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## Strontium isotope evidence for migration in late Pleistocene *Rangifer*: Implications for Neanderthal hunting strategies at the Middle Palaeolithic site of Jonzac, France

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## ABSTRACT

In order to understand the behaviours and subsistence choices of Palaeolithic hunter–gatherers, it is essential to understand the behavioural ecology of their prey. Here, we present strontium isotope data from sequentially-sampled enamel from three reindeer (*Rangifer tarandus* ssp.) and a single bison (*Bison* cf. *priscus*) from the late Middle Palaeolithic site of Jonzac (Chez-Pinaud), France. The results are used to investigate the ranging and migratory behaviours of these important prey species. We found that the bison had isotope values most consistent with a local range, while the three reindeer had values indicating a seasonal migration pattern. Due to the similarity of the patterning of two of the three reindeer and in conjunction with zooarchaeological results, we suggest that they may have been from the same herd, were likely killed around the same point during their seasonal round and may therefore be the product of a single hunting event or a small number of successive hunting events. The isotope analyses complement the zooarchaeological data and have allowed greater insight into the palaeoecology of these species, the palaeoenvironment, and Neanderthal site use and hunting strategies.

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## Introduction

Reconstructing the biogeography of archaeozoofauna is an important aspect of palaeoecology and also vital to understanding the living landscapes of the past. Establishing the seasonal movements, migrations and home-ranging habits of prey species ultimately provides the framework within which the subsistence choices of their human hunters can be interpreted. Herds not only provided game and raw material resources (e.g., 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; Haynes, 2002). Understanding the ranging habits of such animals is therefore essential for reconstructions of landscape ecology and understanding how this may have influenced hunter–gatherer populations and their ‘seasonal-rounds’ (Spiess, 1979). This is especially relevant to Palaeolithic archaeology, where prey species behaviour and ecology have been used to explain relationships between sites, landscape use, seasonal human movements and ranging, and hunting strategies in the Middle (Gaudzinski, 1996, 2006; Gaudzinski and Roebroeks, 2000; e.g., Costamagno et al., 2006) and Upper Palaeolithic (e.g., Bahn, 1977; Gordon, 1988; Straus, 1991; Burke, 1995; Bratlund, 1996; Burke and Pike-Tay, 1997; Enloe and David, 1997; Thacker, 1997; Jochim et al., 1999; Mellars, 2004).

The phenomenon of migratory behaviour in terrestrial animals is the result of a complex interaction of demographic and

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environmental influences, including population size, climate, forage abundance, predation avoidance, and insect pestilence. These factors cannot be known for archaeological populations but are known to influence the occurrence of seasonal movements in modern herds, e.g., their direction, distance, organisation and persistence (Schaefer et al., 2000; Bergerud and Luttich, 2003). European Palaeolithic reindeer are commonly considered to be a bi-annually migrating taxon (Bahn, 1977), their behaviours likened to modern North American caribou herds. However, wild herds of extant caribou and reindeer include both sedentary and migratory ecotypes, although there may be no significant morphological or genetic differences between these groups (Banfield, 1961). Some modern herds occupy ranges of a few hundred square-kilometres, while others have much larger annual ranges and undertake extensive seasonal movements over thousands of kilometres. Some herds undertake the 'classic' long-distance thermo-stress migrations, normally on a north-south trajectory, while others exhibit little or no seasonal movements (Bergman et al., 2000). In addition to these inter-herd differences, chronological variations within the same populations of caribou have also been observed over the last few centuries in Greenland (Meldgaard, 1986), Alaska (Joly et al., 2007) and New England (Bergerud and Mercer, 1989). These changes likely correspond with climatic shifts and population fluctuations. These fluctuations demonstrate the flexibility and instability of animal distributions and movement habits, even in relatively recent history. Given these issues, it is clear that the behaviour of Palaeolithic *Rangifer* populations cannot be sufficiently inferred from present-day or historic observations of extant caribou. Instead, direct methods for the reconstruction of reindeer biogeography are required.

Stable isotope analyses are increasingly used in combination with the serial-sampling of incrementally-developed tissues to identify and characterise seasonal dietary and migratory behaviours in archaeological faunas (Hoppe et al., 1999; Balasse et al., 2002, 2003; Balasse and Tresset, 2002; Pellegrini et al., 2008). Tissues such as enamel and primary dentine are formed sequentially and their sampling can allow the reconstruction of isotopic data within a time-series (i.e., during molariform tooth crown formation). Given the relatively long periods of growth that can be represented in herbivore molariform teeth, the periodicity or seasonality of isotopic variations (due to regular dietary, climatic or location changes) can be established. Such techniques have a range of archaeological applications and have been used to investigate enforced weaning, birth seasonality, foddering, transhumance, and other animal husbandry strategies in archaeological domesticated taxa (Balasse and Tresset, 2002; Balasse et al., 2003, 2006; Bentley and Knipper, 2005). In wild species, these methods can be used to reconstruct seasonal habitat use, dietary changes, niche behaviours, movements and physiology (Hoppe et al., 1999; Gadbury et al., 2000; Pellegrini et al., 2008; Feranec et al., 2009). Such methods also permit the investigation of diachronic assemblages, allowing the exploration of how animal behaviour may have changed through time (e.g., Hoppe and Koch, 2007). Isotopic techniques have also been utilised to assess relatedness of animals in mass death assemblages and to reconstruct the accumulation of bone assemblages in terms of number of hunting episodes, inferring ancient human hunting strategies (Hoppe, 2004).

Here, the sequential-sampling and strontium isotope analysis ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) of *Rangifer* enamel from the Neanderthal site of (Chez-Pinaud) Jonzac, (Charente-Maritime, France) is used to investigate the migratory behaviour of this species in the past. *Rangifer* was arguably the most abundant large herbivore in Northern Eurasia during the late Pleistocene, and these techniques provide insights into the palaeoecology of this important subsistence species and Neanderthal site use in the Middle Palaeolithic of Europe.

