106	111
	M2-2	-11.3	13.0	0.7102	120
	M2-1	-11.2	12.8	0.7100	119
	M3-5	-11.7	14.9	0.7098	89
	M3-4	-11.7	15.3	0.7105	133
	M3-3	-12.0	16.1	0.7112	119
	M3-2	-11.9	16.0	0.7122	118
	M3-1	-12.5	16.4	0.7129	107

Table A.2 Intra-tooth $\delta^{13}C$ and $\delta^{15}N$ values for dentine from *Rangifer tarandus granti* from the Western Arctic herd, Alaska.

Individual	Sample	coll. (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
WACH-2.210	M2-D6	1.6	-20.7	4.0	42.8	14.3	3.5
♀	M2-D5	3.8	-20.0	4.1	37.8	13.6	3.2
	M2-D4	2.6	-20.5	4.0	42.9	14.7	3.4
	M2-D3	1.9	-20.8	4.2	42.9	14.7	3.4
	M2-D2	4.0	-20.4	4.7	43.0	14.9	3.4
	M2-D1	6.7	-20.1	4.5	44.5	16.1	3.2
	M3-D7	1.6	-20.5	3.6	42.7	14.4	3.4
	M3-D6	2.4	-21.0	3.8	42.9	14.6	3.4
	M3-D5	3.0	-20.7	3.9	41.7	14.4	3.4
	M3-D4	3.6	-20.4	4.1	42.6	14.6	3.4
	M3-D3	4.2	-20.4	4.6	42.7	14.8	3.4
	M3-D2	3.6	-20.4	4.7	42.7	14.7	3.4
	M3-D1	5.3	-20.7	4.5	43.2	14.9	3.4
WACH-2000	M2-D7	1.2	-20.7	4.8	41.0	14.6	3.3
♀	M2-D6	1.5	-20.6	4.3	41.9	14.6	3.3
	M2-D5	4.5	-20.5	4.0	38.1	13.2	3.4
	M2-D4	3.8	-20.6	4.5	42.9	15.0	3.3
	M2-D3	4.4	-20.5	4.6	42.3	14.9	3.3
	M2-D2	4.2	-20.8	4.2	42.4	14.7	3.4
	M2-D1	4.4	-21.3	3.8	42.8	14.9	3.4
	M3-D7	1.8	-20.6	3.7	42.0	14.3	3.4
	M3-D6	2.6	-20.8	3.6	42.8	14.4	3.5

	M3-D5	3.7	-20.7	3.9	42.6	14.4	3.5
	M3-D4	4.0	-20.3	4.5	42.9	15.1	3.3
	M3-D3	4.2	-20.1	4.5	42.9	15.0	3.3
	M3-D2	4.5	-20.1	4.2	42.6	15.2	3.3
	M3-D1	5.9	-20.5	3.7	42.9	15.3	3.3
WACH-0.120	M2-D6	0.3	-20.5	4.6	39.4	14.2	3.2
♀	M2-D5	2.1	-20.0	4.7	42.5	15.6	3.2
	M2-D4	5.4	-19.2	4.7	41.9	15.4	3.2
	M2-D3	2.6	-19.3	4.9	41.8	15.3	3.2
	M2-D2	3.2	-19.5	4.8	42.4	15.5	3.2
	M2-D1	6.0	-20.2	4.4	41.0	14.9	3.2
	M3-D7	3.7	-19.4	4.8	42.7	15.3	3.3
	M3-D6	3.5	-19.3	4.6	41.7	15.0	3.2
	M3-D5	5.4	-19.5	4.6	42.5	15.3	3.2
	M3-D4	6.3	-19.8	5.0	42.4	15.6	3.2
	M3-D3	7.2	-19.6	5.4	42.6	15.8	3.2
	M3-D2	6.7	-19.4	5.2	42.5	15.6	3.2
	M3-D1	6.9	-19.4	4.5	42.6	15.6	3.2
WACH-2.230	M2-D8	2.4	-19.9	3.8	43.6	15.4	3.3
♂	M2-D7	3.5	-19.2	3.7	43.9	15.8	3.2
	M2-D6	4.2	-19.2	3.5	43.8	15.6	3.3
	M2-D5	8.7	-19.8	3.8	44.2	16.1	3.2
	M2-D4	6.4	-20.1	3.9	44.2	15.9	3.2
	M2-D3	7.4	-20.2	3.9	44.7	16.0	3.3
	M2-D2	6.6	-20.5	3.7	44.9	15.9	3.3
	M2-D1	7.2	-20.2	3.3	45.0	15.5	3.4
	M3-D8	2.6	-19.4	3.4	43.1	15.5	3.2
	M3-D7	3.2	-19.8	3.2	43.4	15.7	3.2
	M3-D6	5.3	-20.1	3.5	43.6	15.8	3.2
	M3-D5	6.9	-19.7	3.6	43.8	15.8	3.2
	M3-D4	9.0	-20.0	3.8	44.4	16.2	3.2
	M3-D3	9.7	-19.7	3.5	44.3	16.1	3.2
	M3-D2	8.3	-19.9	3.5	44.2	15.9	3.2
	M3-D1	8.5	-20.5	3.0	44.3	15.5	3.3
WACH-153.180	M2-D7	3.2	-20.4	4.5	42.0	15.1	3.2
♂	M2-D6	3.7	-20.2	4.5	42.1	15.3	3.2
	M2-D5	5.5	-19.6	4.4	42.3	15.5	3.2
	M2-D4	7.4	-19.4	4.6	42.9	15.8	3.2
	M2-D3	2.8	-19.2	4.5	41.1	15.2	3.2
	M2-D2	6.9	-19.3	4.3	42.4	15.5	3.2
	M2-D1	8.4	-19.8	3.9	42.7	15.6	3.2
	M3-D7	2.3	-21.2	2.2	67.5	21.0	3.6
	M3-D6	3.2	-19.5	4.0	41.9	15.1	3.2
	M3-D5	4.9	-19.5	4.3	41.8	15.0	3.3
	M3-D4	8.0	-19.3	4.6	42.3	15.6	3.2
	M3-D3	7.2	-19.1	4.3	43.1	15.8	3.2
	M3-D2	6.1	-19.2	4.1	42.4	15.4	3.2
	M3-D1	8.9	-20.0	3.3	43.1	15.5	3.3

