

Rhiannon E. Stevens · Adrian M. Lister
Robert E. M. Hedges

Predicting diet, trophic level and palaeoecology from bone stable isotope analysis: a comparative study of five red deer populations

Received: 17 May 2005 / Accepted: 14 March 2006
© Springer-Verlag 2006

Abstract C and N stable isotope ratios of red deer (*Cervus elaphus*) bone collagen (154 individuals) from five modern populations occupying geographically different habitats are reported. No significant difference was observed between deer occupying forested and non-forested environments subject to similar climatic conditions suggesting a simple “canopy effect” is not observed. Mean population $\delta^{13}\text{C}$ is negatively correlated with temperature whereas mean population $\delta^{15}\text{N}$ is positively correlated with temperature. A weak but significant positive correlation was observed between deer age and collagen $\delta^{13}\text{C}$ values from the Isle of Rum population (Scotland). The amount of intra-population isotope variability is not consistent among populations; thus significant numbers of individuals from each species are required for modern food web studies, for palaeodietary baseline data, and for palaeoecological studies.

Keywords Carbon · Canopy effect · Collagen · Nitrogen · Temperature

Communicated by Jim Ehleringer

R. E. Stevens (✉)
School of Geography, University of Nottingham,
University Park, Nottingham, NG7 2RD, UK
E-mail: Rhiannon.Stevens@Nottingham.ac.uk

R. E. Stevens
NERC Isotope Geosciences Laboratory,
British Geological Survey, Kingsley Dunham Centre,
Keyworth, Nottinghamshire, NG12 5GG, UK

A. M. Lister
Department of Biology, University College London,
Gower Street, London, WC1E 6BT, UK

R. E. M. Hedges
Research Laboratory for Archaeology and the History of Art,
University of Oxford, Dyson Perrins Building,
South Parks Road, Oxford, OX1 3QY, UK

Introduction

Stable isotope analysis of archaeological human and faunal remains has frequently been used to gain a better understanding of diet for both individuals and populations (Richard and Hedges 1999; Privat et al. 2002; Harrison and Katzenberg 2003). However, the extent of C and N isotopic fractionation between food sources and the consumer is not solely dependent on the species involved, but can be strongly influenced by particular features of the local environment. Such natural variability in the stable isotope composition is neither well documented nor understood. At present, there are insufficient data on relevant animals living free in similar environments to provide a clear indication of how much variability may be expected, and therefore what would constitute an adequate sample size which would define isotopic compositions for a given species in a particular habitat. Most palaeodietary reconstructions have been made on the basis of a sample size that is arguably insufficient to provide the statistical power needed to validate the conclusions, although the taphonomy of palaeodeposits may give little choice in the assemblage used, in terms of numbers, contemporaneity, and homogeneity of habitat. Without such a definition of the relevant “baseline”, palaeodietary reconstructions are hard to justify, and liable to lead to circular arguments.

Palaeoenvironmental reconstructions from faunal isotope results have also been made on limited number of samples. Some of the principles on which these reconstructions have been based have not been fully investigated in modern ecosystems. For example, plants within closed (forested) environments are typically depleted in $\delta^{13}\text{C}$ by 2–5‰ in comparison to plants and trees in open environments, a phenomenon known as the “canopy effect” (Van der Merwe and Medina 1989; Tieszen 1991; see Vogel 1978; Medina and Michin 1980; Broadmeadow et al. 1992 for explanation of mechanism). Several archaeological/palaeoenvironmental studies have assumed that these divergent isotope signatures are

passed on to fauna and have used low faunal archaeological $\delta^{13}\text{C}$ values to infer the presence of a forested habitat (e.g. Bocherens et al. 1995; Fizet et al. 1995; Cerling and Harris 1999; Krigbaum 2003). However, comparisons of faunal $\delta^{13}\text{C}$ signatures from closed and open habitats have principally been made across species, with studies comparing the same species currently only available from tropical environments where forests are extremely dense. Thus palaeoenvironmental reconstructions of forest environments in temperate regions based on a limited number of archaeological samples are unlikely to be reliable.

This study aims to: (1) quantify the amount of inter- and intrapopulation variability in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ observed for a single species, red deer (*Cervus elaphus*), (2) determine if a canopy effect signal can be recognised in red deer isotope signatures, and (3) to investigate how the results of this modern study affects our understanding of reconstructing past diet and environments through isotope investigations of ancient populations.