## Strontium isotope analysis and the reconstruction of animal biogeography

$^{87}\text{Sr}$  in rocks forms over time through the radioactive decay of  $^{87}\text{Rb}$  (rubidium), while  $^{86}\text{Sr}$  is stable and does not change. The relative content of  $^{87}\text{Sr}$  to  $^{86}\text{Sr}$  is therefore a function of the age, and also of the original rubidium content of the rock. This leads to generally higher  $^{87}\text{Sr}/^{86}\text{Sr}$  values in older rocks and lower values in younger rocks, most notably in igneous and metamorphic rocks. In herbivores, the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratio of mineralized tissues is directly related to that of plants consumed, and ultimately to the  $^{87}\text{Sr}/^{86}\text{Sr}$  ratios of local soils and waters. Although other influences, such as atmospheric strontium or aeolian deposits, have been shown to affect the Sr composition of local soils (e.g., Miller et al., 1993; Capo et al., 1998; Chadwick et al., 1999), 'bioavailable' Sr in surficial deposits largely reflects local lithologies. Therefore, the strontium isotope composition of mineralized tissues such as bone and tooth enamel often reflects underlying geology, and therefore location, during formation (see review in Bentley, 2006). This principle has been used to explore animal and human mobility in the past, and also has applications to palaeoecology and palaeobiology (e.g., Koch et al., 1998; Hoppe et al., 1999; Gadbury et al., 2000; Feranec et al., 2007), forensics (van der Merwe et al., 1990; Beard and Johnson, 2000; Aggarwal et al., 2008), and modern ecology (see review in Hobson, 1999).

Mammalian enamel is laid down and mineralized in a broadly sequential manner, with the apex forming before material towards the neck of the tooth. In herbivores, this growth can represent many months including multiple seasons, depending on the species in question (e.g., Gadbury et al., 2000; Hoppe et al., 2004). Enamel undergoes no remodelling after formation (Gage et al., 1989), therefore strontium incorporated during mineralization remains during life. Furthermore, the densely packed, crystalline structure of enamel renders it more resistant to diagenesis than other tissues such as bone and dentine (Budd et al., 2000; Hoppe et al., 2003). As a consequence, it may be possible to track seasonal changes in location through the sequential-sampling and strontium isotope analysis of archaeological teeth. A small number of previous studies have used strontium isotope analysis and intra-tooth enamel sampling on archaeological materials to establish animal movements, from both a palaeoecological perspective (Hoppe et al., 1999) or with the aim of establishing relationships between human and animal behaviours (Pellegrini et al., 2008).

However, there are a variety of issues that must be considered that may influence (specifically, attenuate) strontium isotope values determined from herbivore enamel, including the relationship between enamel geometry and the sampling method selected (e.g., Passey and Cerling, 2002; Zazzo et al., 2005), as well as possible physiological factors (Montgomery et al., 2010). The method of continuously sampling herbivore teeth for isotope analysis assumes that tooth enamel mineralizes sequentially (from cusp to cervix) and also at a continuous rate. These assumptions are only partially correct. Attenuation and dampening effects brought about through the successive phasing and multi-dimensional nature of mineralization should always be kept in mind when interpreting this kind of isotope data, along with the homogenizing influence of the transverse sampling methods that are usually employed (e.g., Passey and Cerling, 2002). It should be noted that of the few studies investigating the influence of enamel geometry and sampling approach on isotopic data, most have involved isotope systems other than strontium (e.g., oxygen: Passey and Cerling, 2002; carbon: Zazzo et al., 2005). Where micro-sampling (or even laser ablation) methods are employed, the spatial geometry of enamel and the phasing of enamel mineralization during maturation might still serve to limit the resolution achievable (Zazzo et al., 2005).

The results of a recent study on bovine molariform teeth from a single archaeological sample also appear to confirm the problem of strontium isotope signal attenuation in hypsodont herbivore teeth (Montgomery et al., 2010). However, in this instance, the authors argue that the gradual isotopic transitions in the teeth, observed using both the 'traditional' transverse sampling methods with TIMS and the potentially higher-resolution LA (laser ablation)-MC-ICP-MS methods, are due to the residence time of strontium in the body, potentially further complicating the use of strontium isotope analysis for the reconstruction of palaeomigrations (Montgomery et al., 2010). Given that (as an archaeological sample) neither the origin, movement nor dietary history of the individual involved in the study are known, the results should perhaps be treated with an appropriate degree of caution. As the authors themselves state, "studies of modern migratory cattle of known origin, diet and residence are required if any of these variables are to be unravelled" (Montgomery et al., 2010: 40). Furthermore, Montgomery et al. propose that strontium residence time may increase with age and that, while strontium accumulated during the first year of (a calf's) life may then recirculate in the body after this period, the averaging effect may not be as pronounced in a growing, chemically-active skeleton (Montgomery et al., 2010). Therefore, the implications for studies of brachydonts (i.e., low-crowned species, such as *Rangifer* and other Cervidae) are not clear, as they have much shorter tooth formation/enamel mineralization times than high-crowned herbivores (in the order of months rather than years). Although current research is providing valuable insights, far more work on modern materials is required to better explore and characterise the caveats associated with the gaining of time-resolved isotope data from herbivore teeth.

The only published intra-tooth strontium isotope study conducted on modern material to date involved the analysis of migratory caribou from Alaska (*Rangifer tarandus granti*), demonstrating the capacity for these methods to identify and characterise known patterns of seasonal migratory behaviour in this species (Britton et al., 2009). As with the intra-tooth studies discussed above, the authors also identified some isotopic signal attenuation and discuss possible reasons for this, including influence of feeding ecology and ranging behaviour of the animals themselves (Britton et al., 2009). Whether the result of enamel geometry, sampling strategy, animal physiology or behaviour, such signal attenuation complicates the establishing of 'end member' strontium inputs (Montgomery et al., 2010) and therefore urges caution in the identification of precise points of origin. However, even where 'end members' cannot be established, our modern study does highlight the capacity to identify regular seasonal migrations using these methods. Incorporating oxygen isotope analysis, this study also demonstrated the potential strength of using two independent isotope systems, and strontium and oxygen isotope ratios co-varied synchronously in the migratory individuals (correlating with winter and summer range use). The association of strontium data with fluctuations in oxygen isotope values further suggests a much shorter period of residence for strontium in the body of growing deer, at least during the phase of permanent molariform enamel formation and mineralization. The analysis of multiple individuals from the same modern herd also allowed an assessment of the level of intra-herd variability and demonstrated the potential for such methods to elucidate the movements of populations of this archaeologically-important prey species.