Table A.3 $\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$ values for bone collagen from *Rangifer tarandus granti* from the Western Arctic herd, Alaska.

Individual	Sample	coll. (%)	$\delta^{34}S$ (‰)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
WACH-2.210	Bone	5.2	4.7	-20.4	3.1	43.5	15.5	3.3
WACH-2000	Bone	4.8	2.6	-20.5	2.5	42.3	15.6	3.2
WACH-0.120	Bone	5.0	9.0	-20.0	3.8	44.8	16.4	3.2
WACH-2.230	Bone	4.5	2.8	-20.3	2.0	45.2	16.4	3.2
WACH-153.180	Bone	6.4	3.3	-19.7	2.1	44.9	16.5	3.2

Table A.4 Intra-tooth $\delta^{13}C_{V\text{-}PDB}$, $\delta^{18}O_{V\text{-}SMOW}$ and $^{87}Sr/^{86}Sr$ values and strontium concentration data (ppm) for enamel from *Rangifer tarandus caribou* from the Leaf River herd, Canada.

Individual	Sample	$\delta^{13}C_{V\text{-}PDB}$	$\delta^{18}O_{V\text{-}SMOW}$	$^{87}Sr/^{86}Sr$	Sr conc (ppm)
AFR-1	M2-7	-12.5	14.6	0.7313	24
♀	M2-6	-12.6	14.1	0.7310	143
	M2-5	-13.0	14.3	0.7306	145
	M2-4	-11.8	14.1	0.7299	54
	M2-3	-11.7	13.2	0.7297	172
	M2-2	-11.6	13.1	0.7290	133
	M2-1	-11.7	13.3	0.7290	145
	M3-6	-11.6	14.9	0.7301	114
	M3-5	-12.2	14.6	0.7306	139
	M3-4	-12.2	15.2	0.7310	183
	M3-3	-12.4	15.5	0.7313	182
	M3-2	-12.4	16.2	0.7313	178
	M3-1	-12.5	15.9	0.7314	196
AFR-6	M2-7	-12.2	14.8	0.7259	115
♀	M2-6	-12.2	15.0	0.7261	142
	M2-5	-11.4	14.3	0.7263	153
	M2-4	-11.4	13.4	0.7266	134
	M2-3	-11.1	13.4	0.7266	146
	M2-2	-11.0	13.0	0.7266	142
	M2-1	-11.0	12.9	0.7264	98
	M3-7	-11.4	13.7	0.7279	164
	M3-6	-11.8	14.6	0.7284	138
	M3-5	-11.9	15.5	0.7290	139
	M3-4	-12.2	15.5	0.7298	169
	M3-3	-12.2	15.7	0.7297	152
	M3-2	-12.4	15.9	0.7303	140
	M3-1	-12.3	16.0	0.7303	29
AFR-10	M2-7	-12.4	16.0	0.7335	141
♀	M2-6	-12.6	15.2	0.7329	114
	M2-5	-12.1	14.7	0.7325	127
	M2-4	-12.1	14.7	0.7320	114
	M2-3	-11.7	14.3	0.7315	137
	M2-2	-11.3	14.4	0.7309	143
	M2-1	-11.2	13.9	0.7304	152
	M3-8	-11.0	14.3	0.7308	92
	M3-7	-10.9	15.0	0.7312	55

M3-6	-11.2	14.9	0.7316	116
M3-5	-11.8	15.7	0.7331	116
M3-4	-11.9	15.8	0.7342	114
M3-3	-12.0	16.5	0.7355	101
M3-2	-12.0	16.4	0.7364	121
M3-1	-12.0	16.7	0.7377	105

Table A.5 Intra-tooth $\delta^{13}C$ and $\delta^{15}N$ values for dentine from *Rangifer tarandus caribou* from the Leaf River herd, Canada.