Red deer was chosen as it is one of the few wild large herbivore species that is numerous in both open and forested habitats in north-west Europe both today and through prehistory. A wild species was selected, as humans, through their choice of animal feed, can control a domestic animal's isotope values. Low red deer $\delta^{13}\text{C}$ signatures have been used in a number of palaeoenvironmental studies to infer forested habitats, therefore the results of this study can be used to validate these reconstructions. By choosing bone collagen for analysis, our results can easily be compared to archaeological isotope values. To investigate the canopy effect we would ideally analyse forest and open environment deer from a single population. However, we were unable to obtain significant numbers of deer bones of

known provenance from a single population. Thus we have selected five populations that were subject to relatively similar climatic conditions and altitudes. As red deer, at least in these populations (Table 1), primarily eat grass, isotopic variation due to dietary choice is limited, and we can investigate the typical isotopic variation within and between populations occupying similar environments, with the presence or absence of forest being the major variant.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in bone collagen

Isotopic dietary reconstructions for both ecological and palaeodietary studies are based on the principle that food sources contain different isotopic signatures, which are passed along the food chain to their consumers. Bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values primarily reflect the isotopic composition of dietary protein (DeNiro and Epstein 1978, 1981; Ambrose and Norr 1993; Tieszen and Fagre 1993). The turnover rate for bone collagen is relatively slow, thus $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of bone collagen reflect the average isotopic values of the dietary protein over the last few years of the animal's life (Stenhouse and Baxter 1979; Schwarcz and Schoeninger 1991). Large-scale variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are generally thought to relate to diet. Inputs of marine versus terrestrial protein (e.g. Schoeninger and DeNiro 1984) or C3 versus C4 plants (e.g. Vogel et al. 1977) have been studied in archaeological populations through analysis of $\delta^{13}\text{C}$. $\delta^{15}\text{N}$ values become more enriched with each trophic level, which has allowed consumption of meat (Bocherens et al. 1999), marine fish (Richards and Hedges 1999) and freshwater fish (Katzenberg and Weber 1999) to be identified in archaeological and modern (O'Connell and Hedges

Table 1 Food sources available to each deer population and primary food consumed based on observations and rumen gut contents analysis

Site	Environment and possible foods	Predominant food	Typical temperatures (°C)	Annual precipitation (mm)	Altitude (m)
Exmoor (southern England)	Woodland and moorland. Wide range of plant species both broad-leaved and coniferous browse and grass	Grass in both summer and winter (Langbein 1997)	Mean=9.8 Maximum=20.7 Minimum=1.8	1,018	0–350
Sutherland (northern Scotland)	Upland vegetation, grass, heather	Grass in summer but also heather in winter and spring (Fraser and Gordon 1997)	Mean=7.1 Maximum=17.9 Minimum=-1.3	993	100–350
Duror (west coast, Scotland)	Conifer plantation forest. Grass, sedges, rushes, and heaths (especially heather)	Grass in both summer and winter (Latham et al. 1999)	Mean=6.1 Maximum=17.7 Min=2.1	1,660	50–410
Isle of Rum (west coast, Scotland)	Grasslands, heathland, bogs and fens, heathers	Grass (Alison Donald, personal communication)	Mean=8.7 Maximum=14.0 Minimum=3.6	2,705	0–300
Slowinski National Park (Poland)	Relatively open, composed of both deciduous and coniferous vegetation. Three categories of deer habitat include: (1) forests (predominantly coniferous), (2) reeds and lake shore shrubs, (3) forest bogs, overgrown meadows and dunes	Grasses and forbs in both summer and winter (Dzieciolowski et al. 1995)	Mean=7.5 Maximum=16.5 Minimum=-1.2	665	0–115

1999) studies. The amount of $\delta^{15}\text{N}$ enrichment at each trophic level is under much debate but is generally quoted as a 3–5‰ enrichment over dietary protein at each trophic level (DeNiro and Epstein 1981; Schoeninger and DeNiro 1984; Bocherens and Drucker 2003; Van der kluft and Ponsard 2003). The deer in this study all predominantly eat grass (Table 1), consequently limiting isotope variability due to different diets. Although diet is often the primary control determining collagen isotope values, small-scale isotopic variability may be created by climatic and environmental conditions such as temperature, precipitation or altitude (Vogel 1978; Van der Merwe and Medina 1989; Van Klinken et al. 1994; Schwarcz et al. 1999; Stevens and Hedges 2004; Hedges et al. 2005). These variables tend to influence plant isotope values, with the resulting variation being passed up the food chain to fauna. The influence of these parameters on plant and faunal isotope values are discussed below.