### The site of Jonzac

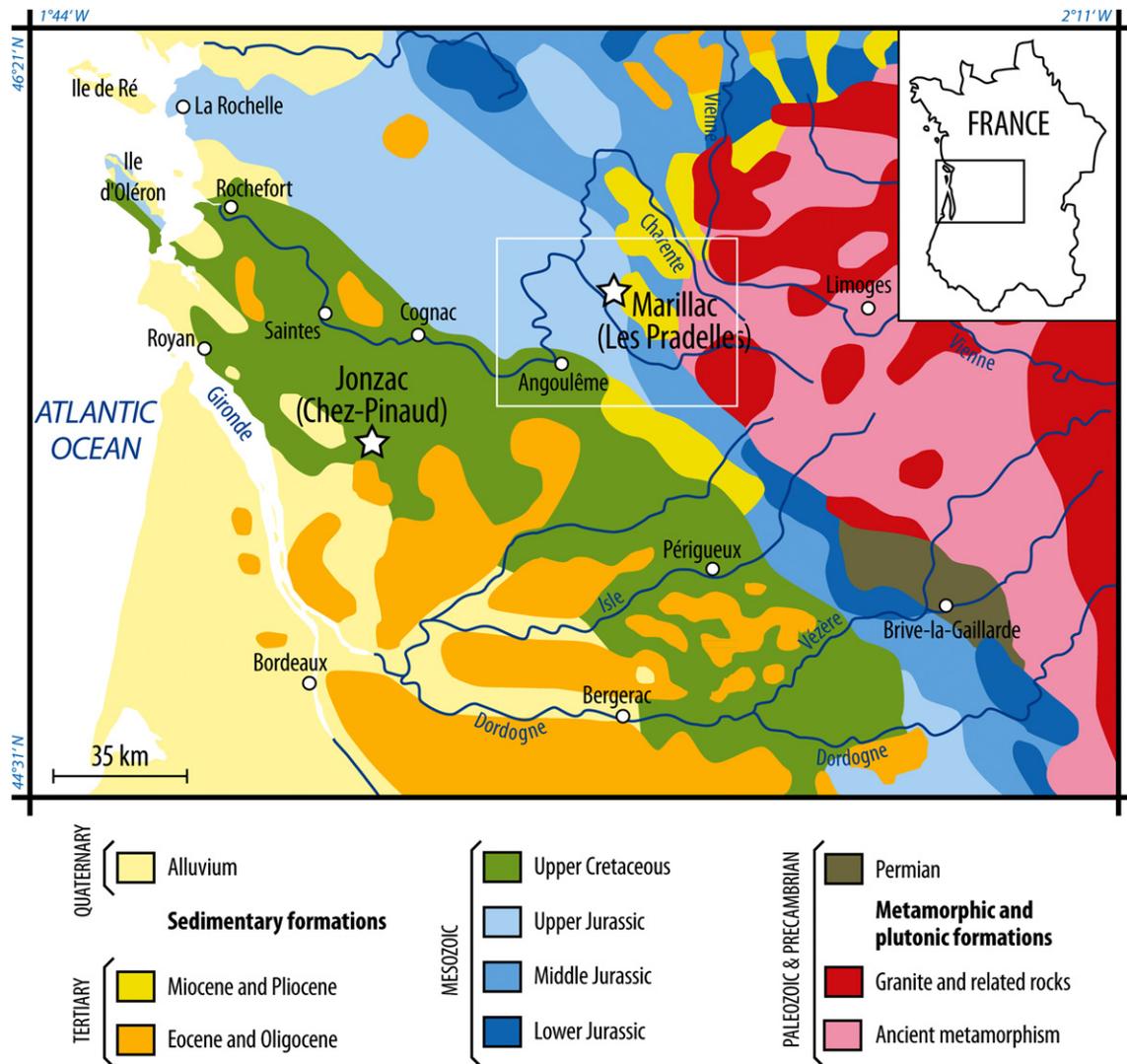
The site of Jonzac, also known as Chez-Pinaud, is a collapsed rock shelter located in the Charente-Maritime region of southwest France, approximately 80 km north of Bordeaux and 110 km

southeast of La Rochelle (Fig. 1). The site was discovered in the 1990s and has been excavated during two campaigns; the first led by Jean Airvaux (1998–1999, 2002–2003) (Airvaux, 2004; Airvaux and Soressi, 2005) and the second as a larger scale multi-disciplinary collaboration between the Max Planck Institute of Evolutionary Anthropology in Leipzig (led by Jean-Jacques Hublin) and the Université de Bordeaux I (led by Jacques Jaubert) (Jaubert et al., 2008; Richards et al., 2008).

The cultural sequence at the site from bottom to top includes Quina Mousterian, Denticulate Mousterian, Mousterian of Acheulian Tradition (MTA), and Aurignacian. The stratigraphic units include rich lithic industries, anthropogenically-modified animal bone and an MTA Neanderthal premolar. The carbon and nitrogen stable isotope analysis of this Neanderthal, along with the associated MTA fauna, has been previously published (see Richards et al., 2008).