Individual	Sample	coll. (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
AFR-1	M2-D6	3.0	-19.6	5.8	42.5	15.0	3.3
♀	M2-D5	2.4	-19.3	5.9	41.7	14.7	3.3
	M2-D4	4.7	-19.3	5.6	42.3	15.2	3.2
	M2-D3	11.1	-19.5	5.8	43.5	15.6	3.3
	M2-D2	7.5	-20.0	5.9	43.8	15.7	3.3
	M2-D1	7.0	-19.7	6.1	43.4	15.7	3.2
	M3-D7	2.3	-19.2	4.4	43.2	15.2	3.3
	M3-D6	3.5	-19.7	4.7	40.6	14.3	3.3
	M3-D5	4.5	-19.8	5.1	40.8	14.7	3.2
	M3-D4	5.0	-19.3	5.8	42.6	15.3	3.3
	M3-D3	7.6	-19.1	5.7	43.4	15.4	3.3
	M3-D2	7.0	-19.3	5.4	43.8	15.5	3.3
	M3-D1	6.7	-19.7	4.8	44.3	15.2	3.2
AFR-6	M2-D8	1.3	-20.8	4.1	42.5	14.0	3.6
♀	M2-D7	1.6	-20.0	4.1	42.5	14.7	3.4
	M2-D6	2.0	-19.7	4.0	42.9	14.6	3.4
	M2-D5	4.2	-19.3	3.7	43.1	14.8	3.4
	M2-D4	3.7	-19.6	4.4	43.3	15.3	3.3
	M2-D3	6.3	-19.9	5.2	43.5	15.6	3.3
	M2-D2	2.7	-20.3	5.5	44.4	15.5	3.3
	M2-D1	3.7	-20.7	5.3	46.1	14.8	3.6
	M3-D8	1.6	-19.3	2.8	43.5	14.9	3.4
	M3-D7	2.3	-19.5	3.1	42.7	14.9	3.3
	M3-D6	2.4	-20.2	3.9	42.3	14.4	3.4
	M3-D5	4.8	-20.1	4.7	42.1	14.8	3.3
	M3-D4	4.4	-19.9	5.3	42.3	14.9	3.3
	M3-D3	6.5	-19.6	5.6	43.3	15.7	3.2
	M3-D2	5.5	-20.3	5.3	43.8	15.1	3.4
	M3-D1	7.1	-21.4	5.2	45.9	14.4	3.7
AFR-10	M2-D8	2.1	-20.4	4.3	42.8	15.1	3.3
♀	M2-D7	3.3	-19.7	4.1	42.8	15.5	3.3
	M2-D6	5.9	-19.1	3.8	43.1	15.3	3.3
	M2-D5	8.3	-19.7	4.3	43.7	16.0	3.2
	M2-D4	6.8	-20.0	4.7	43.4	15.8	3,2

M2-D3	8.1	-20.4	5.0	43.1	15.6	3.2
M2-D2	8.1	-20.7	5.0	43.4	15.5	3.3
M2-D1	8.7	-20.6	5.0	43.8	15.2	3.4
M3-D8	1.7	-18.9	2.7	42.7	15.1	3.3
M3-D7	2.2	-19.3	3.1	42.3	15.0	3.3
M3-D6	3.2	-19.6	4.0	42.3	15.1	3.3
M3-D5	5.0	-20.1	5.3	42.3	15.2	3.2
M3-D4	6.2	-19.8	5.4	43.2	15.3	3.3
M3-D3	7.6	-19.4	5.5	43.3	15.5	3.2
M3-D2	7.3	-19.4	5.2	42.6	15.3	3.3
M3-D1	7.3	-19.6	4.4	43.3	15.0	3.4

Table A.6 $\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$ values for bone collagen from *Rangifer tarandus caribou* from the Leaf River herd, Canada.

Individual	Sample	coll. (%)	$\delta^{34}S$ (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
AFR-1	Bone	4.7	7.5	-19.9	4.0	43.2	15.9	3.2
AFR-5	Bone	5.6	7.2	-19.6	3.1	43.1	15.6	3.2
AFR-6	Bone	5.7	7.4	-19.9	3.7	43.1	15.8	3.2
AFR-7	Bone	5.0	8.3	-19.9	3.5	43.3	16.0	3.1
AFR-10	Bone	5.9	7.6	-20.1	3.3	43.1	15.9	3.2
AFR-13	Bone	4.8	7.5	-19.6	3.2	42.9	15.8	3.2
AFR-14	Bone	4.8	7.5	-19.9	2.6	43.9	16.2	3.2
AFR-15	Bone	5.4	7.9	-20.1	3.6	43.6	16.1	3.2
AFR-16	Bone	3.9	7.5	-19.6	3.0	43.2	15.8	3.2
AFR-18	Bone	4.4	7.3	-19.8	4.0	43.7	16.0	3.2

Table A.7 Intra-tooth $\delta^{13}C_{V\text{-}PDB}$, $\delta^{18}O_{V\text{-}SMOW}$ and $^{87}Sr/^{86}Sr$ values and strontium concentration data (ppm) for enamel from *Rangifer tarandus caribou* from the George River herd, Canada.

Individual	Sample	$\delta^{13}C_{V\text{-}PDB}$	$\delta^{18}O_{V\text{-}SMOW}$	$^{87}Sr/^{86}Sr$	Sr conc (ppm)
GR-3	M2-5	-11.3	15.0	0.7307	141
♀	M2-4	-11.2	14.6	0.7294	137
	M2-3	-10.9	13.8	0.7288	120
	M2-2	-11.1	13.7	0.7285	136
	M2-1	-11.0	13.6	0.7282	135
	M3-6	-11.3	16.3	0.7299	130
	M3-5	-11.4	16.8	0.7305	142
	M3-4	-11.7	17.3	0.7308	107
	M3-3	-11.9	17.0	0.7315	142
	M3-2	-11.8	16.6	0.7324	168
	M3-1	-11.8	16.1	0.7328	116
GR-8	M2-5	-11.7	12.1	0.7279	230
♀	M2-4	-11.3	11.2	0.7283	249
	M2-3	-10.9	10.5	0.7280	203