Materials and methods

Samples

Deer bone samples were obtained between 1986 and 2002 from five deer populations living in geographically different habitats (Isle of Rum, Sutherland and Duror Forest, Scotland; Exmoor, southern England; and Slowinski National Park, Poland) (Fig. 1). Details of sex were available only for the Rum deer population. Age was available for the Rum population through field observations and tagging. Age information was not available for the Duror and Slowinski populations; however, all animals sampled were adults. Prior to this study age was determined for the Exmoor and Sutherland deer through molar tooth eruption patterns and wear according to Lowe (1967) (Sarah Collinge, personal communication). However, estimates of age based on molar eruption and tooth wear can be inaccurate. Hewison et al. (1999) tested the ability of ten observers to accurately estimate the age using molar tooth eruption patterns and wear of known-age roe deer (*Capreolus capreolus*). Observers generally over-estimated the age of young animals and underestimated the age of older animals, with an average error of ± 1.03 years and maximum errors of -5 to $+6$ years. Thus absence or presence of correlations between isotopes and age estimated must be critically considered.

A description of the different habitats occupied by the deer populations and the predominant food source (established through either rumen contents of culled deer or from field survey) are described in Table 1. Climate data were obtained from the weather stations nearest each population site (data from Meteorological office web page <http://www.met-office.gov.uk/index.html>) and (<http://www.hum.amu.edu.pl/~zbcw/ph/pnp/slow.htm>).

Samples were prepared and analysed at the Research Laboratory for Archaeology and the History of Art,

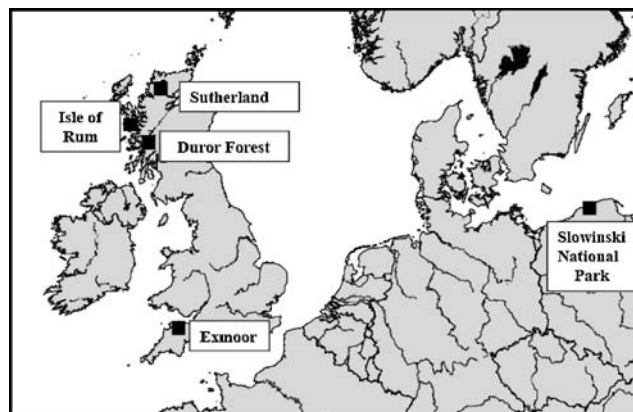


Fig. 1 Map of geographical location of deer populations

Oxford by R. Stevens as part of a NERC studentship (NER/S/A/2000/03522). Approximately 500-mg slices of bone were taken from 154 individual deer. Mandibles were sampled in 100 deer (25 from each site, with the exception of Rum) whereas vertebrae were sampled for 54 deer (Isle of Rum population). Collagen was extracted from each bone sample in the manner described by O'Connell et al. (2001). Samples were isotopically analysed using an automated Carlo Erba carbon and nitrogen elemental analyser coupled to a continuous flow isotope ratio-monitoring (PDZ Europa Geo 20/20) mass spectrometer. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ results are reported in per mil (‰) relative to VPDB and AIR standards, respectively (Mariotti 1983; Gonfiantini et al. 1990). Each sample was run in duplicate, with analytical errors of $\pm 0.2\text{‰}$ for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for each analysis.

Results

The results of the red deer isotope analyses are shown in Fig. 2. The atomic C/N ratios calculated for all of the samples in this study were between 3.1 and 3.3 which is within the range expected for fresh pure collagen.

Overall variability

For all the red deer samples analysed the $\delta^{13}\text{C}$ ranged from -24.8 to -21.2‰ (range = 3.6‰ , mean = $-23.0\text{‰} \pm 0.7$), and the $\delta^{15}\text{N}$ ranged from 1.4 to 7.9‰ (range = 6.4‰ , mean = $4.1\text{‰} \pm 1.3$) Table 2 shows the mean, range and SD of the isotope values measured for each of the five deer populations.