Near the base of the sequence is stratigraphic unit W-22 (W-US22), a thick (>1 m), dense accumulation of fauna ('bonebed') associated with a Quina Mousterian lithic industry (Jaubert et al., 2008). The Quina fauna are dominated by *Rangifer*, with prime-age individuals most commonly represented. Archaeozoological data indicate Neanderthal hunting of reindeer during the winter/spring and probably an additional event in autumn (Jaubert et al., 2008; Steele et al., 2009). Smaller numbers of other species such as horse (*Equus* sp.) and bison (*Bison* cf. *priscus*) were also found. There is little evidence for post-depositional disturbance in the bonebed and the faunal remains are in an excellent state of preservation, including *in situ* articulated limb units and complete hemi-mandibles. Skeletal element abundances indicate that a number of complete or nearly complete reindeer (NISP = 5232; MNI = 18) were introduced to the site for butchering (Jaubert et al., 2008). Stone-tool cut marks are frequent, indicating disarticulation and meat removal. Long bones were also systematically fractured during marrow extraction (Jaubert et al., 2008).

The area surrounding Jonzac is dominated by limestone, consisting of both Late Cretaceous and older Jurassic deposits (Fig. 1). The site itself lies on Late Cretaceous (Turonian) lithologies, including fossiliferous, bioclastic and argillaceous limestones. These limestones continue eastwards throughout the surrounding region into the Dordogne (Pomerol and Debelmas, 1980; Girard, 2009; Fig. 1). Plant and soil strontium values for this area can give an indication of what is the local or 'bioavailable' strontium isotope signature (i.e., that can become assimilated into the mineralized tissues of animal living in the area). An extensive strontium bioavailability study has been conducted in this area by one of the authors (TK) as part of a separate study (Kelly, 2007), with analysis carried out at the Australian National University, Research School of Earth Sciences. Although focussing on the area surrounding another archaeological site (Marillac, also known as Les Pradelles), Kelly's survey incorporated analyses of soil (including topsoil and deeper soils), plants and rock from the major geological units of the region, including those surrounding Jonzac. The mean environmental strontium value for sampling sites on the limestone lithologies is  $0.7088 \pm 0.0013$  ( $1\sigma$ ,  $n = 22$ ), which is typical for Cretaceous and Jurassic limestones, reflecting  $^{87}\text{Sr}/^{86}\text{Sr}$  in contemporary seawater (Bentley, 2006). Furthermore, this mean corresponds to the range of  $^{87}\text{Sr}/^{86}\text{Sr}$  values determined for local mineral waters ( $0.7070$ – $0.7090$  from Voerkelius et al., 2010) and local wines (Almeida and Vasconcelos, 2001). Further to the east is the Massif Central. This area is more elevated and consists of fine and coarse grained, mica-rich Devonian granitoids. These older, more radiogenic areas had sites with normally higher 'bioavailable' strontium isotope values ( $0.7166 \pm 0.0060$ ,  $1\sigma$ ,  $n = 9$ ; Kelly, 2007). These higher values are similar to the range of values determined for local mineral waters from the ancient lithologies of the Massif



**Figure 1.** Simplified geological map of southwest France (after Pomerol and Debelmas, 1980; Wilson, 1999, Colour Plate 1; Girard, 2009: Fig. 1), showing location of Jonzac (Chez-Pinaud) and the proximal site of Marillac (Les Pradelles). The area of Kelly's environmental sampling study is highlighted (Kelly, 2007). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Central (0.7130–0.7200, Voerkelius et al., 2010). This region of southwest France also features some biotite-rich gneiss, partially mixed with the granites (0.7213 ± 0.0050, 1σ, n = 2; Kelly, 2007). In addition to limestone lowlands and granitoid uplands, there are also some areas of Tertiary and Quaternary clays and clay sands (Pomerol and Debelmas, 1980). Sampling sites on the Tertiary and Quaternary lithologies also yielded higher mean values than the limestones (0.7109 ± 0.0012, 1σ, n = 23; Kelly, 2007).

Given the density of anthropogenically-modified faunal remains at Jonzac and excellent preservational conditions (including multiple hemi-mandibles with complete cheek–tooth rows), the site represents an ideal opportunity to use strontium isotope analysis for exploring the seasonality of animal movements in the Middle Palaeolithic. This study utilises the strontium isotope analysis of sequentially-sampled enamel of reindeer from the Quina Mousterian deposits (W-US22) in order to explore their biogeography. A single bison was also sampled from the same stratigraphic unit for comparative purposes. Here, the application of the same technical and analytical methods applied to previously-published modern materials (Britton et al., 2009) reveals information about the range use of these different taxa. Intra-tooth strontium data is assessed to identify migratory behaviour in these

species, facilitated by the existence of an environmental strontium isotope data set from a proximal area (Kelly, 2007; mean values cited above). Patterns of intra-tooth strontium isotope variation are used to comment on the seasonal availability of these species at Jonzac and the influence that their seasonal migratory behaviour may have had upon Neanderthal hunters.

### Materials and methods

Second (M2) and third (M3) molars were extracted from three W-US22 right hemi-mandibles from three individual reindeer (specimen numbers: G9-2068, H9-2221 and H10-1002) and selected for analysis. Based on dental eruption and wear, these individuals were aged between two and four years, with crown heights averaging between 9.4 and 14.2 mm (M2), and 14.3 and 16.2 mm (M3). Given that there is currently no published material on the timing of crown formation or enamel mineralization in *Rangifer*, these two molariform teeth were selected on the basis of mandibular radiography studies of other deer species (Brown and Chapman, 1991a, b). Using these studies as a guideline, it is suggested that a complete, unerupted and unworn *Rangifer* M2 or M3 represents between six and nine months of growth, and that these teeth form sequentially