	M2-2	-10.4	11.0	0.7279	231
	M2-1	-9.8	12.8	0.7277	220
	M3-5	-11.6	15.1	0.7263	257
	M3-4	-12.1	15.0	0.7263	209
	M3-3	-12.9	15.8	0.7264	185
	M3-2	-12.9	14.8	0.7264	189
	M3-1	-12.8	14.3	0.7263	157
GR-16	M2-7	-11.3	14.0	0.7195	241
♀	M2-6	-10.7	13.3	0.7192	234
	M2-5	-10.5	12.7	0.7187	205
	M2-4	-10.4	12.7	0.7187	244
	M2-3	-10.4	12.7	0.7185	203
	M2-2	-10.2	12.6	0.7180	240
	M2-1	-10.0	12.8	0.7178	273
	M3-7	-10.9	15.2	0.7194	259
	M3-6	-11.1	15.6	0.7202	234
	M3-5	-11.3	16.0	0.7220	241
	M3-4	-11.7	16.6	0.7228	240
	M3-3	-12.0	16.7	0.7246	73
	M3-2	-12.3	16.9	0.7261	234
	M3-1	-12.4	16.2	0.7283	242

Table A.8 Intra-tooth $\delta^{13}C$ and $\delta^{15}N$ values for dentine from *Rangifer tarandus caribou* from the George River herd, Canada.

Individual	Sample	coll. (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
GR-3	M2-D7	2.7	-19.2	3.1	43.9	16.2	3.2
♀	M2-D6	3.1	-19.1	3.0	43.8	16.3	3.1
	M2-D5	6.5	-19.0	3.2	42.2	15.3	3.2
	M2-D4	8.1	-19.5	4.0	43.1	15.6	3.2
	M2-D3	7.3	-19.7	4.4	43.8	15.8	3.2
	M2-D2	11.5	-19.7	4.6	43.5	15.8	3.2
	M2-D1	8.3	-19.7	3.7	43.2	15.5	3.2
	M3-D7	1.8	-19.8	2.2	44.3	15.5	3.3
	M3-D6	2.5	-20.1	2.8	43.5	15.5	3.3
	M3-D5	5.2	-19.9	3.5	42.9	15.9	3.2
	M3-D4	6.8	-19.6	4.3	51.7	19.2	3.1
	M3-D3	7.6	-19.5	4.8	43.4	16.2	3.1
	M3-D2	7.9	-19.8	5.1	44.4	16.3	3.2
	M3-D1	8.9	-20.4	4.4	43.8	16.2	3.2
GR-8	M2-D7	1.1	-20.4	3.7	42.0	14.7	3.3
♀	M2-D6	1.9	-19.5	3.6	42.2	15.2	3.2
	M2-D5	4.2	-19.5	3.5	42.3	15.3	3.2
	M2-D4	4.7	-20.2	4.1	42.4	15.4	3.2
	M2-D3	4.6	-20.4	4.5	42.9	15.6	3.2
	M2-D2	6.0	-20.4	4.6	42.5	15.5	3.2

	M2-D1	5.5	-20.2	4.0	43.4	15.6	3.2
	M3-D7	1.6	-20.1	2.7	42.2	15.0	3.3
	M3-D6	2.5	-20.6	3.3	41.0	14.8	3.2
	M3-D5	3.9	-20.5	3.9	41.9	15.2	3.2
	M3-D4	4.6	-20.1	4.0	42.4	15.3	3.2
	M3-D3	4.8	-19.8	4.1	43.0	15.7	3.2
	M3-D2	4.6	-20.0	4.1	43.3	15.8	3.2
	M3-D1	6.2	-20.4	3.3	43.5	15.7	3.2
GR-16	M2-D7	1.7	-20.1	5.1	45.5	16.5	3.2
♀	M2-D6	2.7	-19.4	5.4	45.2	16.6	3.2
	M2-D5	3.8	-19.8	5.4	45.5	16.6	3.2
	M2-D4	1.4	-20.0	5.9	45.5	16.7	3.2
	M2-D3	5.5	-20.1	5.8	49.0	18.2	3.2
	M2-D2	3.9	-20.4	5.2	45.3	16.6	3.2
	M2-D1	5.6	-20.8	5.1	45.6	16.7	3.2
	M3-D8	1.1	-19.6	3.9	45.3	15.3	3.5
	M3-D7	1.9	-19.4	4.5	44.8	16.5	3.2
	M3-D6	3.4	-19.8	5.2	44.3	16.5	3.1
	M3-D5	5.0	-20.0	6.0	44.9	16.8	3.1
	M3-D4	6.2	-19.7	6.0	45.2	17.1	3.1
	M3-D3	5.7	-19.7	5.5	45.7	17.1	3.1
	M3-D2	4.6	-19.9	5.1	45.8	16.8	3.2
	M3-D1	6.1	-20.2	4.3	45.7	16.7	3.2

Table A.9 $\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$ values for bone collagen from *Rangifer tarandus caribou* from the George River herd, Canada.