Inter-population variability

For both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ there is overlap in the ranges for all the different populations analysed. Table 3 describes the significance of the differences observed

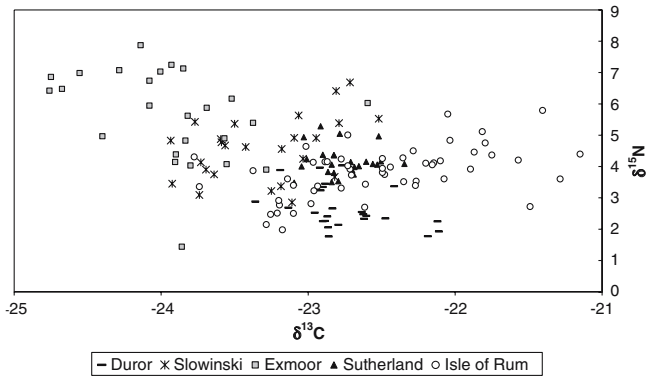


Fig. 2 Plot of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ bone collagen values of 154 red deer (*Cervus elaphus*) from five different populations

between the means of each population (two-tailed Student's independent *t*-test). The difference in mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among all populations is significant with the exception of Duror and Sutherland $\delta^{13}\text{C}$ values and Slowinski and Sutherland $\delta^{15}\text{N}$ values. A negative correlation is observed between annual maximum temperature and deer $\delta^{13}\text{C}$ ($R^2=0.5882$) (Fig. 4), whereas a weak negative correlation is observed between mean annual temperature and deer $\delta^{13}\text{C}$ ($R^2=0.3466$) (Fig. 5). A positive correlation ($R^2=0.6563$) (Fig. 6) is observed between mean annual temperature of the habitat occupied by each population and mean population $\delta^{15}\text{N}$.

Intra-population variability

The within-population range in $\delta^{13}\text{C}$ varies from 0.8 to 2.6‰, and in $\delta^{15}\text{N}$ from 1.8 to 6.4‰. Information on sex

was only available for the Isle of Rum deer population, for which no significant difference between male (mean $\delta^{13}\text{C}=-22.6\text{‰} \pm 0.6$, $\delta^{15}\text{N}=4.0\text{‰} \pm 0.8$) and female (mean $\delta^{13}\text{C}=-22.5\text{‰} \pm 0.7$, $\delta^{15}\text{N}=3.6\text{‰} \pm 0.8$) deer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values was observed. A weak, but significant, positive correlation ($R^2=0.2318$, $P<0.001$) with age was found for the $\delta^{13}\text{C}$ of the Rum population (all >6 months old) (Fig. 3). No correlation is observed between age and $\delta^{15}\text{N}$ for the Rum population. There is no significant difference in the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of weaned and non-weaned deer for the Rum population. The Exmoor and the Sutherland deer populations' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (all >1 year old and weaned) do not correlate with age.

Discussion

Inter-population variability

Canopy effect

Although the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for all populations overlap, the mean isotope values are different. For $\delta^{13}\text{C}$, the difference between the means is statistically significant except between the Duror and Sutherland populations. We expected to observe lower $\delta^{13}\text{C}$ values for the population that occupied a forest environment (Duror) compared to those living in open habitat due to the canopy effect. As previously mentioned, ground level undergrowth in dense forests is typically depleted in $\delta^{13}\text{C}$ by 2–5‰ in comparison to plants and trees in open environments (Tieszen 1991). As herbivores incorporate the isotopic signatures of the plants they eat into their body tissues,

Table 2 Mean, range and SD of the isotope values measured for five deer populations

Population	Number of individuals	Mean $\delta^{13}\text{C}$ ‰	Range of $\delta^{13}\text{C}$ ‰	SD $\delta^{13}\text{C}$ ‰	Mean $\delta^{15}\text{N}$ ‰	Range of $\delta^{15}\text{N}$ ‰	SD $\delta^{15}\text{N}$ ‰
Duror	25	-22.8	1.3	0.3	2.9	2.3	0.7
Sutherland	25	-22.8	0.8	0.2	4.2	1.8	0.5
Exmoor	25	-23.9	2.2	0.5	5.7	6.4	1.5
Slowinski	25	-23.3	1.4	0.4	4.6	3.8	1.0
Rum	54	-22.5	2.6	0.6	3.8	3.8	0.8

Table 3 Results of two-tailed Student's *t*-test between deer populations

Population 1	Population 2	Significance of difference in mean $\delta^{13}\text{C}$	Significance of difference in mean $\delta^{15}\text{N}$
Exmoor ($n=25$)	Duror ($n=25$)	$P \leq 0.001$	$P \leq 0.001$
Exmoor ($n=25$)	Slowinski ($n=25$)	$P \leq 0.001$	$P = 0.004$
Exmoor ($n=25$)	Sutherland ($n=25$)	$P \leq 0.001$	$P \leq 0.001$
Exmoor ($n=25$)	Rum ($n=54$)	$P \leq 0.001$	$P \leq 0.001$
Duror ($n=25$)	Slowinski ($n=25$)	$P \leq 0.001$	$P \leq 0.001$
Duror ($n=25$)	Sutherland ($n=25$)	Not significant	$P \leq 0.001$
Duror ($n=25$)	Rum ($n=54$)	$P = 0.032$	$P \leq 0.001$
Slowinski ($n=25$)	Sutherland ($n=25$)	$P \leq 0.001$	Not significant
Slowinski ($n=25$)	Rum ($n=54$)	$P \leq 0.001$	$P = 0.001$
Sutherland ($n=25$)	Rum ($n=54$)	$P = 0.012$	$P = 0.016$