between the ages of <3.5 and nine months (M2) and nine and <18 months (M3) (Brown and Chapman, 1991a). This phasing appears to be confirmed by recent sequential oxygen isotope studies of M2 and M3 enamel in modern caribou (Britton et al., 2009; Britton, 2010). A single bison first/second maxillary molar (G8-2285) from the same stratigraphic unit – the only suitable sample available – was also selected, allowing for inter- as well as intra-species comparisons to be drawn. As an isolated tooth in full wear, no estimation of age was possible for this individual, although crown heights of 32.1 mm indicate that it was an adult but not old. As a high-crowned herbivore, the period of crown formation and mineralization is considerably longer in the bison than in the reindeer. The phasing of enamel formation and mineralization has been better established for modern bison and cattle than for other herbivores (Brown et al., 1960; Gadbury et al., 2000). The M1 begins to form several months before birth until around four months of age and the M2 forms between birth and ~13 months (Brown et al., 1960; Gadbury et al., 2000). Although modern bison cows may take up to one year to wean their calves (McHugh, 1958), there is no fractionation or ‘weaning’ influence observable in strontium isotope studies (see Bentley, 2006). All samples were drawn from a 15 cm subunit within W-US22. Work is currently in progress to date W-US22 by thermoluminescence (TL). However, we can estimate its age based on the overlying stratigraphy. W-US21 to W-US09 are dominated by reindeer and thus indicate cold conditions. A shift towards more temperate conditions is indicated by the fauna in SW-US08 (overlying W-US09), which was dated by TL to  $49 \pm 5$  ka (Jaubert et al., 2008). It is very likely, therefore, that W-US22 dates to MIS4.

A detailed account of the methods used in the preparation of these samples for strontium isotope analysis can be found in Britton et al. (2009). An in-depth description of the solution strontium analysis (wet chemistry, ion-exchange columns and mass spectrometry) can be found in Copeland et al. (2008).

After being extracted from the mandibles, all teeth were mechanically abraded using a tungsten carbide burr (MTI-Kahla, Germany). This was done to remove surficial enamel, which is more likely to be diagenetically altered or contaminated with exogenous strontium from within the burial environment (Budd et al., 2000; Trickett et al., 2003). Intra-tooth sampling was performed with superfine diamond-coated circular drilling discs. Cross-contamination was avoided through the cleaning of all drill-bits prior to use and between samples using a weak nitric acid solution, ultrasonic bath and water rinse.

The buccal face of the anterior loph of each tooth was removed for analysis. This was selected due to the slightly thicker enamel found in this portion of the tooth. Adhering dentine in the interior of each portion of enamel was removed using a clean tungsten carbide burr and a little dentine (~20 mg) was retained for strontium isotope analysis. A final thorough cleaning of all external and internal surfaces was conducted, ensuring that all dentine was removed and only enamel would be analysed in the intra-tooth samples. 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).

Intact faces of enamel were marked for horizontal sequential-sampling using the diamond-coated disc and done at ~1.5 mm intervals. Whole enamel faces were ultrasonicated in deionised (Milli-Q®, 18.7 M $\Omega$ ) water for 10 minutes and dried at room temperature. Sections were cut using the drilling disc and each section was ultrasonicated in deionised water (5 minutes) and dried. These washing procedures ensured the removal of any adhering enamel powder from adjacent sections. Sections were given sequential numerical sample assignments, starting from the cementum–enamel junction.

Enamel sub-samples were prepared for solution strontium analysis in the clean laboratory and MC-ICP-MS facility at the MPI-

EVA, Leipzig. The methods used were similar to those detailed by Deniel and Pin (2001) with modifications outlined in Copeland et al. (2008).

The initial pre-treatment involved an additional cleaning step, including rinsing with high purity deionised (18.7 M $\Omega$ ) water (Milli-Q® Element A10 ultrapure water purification system, Millipore GmbH, Schwalbach, Germany), followed by ultrapure acetone (GR for analysis grade,  $\geq 99.8\%$ , Merck KGaA, Darmstadt, Germany). Samples were dried overnight in a closed, clean environment under constant airflow (HEPA filtered, Class 10). Clean enamel samples (5–15 mg) were then dissolved in 3 mL Savillex® vials (Minnetonka, MN, USA) with 1 mL of 14.3 M HNO<sub>3</sub> (SupraPur® grade, Merck KGaA). Following complete dissolution, the samples were evaporated to dryness on a hot plate (~8 h; 120 °C). The resulting residue was re-dissolved in 1 mL of 3 M HNO<sub>3</sub> (SupraPur® grade, Merck KGaA) and then passed through 2 mL micro-columns containing pre-conditioned Sr-Spec® (EiChroM Industries, Darien, IL, USA) resin suspended in water. Three wash cycles of 1 mL 3 M HNO<sub>3</sub> were passed through the columns prior to the elution of strontium from the resin in 1 mL Milli-Q (18.7 M $\Omega$ ) deionised water. This solution was dried and then re-dissolved in 3% HNO<sub>3</sub> (SupraPur® grade, Merck KGaA) for analysis of <sup>87</sup>Sr/<sup>86</sup>Sr ratios using MC-ICP-MS.

Strontium isotope measurements were determined using a Thermo Fisher Neptune™ plasma ionization multicollector mass spectrometer. <sup>87</sup>Sr/<sup>86</sup>Sr measurements were corrected for Krypton (Kr) and Rubidium (Rb) interferences and normalized for instrumental mass bias using <sup>88</sup>Sr/<sup>86</sup>Sr = 8.375209. Repeated analysis of an international standard (NIST SRM987) was used for external normalization of all data. The long-term <sup>87</sup>Sr/<sup>86</sup>Sr value, determined over a 10-month period, was  $0.710273 \pm 0.000033$  (46 ppm,  $2\sigma$ ,  $n = 97$ ). The average internal error of any given measurement was  $0.000006 \pm 0.000004$  (8 ppm,  $2\sigma$ ,  $n = 97$ ) (Copeland et al., 2008). The reported <sup>87</sup>Sr/<sup>86</sup>Sr values were adjusted to the standard SRM987 using a published value of 0.710240 (Terakado et al., 1988; Johnson et al., 1990), and strontium concentrations were determined with an accuracy of  $\pm 31$  ppm (Copeland et al., 2008; Britton et al., 2009).

## Results

The results of the strontium isotope measurements for the herbivore enamel are summarised in Table 1 and the accompanying strontium isotope data from the dentine of each individual can be found in Table 2. Sequential strontium data for the three W-US22 reindeer are shown in Fig. 2, along with dentine values, the mean limestone value (soil and plant; Kelly, 2007) and average modern rainwater value (Capo et al., 1998). Fig. 3 demonstrates the sequential strontium data and total strontium intra-tooth variability in each of the individuals analysed, including the single bison sample. Given the number of individuals under analysis and the nature of the data, no statistical approaches have been employed with the analysis of the serial strontium data.