Individual	Sample	coll. (%)	$\delta^{34}S$ (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
GR-3	Bone	5.6	6.0	-20.1	2.5	43.2	15.9	3.2
GR-5	Bone	4.1	8.0	-19.7	3.2	43.6	16.0	3.2
GR-6	Bone	5.1	7.0	-19.8	3.2	43.2	15.9	3.2
GR-7	Bone	4.8	6.4	-20.5	3.2	43.6	16.1	3.2
GR-8	Bone	6.6	6.6	-20.0	3.1	43.2	15.8	3.2
GR-9	Bone	5.6	6.6	-19.9	2.8	43.4	16.0	3.2
GR-13	Bone	5.2	7.7	-20.0	3.0	43.7	16.0	3.2
GR-15	Bone	4.9	7.5	-20.1	2.9	44.0	16.2	3.2
GR-16	Bone	5.5	6.9	-20.0	3.1	43.5	15.9	3.2
GR-17	Bone	5.4	7.0	-19.6	2.9	43.9	16.0	3.2

Table A.10 Intra-tooth $\delta^{13}C_{V\text{-}PDB}$, $\delta^{18}O_{V\text{-}SMOW}$ and $^{87}Sr/^{86}Sr$ values and strontium concentration data (ppm) for enamel from *Bison bison* from the Henry Mountains herd, Utah.

Individual	Sample	$\delta^{13}C_{V\text{-}PDB}$	$\delta^{18}O_{V\text{-}SMOW}$	$^{87}Sr/^{86}Sr$	Sr conc (ppm)
FS-768	M3-12	-6.9	23.4	0.7086	166
♂	M3-11	-6.6	23.0	0.7086	110
	M3-10	-6.6	23.2	0.7086	113
	M3-9	-6.9	23.1	0.7086	96
	M3-8	-7.1	23.1	0.7087	143
	M3-7	-7.2	23.4	0.7087	108
	M3-6	-8.4	24.3	0.7086	121
	M3-5	-9.3	25.1	0.7086	134
	M3-4	-9.0	25.7	0.7086	129
	M3-3	-8.2	24.9	0.7086	135
	M3-2	-7.4	23.8	0.7087	118
	M3-1	-6.8	23.0	0.7087	110

Table A.11 Intra-tooth $\delta^{13}C$ and $\delta^{15}N$ values for dentine from *Bison bison* from the Henry Mountains herd, Utah.

Individual	Sample	coll. (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
FS-768	M3-D19	2.6	-18.2	5.0	39.8	14.4	3.2
♂	M3-D18	3.5	-17.5	5.1	38.2	14.1	3.2
	M3-D17	2.9	-17.4	5.1	39.8	14.7	3.2
	M3-D16	4.2	-17.1	5.0	37.6	14.1	3.1
	M3-D15	3.1	-16.9	5.0	37.4	14.0	3.1
	M3-D14	3.3	-16.9	5.1	38.0	14.3	3.1
	M3-D13	4.5	-16.9	5.2	37.5	13.8	3.2
	M3-D12	3.7	-16.7	5.3	40.2	14.8	3.2
	M3-D11	5.7	-17.2	5.3	40.4	15.0	3.1
	M3-D10	5.2	-17.2	5.5	39.1	14.5	3.1
	M3-D9	7.1	-17.1	5.9	30.6	11.5	3.1
	M3-D8	7.1	-17.1	5.9	39.7	14.8	3.1
	M3-D7	7.2	-17.0	5.5	40.7	15.0	3.2
	M3-D6	8.1	-16.7	5.1	39.9	14.8	3.1
	M3-D5	7.2	-16.7	5.1	40.4	14.9	3.2
	M3-D4	8.0	-17.3	5.0	40.5	14.9	3.2
	M3-D3	7.5	-17.6	5.0	40.7	15.0	3.2
	M3-D2	7.7	-17.6	5.0	40.8	14.9	3.2
	M3-D1	8.2	-17.6	5.1	40.7	14.9	3.2

Table A.12 Intra-tooth $\delta^{13}C_{V\text{-}PDB}$, $\delta^{18}O_{V\text{-}SMOW}$ and $^{87}Sr/^{86}Sr$ values and strontium concentration data (ppm) for enamel from *Bison bison* from the Wind Cave National Park herd, South Dakota.

Individual	Sample	$\delta^{13}C_{V\text{-}PDB}$	$\delta^{18}O_{V\text{-}SMOW}$	$^{87}Sr/^{86}Sr$	Sr conc (ppm)
WCNPB-2	M3-15	-9.2	19.7	0.7128	56
♀/♂	M3-14	-9.5	19.3	0.7128	36
	M3-13	-9.6	19.8	0.7128	81
	M3-12	-9.7	19.7	0.7129	65
	M3-11	-9.7	20.1	0.7128	43
	M3-10	-10.1	20.5	0.7128	45
	M3-9	-9.6	21.3	0.7129	50
	M3-8	-9.6	21.7	0.7131	42
	M3-7	-9.6	22.0	0.7132	58
	M3-6	-9.6	21.4	0.7133	21
	M3-5	-9.7	21.0	0.7132	74
	M3-4	-9.1	21.0	0.7132	48
	M3-3	-9.5	20.1	0.7134	75
	M3-2	-9.4	20.0	0.7138	80
	M3-1	-9.4	19.8	0.7138	72
WCNPB-3	M3-14	-9.2	23.4	0.7142	85
♀/♂	M3-13	-9.3	22.7	0.7139	86
	M3-12	-9.2	21.4	0.7136	91
	M3-11	-9.1	21.0	0.7135	94
	M3-10	-9.3	20.6	0.7135	84
	M3-9	-9.7	20.2	0.7134	86
	M3-8	-9.8	20.2	0.7134	87
	M3-7	-9.6	20.5	0.7135	88
	M3-6	-9.7	21.0	0.7138	95
	M3-5	-9.4	21.2	0.7141	87
	M3-4	-8.9	21.9	0.7143	88
	M3-3	-7.9	21.8	0.7138	84
	M3-2	-8.5	21.2	0.7134	103
	M3-1	-9.0	19.1	0.7132	125

Table A.13 Intra-tooth $\delta^{13}C$ and $\delta^{15}N$ values for dentine from *Bison bison* from the Wind Cave National Park herd, South Dakota.

Individual	Sample	coll. (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
WCNPB-2	M3-D17	2.6	-17.4	4.7	42.7	15.3	3.2
♀/♂	M3-D16	3.6	-17.5	4.7	42.8	15.7	3.2
	M3-D15	3.0	-17.7	4.8	42.9	15.5	3.2
	M3-D14	3.0	-18.2	4.8	42.2	15.4	3.2
	M3-D13	2.6	-18.5	4.8	42.5	15.5	3.2
	M3-D12	1.9	-18.7	4.6	41.3	15.0	3.2
	M3-D11	2.4	-18.6	4.6	41.9	15.1	3.2
	M3-D10	3.9	-18.2	4.6	43.0	15.6	3.2
	M3-D9	3.3	-18.3	4.6	40.7	14.8	3.2
	M3-D8	3.8	-18.2	4.6	40.4	14.7	3.2
	M3-D7	4.6	-18.0	4.5	38.9	14.2	3.2
	M3-D6	4.5	-17.8	4.5	37.3	13.6	3.2
	M3-D5	3.8	-18.2	4.6	41.7	15.2	3.2
	M3-D4	5.3	-18.4	4.5	42.3	15.4	3.2
	M3-D3	7.7	-18.2	4.5	42.2	15.4	3.2
	M3-D2	7.4	-18.2	4.4	43.5	15.8	3.2
	M3-D1	6.7	-18.5	4.3	42.6	15.4	3.2
WCNPB-3	M3-D18	2.9	-18.5	4.8	45.3	16.4	3.2
♀/♂	M3-D17	4.6	-17.9	4.9	42.8	16.2	3.1
	M3-D16	4.7	-18.0	4.9	41.8	16.1	3.0
	M3-D15	4.6	-18.2	5.0	42.9	16.5	3.0
	M3-D14	3.3	-18.7	5.1	42.4	16.2	3.1
	M3-D13	4.2	-18.6	5.0	43.3	16.6	3.1
	M3-D12	3.1	-18.8	4.8	38.9	14.4	3.2
	M3-D11	3.8	-18.7	4.6	39.1	14.4	3.2
	M3-D10	2.1	-18.6	4.7	41.3	15.2	3.2
	M3-D9	2.4	-18.6	4.4	38.1	14.0	3.2
	M3-D8	1.6	-18.7	4.5	37.5	13.7	3.2
	M3-D7	2.7	-19.2	4.3	41.9	14.5	3.4
	M3-D6	1.9	-18.2	4.4	39.2	14.4	3.2
	M3-D5	3.2	-17.8	4.5	39.2	14.5	3.1
	M3-D4	5.6	-17.9	4.7	40.9	15.1	3.2
	M3-D3	5.9	-17.9	4.6	42.7	15.7	3.2
	M3-D2	5.0	-17.7	4.4	42.8	15.7	3.2
	M3-D1	4.1	-18.0	4.1	42.8	15.3	3.3

Table A.14 Intra-tooth $\delta^{13}C_{V\text{-}PDB}$, $\delta^{18}O_{V\text{-}SMOW}$ and $^{87}Sr/^{86}Sr$ values and strontium concentration data (ppm) for enamel from *Bison bison* from the Wichita Mountains herd, Oklahoma.

Individual	Sample	$\delta^{13}C_{PDB}$	$\delta^{18}O_{SMOW}$	$^{87}Sr/^{86}Sr$	Sr conc (ppm)
WMB-11	M3-12	-4.1	29.9	0.7106	87
♀/♂	M3-11	-4.1	29.5	0.7106	81
	M3-10	-4.4	29.0	0.7106	85
	M3-9	-4.4	28.7	0.7106	91
	M3-8	-4.2	29.4	0.7107	82
	M3-7	-4.3	29.3	0.7107	89
	M3-6	-5.0	28.9	0.7107	89
	M3-5	-3.8	29.3	0.7107	66
	M3-4	-3.8	29.3	0.7107	75
	M3-3	-3.1	29.5	0.7108	86
	M3-2	-2.6	29.5	0.7108	76
	M3-1	-2.7	29.0	0.7108	93
WMB-12	M3-12	-4.0	30.8	0.7107	54
♀/♂	M3-11	-3.9	30.8	0.7107	54
	M3-10	-3.8	30.6	0.7107	57
	M3-9	-4.0	29.9	0.7107	55
	M3-8	-4.2	29.2	0.7107	57
	M3-7	-4.3	28.7	0.7107	58
	M3-6	-4.4	28.0	0.7106	58
	M3-5	-3.9	28.1	0.7107	61
	M3-4	-3.4	27.6	0.7106	73
	M3-3	-3.7	27.2	0.7106	55
	M3-2	-3.7	26.8	0.7106	62
	M3-1	-3.5	27.4	0.7107	68

Table A.15 Intra-tooth $\delta^{13}C$ and $\delta^{15}N$ values for dentine from *Bison bison* from the Wichita Mountains herd, Oklahoma.