The total isotopic range of strontium data for all of the enamel samples and all of the animals (including bison and reindeer) involved in this study is fairly large (from 0.7090 to 0.7104). Strontium concentrations in the enamel range from 13 to 166 ppm, with a mean of 76 ppm ( $n = 49$ ). These values are comparable with those observed in domestic cattle from England and modern Alaskan caribou (Evans et al., 2007; Britton et al., 2009). The strontium isotope values determined from the herbivore dentine are lower than the values measured in the enamel (range = 0.7088–0.7092, mean = 0.7089,  $n = 9$ ) and the strontium concentrations are generally higher (mean = 101 ppm,  $n = 9$ ). These data indicate that diagenetic alteration of dentine within the burial environment has occurred, moving dentine strontium isotope values towards the likely strontium isotopic composition of the surrounding limestone

**Table 1**  
Summary of isotopic results ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) from sequentially-sampled enamel of from three Jonzac reindeer and one bison.

Individual	Sample	$^{87}\text{Sr}/^{86}\text{Sr}$	Sr conc. (ppm)
G9-2068 <i>Rangifer</i>	M2-5	0.7096	100
	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 <i>Rangifer</i>	M2-6	0.7095
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 <i>Rangifer</i>		M2-6	0.7096
	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 <i>Bison</i>	M-13	0.7091
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

Sections were given numerical assignments commencing from the neck of the tooth to the occlusal surface/apex.

soils (mean = 0.7088; Kelly, 2007). This type of diagenetic alteration is expected in dentine, confirming it as an unsuitable analyte for archaeological strontium isotope studies (Budd et al., 2000; Hoppe et al., 2003).

**Table 2**  
Isotopic results ( $^{87}\text{Sr}/^{86}\text{Sr}$ ) from dentine of three Jonzac reindeer and one bison.

Individual	Sample	$^{87}\text{Sr}/^{86}\text{Sr}$	Sr conc. (ppm)
G9-2068	dM2	0.7088	125
	dM3	0.7090	118
H10-1002	dM2	0.7090	86
	dM3	0.7092	105
H9-2221	dM2	0.7089	120
	dM3	0.7089	88
G8-2285	dM-i	0.7088	94
	dM-ii	0.7088	81
	dM-iii	0.7088	95

A single sample of dentine was taken from each reindeer tooth, and three (dM-i, dM-ii, dM-iii) were taken from the larger bison tooth.

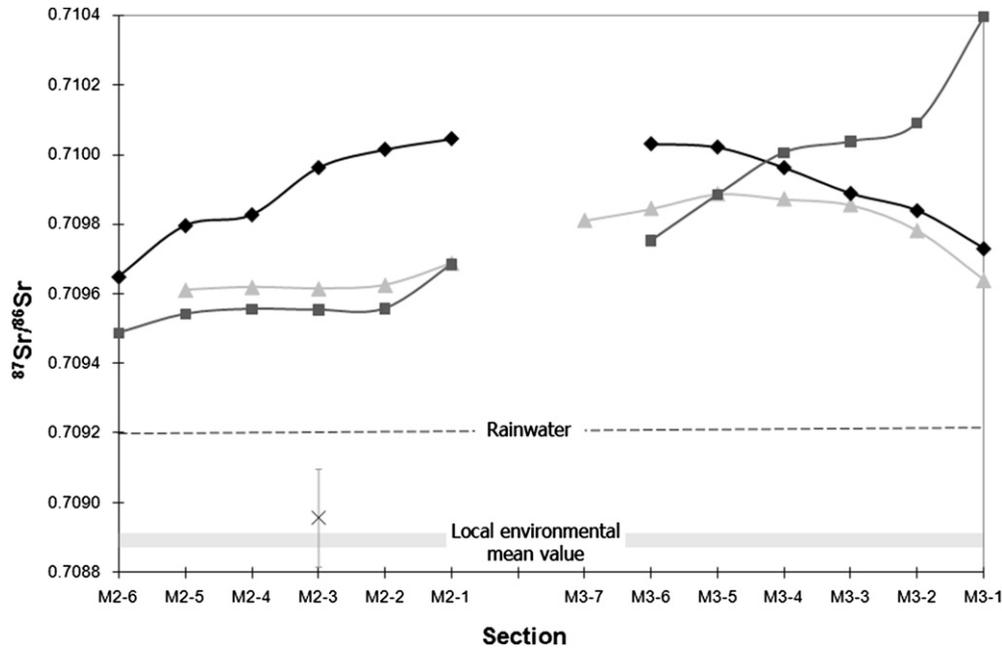
The total range of enamel  $^{87}\text{Sr}/^{86}\text{Sr}$  isotope data for the reindeer is 0.7095–0.7104 with a mean of  $0.7098 \pm 0.0002$  ( $1\sigma$ ). These three individuals display a similar overall trend in the first-forming second molar, from lower values in the earliest forming parts of the M2 ( $0.7096 \pm 0.0001$  ( $1\sigma$ ) at point M2-5) to slightly higher values ( $0.7098 \pm 0.0002$  ( $1\sigma$ ) 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 ( $0.7099 \pm 0.0001$  ( $1\sigma$ ) at point M3-6 and  $0.7099 \pm 0.0001$  ( $1\sigma$ ) at point M3-4). Individuals G9-2068 and H9-2221 remain similar ( $0.7097 \pm 0.0001$  ( $1\sigma$ ) at point M3-1) but H10-1002 differs slightly at this point, rising to 0.7104 at point M3-1. The total amount of time represented by these isotopic fluctuations is inferred to be approximately one year of life in these animals (Brown and Chapman, 1991a, b; Britton et al., 2009). Despite some inter-individual variations (e.g., H10-1002 in the latest forming parts of the M3), the intra-group variability within this small sample of late Pleistocene *Rangifer* is as small as, or smaller than, variability displayed in modern herds (Britton et al., 2009). The strontium isotope values measured in the reindeer enamel are universally higher than the mean soil and plant strontium value from a proximal area of similar geology (Kelly, 2007). The amount of intra-tooth variation and general pattern of strontium isotope variation is consistent with a non-local, seasonally migrating animal.