Individual	Sample	coll. (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
WMB-11	M3-D17	2.2	-12.8	4.1	42.7	15.5	3.2
♀/♂	M3-D16	2.7	-12.7	4.0	42.1	15.3	3.2
	M3-D15	2.6	-12.7	4.0	42.6	15.5	3.2
	M3-D14	2.8	-12.5	4.0	42.8	15.6	3.2
	M3-D13	3.2	-12.8	4.0	42.2	15.5	3.2
	M3-D12	2.6	-12.9	3.9	40.7	14.9	3.2
	M3-D11	4.2	-13.0	3.8	38.8	14.2	3.2
	M3-D10	2.1	-13.0	3.8	42.0	15.3	3.2
	M3-D9	2.3	-12.9	3.8	41.9	15.2	3.2
	M3-D8	4.0	-12.7	3.9	42.6	15.6	3.2
	M3-D7	5.2	-12.2	3.8	41.7	15.2	3.2
	M3-D6	6.2	-11.7	3.7	42.4	15.4	3.2
	M3-D5	6.0	-11.6	3.6	43.2	15.8	3.2
	M3-D4	6.3	-11.8	3.5	43.0	15.7	3.2

	M3-D3	6.9	-11.9	3.3	42.9	15.6	3.2
	M3-D2	5.8	-11.7	3.3	42.8	15.5	3.2
	M3-D1	6.3	-11.6	3.1	42.8	15.5	3.2
WMB-12	M3-D15	2.6	-12.5	4.2	42.2	16.2	3.0
♀/♂	M3-D14	5.0	-12.7	4.1	38.5	15.2	3.0
	M3-D13	3.0	-12.3	4.0	42.1	16.5	3.0
	M3-D12	3.3	-12.6	4.0	42.5	16.7	3.0
	M3-D11	3.6	-12.9	3.8	42.2	16.6	3.0
	M3-D10	3.7	-13.0	4.1	41.6	16.4	3.0
	M3-D9	3.3	-13.2	4.2	42.4	16.7	3.0
	M3-D8	3.2	-14.0	4.2	41.8	16.4	3.0
	M3-D7	3.3	-13.9	4.2	41.4	16.2	3.0
	M3-D6	4.5	-13.8	4.2	42.3	16.5	3.0
	M3-D5	4.6	-13.8	4.5	42.8	16.6	3.0
	M3-D4	5.8	-14.1	4.2	43.0	16.4	3.1
	M3-D3	5.0	-14.0	3.8	45.3	15.9	3.3
	M3-D2	5.2	-13.9	3.5	45.1	16.0	3.3
	M3-D1	6.4	-13.8	3.4	46.5	15.5	3.5

Table A.16 $\delta^{34}S$, $\delta^{13}C$ and $\delta^{15}N$ values for bone collagen from *Bison bison* from the Wichita Mountains herd, Oklahoma.

Individual	Sample	coll. (%)	$\delta^{34}S$ (%)	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	C(%)	N (%)	C:N
WMB-11	Bone	4.6	4.7	-11.7	2.9	44.8	16.6	3.1
WMB-12	Bone	5.1	3.0	-13.0	3.2	44.7	16.5	3.2
WMB-13	Bone	5.2	3.2	-12.7	2.4	44.1	16.1	3.2
WMB-14	Bone	5.2	3.6	-13.0	3.4	44.4	16.4	3.2
WMB-15	Bone	3.0	4.5	-12.8	2.3	45.1	16.7	3.2

Table A.17 Intra-tooth strontium isotope values and strontium concentrations for reindeer and bison sampled from Level 22 at Jonzac.

Individual	Sample	$^{87}Sr/^{86}Sr$	Sr conc (ppm)
G9-2068	M2-5	0.7096	100
Rangifer	M2-4	0.7096	70
	M2-3	0.7096	61
	M2-2	0.7096	63
	M2-1	0.7097	83
	M3-7	0.7098	63
	M3-6	0.7098	84
	M3-5	0.7099	87
	M3-4	0.7099	65
	M3-3	0.7099	85
	M3-2	0.7098	77
	M3-1	0.7096	105
H10-1002	M2-6	0.7095	74

Rangifer	M2-5	0.7095	64
	M2-4	0.7096	73
	M2-3	0.7096	57
	M2-2	0.7096	59
	M2-1	0.7097	48
	M3-6	0.7098	89
	M3-5	0.7099	55
	M3-4	0.7100	51
	M3-3	0.7100	48
	M3-2	0.7101	68
	M3-1	0.7104	60
H9-2221	M2-6	0.7096	84
Rangifer	M2-5	0.7098	66
	M2-4	0.7098	73
	M2-3	0.7100	46
	M2-2	0.7100	94
	M2-1	0.7100	83
	M3-6	0.7100	110
	M3-5	0.7100	87
	M3-4	0.7100	73
	M3-3	0.7099	80
	M3-2	0.7098	82
	M3-1	0.7097	73
G8-2285	M-13	0.7091	91
Bison	M-12	0.7091	111
	M-11	0.7091	83
	M-10	0.7092	82
	M-9	0.7092	56
	M-8	0.7092	166
	M-7	0.7092	155
	M-6	0.7092	13
	M-5	0.7092	32
	M-4	0.7092	107
	M-3	0.7091	92
	M-2	0.7090	84
	M-1	0.7090	87

Table A.18 Intra-tooth enamel strontium isotope values ($^{87}Sr/^{86}Sr$) and strontium concentrations (ppm) for a single reindeer individual sampled from Level 8 at Jonzac.