The bison  $^{87}\text{Sr}/^{86}\text{Sr}$  values range from 0.7090 to 0.7091 ( $0.7091 \pm 0.0001$  ( $1\sigma$ )) throughout the formation of this molar. These values are lower than the contemporary *Rangifer* and a lower amount of intra-tooth variation is displayed in this animal compared with the second or third molars of any of the reindeer (Fig. 3). Bison are high-crowned herbivores and this tooth represents a longer period of growth than the individual reindeer teeth, the enamel of a first or second molar taking more than one year to form (Brown et al., 1960; Gadbury et al., 2000). All strontium values displayed in this individual are also far more similar to the mean local soil and plant values than the reindeer. This, combined with a lack of intra-tooth variability, is consistent with a more local, non-migratory animal, which may have been available in the local area throughout the year.

## Discussion

### Reindeer intra-group variation

Bulk isotopic techniques have previously been employed to explore relatedness in archaeological animal bone assemblages, to identify potential herds or family groups, and therefore to infer the nature of the accumulation in terms of single or multiple hunting events (Hoppe, 2004; Fenner, 2008, 2009). Here, intra-tooth data from multiple individuals can not only be used to examine relatedness in terms of overall values, but can also be used to compare strontium isotope variations through time (i.e., during dental formation/mineralization) and therefore migratory behaviour during this period. Although the number of samples involved in this initial study is small compared with bulk isotope studies (yet comparable with other intra-tooth studies), it is possible to draw comparisons between the strontium isotope values determined in the different individuals and assess the intra-group variation. This is facilitated by the existence of published data from a modern herd of migratory Alaskan caribou (Britton et al., 2009), in addition to a large quantity of available data from other North American caribou and bison herds (Britton, 2010). The three reindeer analysed generally exhibit a low degree of intra-group strontium isotope variation, which is comparable to the variation expected within the modern caribou herds. The slight differences observed



**Figure 2.** Sequential  $^{87}\text{Sr}/^{86}\text{Sr}$  data from *Rangifer* enamel from the Quina Mousterian deposits (W-US22) at Jonzac (diamonds = H9-2221, squares = H10-1002, triangles = G9-2068). Also shown are dentine strontium isotope data from the same individuals (cross = mean value, with total range shown,  $n = 6$ ) and the mean local environmental strontium isotope value (Kelly, 2007). The dashed line shows the  $^{87}\text{Sr}/^{86}\text{Sr}$  value of modern rainwater. Analytical error is within the point markers.

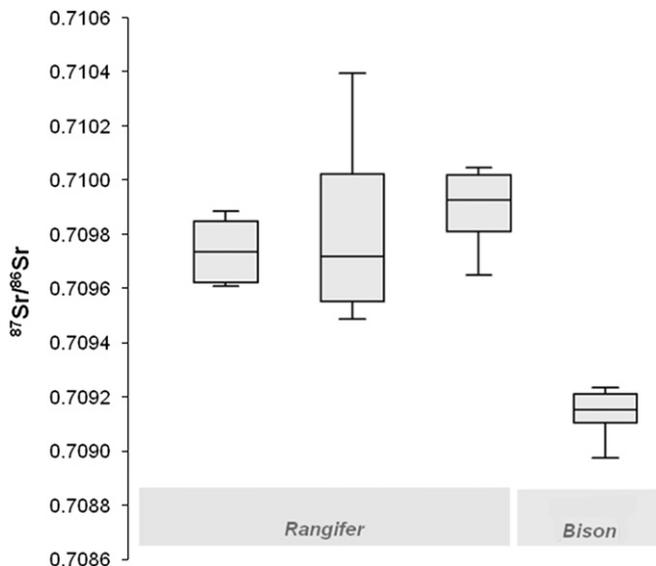
between H10-1002 and the other reindeer in the latest forming portions of the M3 are noteworthy and could be attributed to differences in migratory behaviour. However, given that these differences are similar to or even lower than those observed in modern herds (Britton et al., 2009; Britton, 2010), it is unlikely that this represents a behavioural outlier. Within modern herds, similar intra-group variation has been attributed to natural dispersal within large herds and/or across large geographical ranges (which may incorporate different lithologies), rather than a lack of behavioural fidelity (Britton et al., 2009; Britton, 2010).

It is suggested that the Jonzac reindeer indicate a relatively high degree of intra-group homogeneity and therefore 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). These inter-individual similarities lead to two interpretative scenarios: 1) that reindeer migratory behaviour was relatively stable in the late Pleistocene, or 2) that the animals sampled in this study originate from the same herd and possibly even the same hunting episode. In the first instance, with this data we could presume that herd behaviour (both inter-individually and inter-annually) was more stable in the late Pleistocene than observed in many modern herds. This could be due to the lack of interferences of modern infrastructure, range disruption, herd management and humanly-induced climatic/environmental changes that have been demonstrated to influence migration habits in modern herbivore species (e.g., Serneels and Lambin, 2001; Joly et al., 2002, 2003; Dahle et al., 2008). However, given the close proximity of all samples within the deposits (restricting temporal span of individuals sampled), the latter explanation may be more likely. In this scenario, these reindeer may have originated from the same herd, were killed in close chronological succession and are therefore the product of a small number of hunting episodes.

#### Reindeer and bison movements

Intra-tooth strontium isotope variations from the reindeer at Jonzac indicate movement across different geological terrains during enamel formation in the M2 and M3, a period of at least one year. This behaviour appears to be regular and seasonal, indicating a true migration. The strontium values are universally higher than environmental values typical of this geology (Kelly, 2007). Therefore, the strontium isotopic evidence does not indicate that they were a local species and that lithologies other than those found at the site contributed to strontium isotope ratios observed in the dentition. Furthermore, measured strontium isotope values are not as high as the nearby clay and granite zones (0.7109 and 0.7166, respectively; Kelly, 2007). Therefore, although the shape of the intra-tooth strontium isotopic profiles indicates seasonal movement, the isotopic data does not confidently tie these animals to any of the proximal geological units.



**Figure 3.** Sequential  $^{87}\text{Sr}/^{86}\text{Sr}$  data from *Rangifer* and *Bison* enamel. Box plots display the first and third quartile, median, minimum and maximum values.

However, despite being identified as non-locals and migrants, these reindeer clearly spent a portion of their annual movement cycle in the area close to the site of Jonzac. The large volume of remains and primary butchering processing evidence at Jonzac make it unlikely that these materials were transported long distances from other areas. Like modern caribou, the Jonzac reindeer may have moved quickly through the local area during their annual migrations, with contributions from the local strontium isotope signature becoming dampened or diluted through additions from other geological areas. This is likely due to the rapidity of the movement, combined with the phasing of mineralization and influenced by the ranging/feeding behaviour of the animals. A similar effect has been observed in the modern herds, where the isotopic inputs from migratory zones (i.e., areas between the summer and winter ranges) are not preserved in the sequentially-sampled strontium data (Britton et al., 2009). It is also suggested that the total range size of these animals could have been very large, with geographically distant and geologically distinct summer and winter ranges, producing specific isotope signatures in the teeth. It is also suggested that, as with many modern caribou herds, the seasonal ranges themselves would have been very large, likely incorporating a range of geological substrates and therefore a mixed signal in the teeth.

Although a location of summer and winter range cannot be inferred, using the isotopic data we can deduce that these animals shared similar life histories, were non-local for at least some part of their maturation, and engaged in seasonal migratory movements. In contrast, data from a single, contemporary bison at the same site, suggest that this species was not undertaking regular seasonal movements during this period. The lower strontium isotope values and lack of intra-tooth variation indicate that this animal did not undertake movements over different geological terrains during molar enamel formation and that local strontium sources (i.e., the Cretaceous and Jurassic limestones) made a large contribution to the strontium isotope values found in the tooth.

#### *Herbivore biogeography and Neanderthal hunting at Jonzac*

Based on the isotopic data, we suggest that these late Pleistocene reindeer, like many modern Alaskan and Canadian caribou populations, undertook bi-annual migrations. The level of intra-group homogeneity shown in the reindeer may be demonstrative of closely-allied behaviour in contemporary individuals. The isotope data supports the idea of a rapid accumulation of W-US22, the product of hunting events in which Neanderthals targeted the same reindeer herd. Bulk sampling techniques have previously been employed to assess the isotopic-relatedness between individuals in an assemblage and therefore to identify single or multiple kill events in archaeological contexts (Hoppe, 2004; Fenner, 2008, 2009). Here, the serial-sampling techniques have not only allowed the identification of a group – the possible product of a single hunting event or closely-timed series of successive episodes – but also revealed the movement habits of the animals in question.

The strontium isotope values obtained from these individuals imply that these animals spent large portions of their lives on non-local lithologies, at least during the period of M2 and M3 enamel formation. As with modern migratory caribou, if the movements during this first year of life were indicative of lifetime migration habits, this may also support the conjecture that the rock shelter of Jonzac was situated close to the migration route of these seasonally-moving animals. This complements reindeer season-of-death at the site based on zooarchaeological analyses (Jaubert et al., 2008) and implies that the *Rangifer* remains are the result of intensive seasonal exploitation of this species during their annual migration.

It is this seasonal availability of large number of reindeer in the local area that accounts for the abundance of prime-age *Rangifer* in

the faunal assemblage. 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-predictable resources. This seasonally-restricted use is also indicated by the low density of remains from other species in the W-US22 deposits, with species such as bison likely to have been local and available all year round, as confirmed by the strontium isotope data. This may also be true of horses, which are also represented in low-densities in the Quina Mousterian deposits at Jonzac (Jaubert et al., 2008).

It is hoped that future work incorporating additional species and from other contexts at Jonzac could be used to measure changes in the behaviours of the same 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 to 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.

#### **Conclusions**

This study has provided insight into the movements and palaeoecology of late Pleistocene *Rangifer* and *Bison*. Here, strontium isotope analysis and the sequential-sampling of enamel 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 bonebed at Jonzac has revealed clear similarities in the seasonality and route of migration in this ancestral species. The inter-individual variability within this group is low, suggesting a strong fidelity to migration routes at this time and/or the contemporaneity of these individuals, their birth, death and deposition. When combined with season-of-death and seasonality data from Jonzac, it is possible to deduce that Neanderthal hunters intensively exploited the reindeer as the herds passed through the area, with the rockshelter of Jonzac located near their migration routes. Strontium isotope values from the single bison indicate that this was a local, non-migratory animal. Representation of this and other species is significantly lower than reindeer in these deposits, again emphasising the seasonality and nature of site use. Evidence for reindeer interception hunting is becoming increasingly clear at Mousterian sites (Gaudzinski and Roebroeks, 2000; Costamagno et al., 2006; Gaudzinski, 2006), as well as at Upper Palaeolithic sites (White, 1985; Enloe, 1993; Burke, 1995; Boyle, 1996; Jochim et al., 1999) and amongst contemporary/historic hunter–gatherer groups (Ingold, 1986). This indicates that that reindeer interception hunting was a subsistence strategy amongst both Neanderthals and anatomically modern humans, and emphasises the deep antiquity and long-endurance of this hunting strategy in the human past.

This case study demonstrates the potential for strontium isotope methods and sequential enamel sampling to reconstruct the biogeography of archaeologically-important prey species, and to distinguish between contemporary migrants and non-migrant species at the same site. The establishing of biogeochemical landscapes of the past is clearly not only an important part of palaeoecology but can also shape our understanding of hominin site-selection and predation behaviour.

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