Individual	Sample	$^{87}Sr/^{86}Sr$	Sr conc (ppm)
F15-557	M2-5	0.70925	63
Rangifer	M2-4	0.70919	55
	M2-3	0.70910	54
	M2-2	0.70915	53
	M2-1	0.70933	52

Table A.19 Strontium isotope values ($^{87}Sr/^{86}Sr$) and strontium concentrations (ppm) from dentine of all reindeer and bison teeth sampled from Level 22 and Level 8 at Jonzac.

Individual	Sample	$^{87}Sr/^{86}Sr$	Sr conc (ppm)
G9-2068	M2	0.7088	125
	M3	0.7090	118
H10-1002	M2	0.7090	86
	M3	0.7092	105
H9-2221	M2	0.7089	120
	M3	0.7089	88
G8-2285	M-i	0.7088	94
	M-ii	0.7088	81
	M-iii	0.7088	95
F15-557	M2	0.7087	92

Table A.20 Carbon and nitrogen isotope data for animal bones from different levels at Jonzac. All isotope, compositional and yield data is for the >30kDa fraction only. $\delta^{13}C$ and $\delta^{15}N$ were measured relative to the V-PDB and AIR standards respectively.
(* denotes samples that have been identified with a high level of confidence but, due to fragmentation or the loss of non-diagnostic components cannot conclusively be assigned to species).

Jonzac square ID	Species	Level	$\delta^{13}C$	$\delta^{15}N$	%C	%N	C:N	%'collagen'
D19-726	*Equus*	6	-20.1	6.1	21.3	7.7	3.2	1.3
E13-872	*Bos*	8	-20.2	4.7	36.1	13.0	3.2	0.3
G16-679	*Bos*	8	-20.1	4.8	23.8	8.6	3.2	0.8
E13-974	*Bos*	8	-19.8	6.1	34.6	12.5	3.2	0.3
E16-1327	*Bos*	8	-20.0	4.0	32.5	11.8	3.2	0.6
E18-1610	*Crocuta*	8	-18.5	8.2	28.4	10.1	3.3	0.3
D19-1296	*Castor*	8	-21.4	6.2	21.1	7.2	3.4	0.2
E18-404	*Equus*	8	-20.4	3.9	31.6	11.4	3.2	0.8
F12-669	*Equus*	8	-19.8	5.5	25.0	9.1	3.2	1.0
E13-1491	*Equus*	8	-20.2	4.5	15.7	5.5	3.4	0.3
G16-669	*Megaceros*	8	-20.0	4.6	26.8	9.7	3.2	0.4
F15-557	*Rangifer*	8	-18.4	7.7	21.7	7.7	3.3	0.7
F14-406	*Rangifer*	9	-18.8	5.8	17.8	6.2	3.4	0.6
F12-549	*Rangifer*	9	-19.0	8.2	29.4	10.6	3.3	0.9
F16-1144	*Rangifer*	9	-19.4	8.3	18.8	6.2	3.5	0.2
F16-1143	*Rangifer**	9	-19.5	5.1	30.0	10.8	3.2	0.6
F12-607	*Rangifer*	10	-19.4	5.4	39.0	13.8	3.3	0.2
F12-590	*Rangifer*	10	-19.1	5.9	29.0	10.4	3.2	0.9
F13-823	*Rangifer*	10	-19.2	4.4	31.9	11.5	3.2	0.6
D17-3	*Rangifer**	10	-18.5	4.3	25.7	9.2	3.3	0.3
F12-569	*Rangifer**	10	-19.4	4.7	30.4	10.9	3.2	0.5
F11-166	*Rangifer*	12	-19.2	7.5	35.2	12.5	3.3	0.3
F11-188	*Rangifer*	12	-19.2	7.8	18.7	6.6	3.3	1.3
G9-3202	*Bison/Bos*	22	-19.1	9.0	21.8	7.7	3.3	0.5
G8-2285	*Bison/Bos*	22	-19.4	8.5	35.4	12.6	3.3	0.3
H8-2774	*Bison/Bos**	22	-20.1	7.0	20.3	7.3	3.3	1.0
G9-3012	*Bison/Bos**	22	-19.2	5.6	24.4	8.8	3.2	1.5
G9-2068	*Rangifer*	22	-19.6	7.5	22.0	7.7	3.3	0.4
G9-2156	*Rangifer*	22	-19.0	6.5	40.7	14.4	3.3	0.2
H10-1002	*Rangifer*	22	-18.8	7.4	40.7	14.6	3.3	0.4
H10-1356	*Rangifer*	22	-19.8	6.5	34.7	11.7	3.5	0.1
H10-1399	*Rangifer*	22	-19.1	6.7	38.6	14.0	3.2	0.4
H9-2221	*Rangifer*	22	-18.8	7.3	21.2	7.4	3.3	0.8