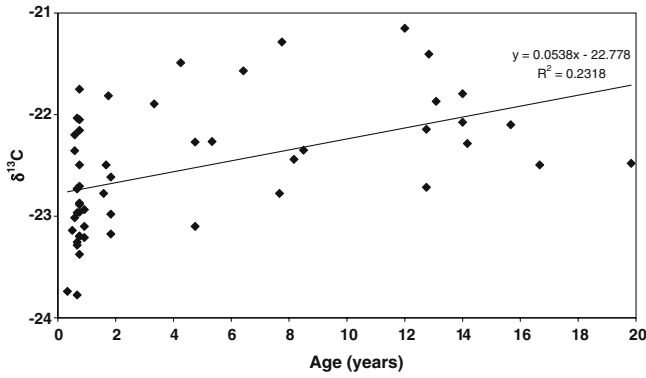


Fig. 3 Plot of $\delta^{13}\text{C}$ versus age of deer: Isle of Rum population

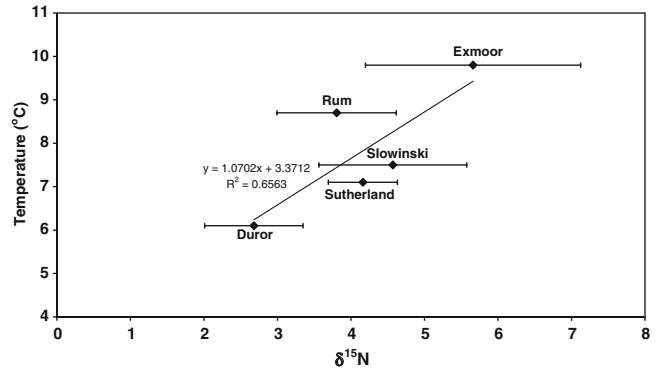


Fig. 6 Mean population bone collagen $\delta^{15}\text{N}$ (error bars=SD) versus mean annual temperature for each deer population habitat

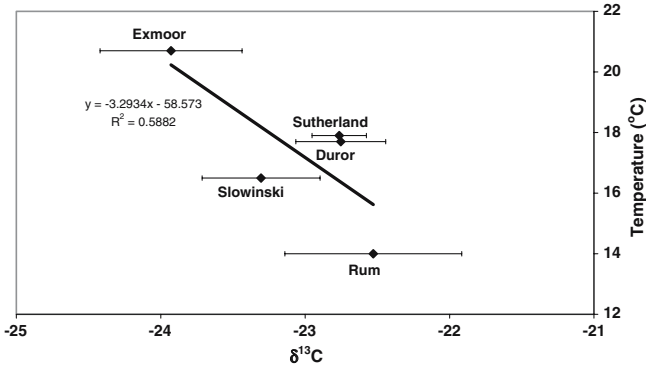


Fig. 4 Mean population bone collagen $\delta^{13}\text{C}$ (error bars=SD) versus mean annual maximum temperature for each deer population habitat

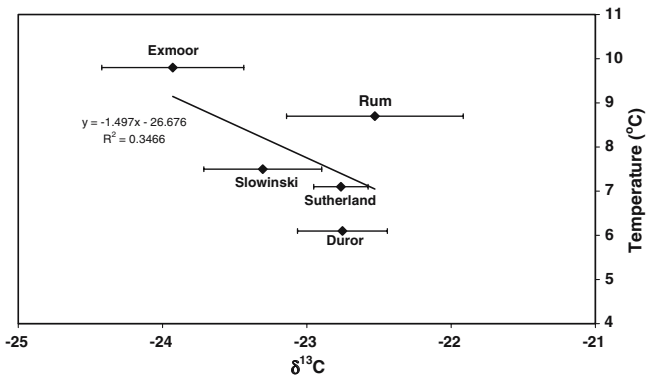


Fig. 5 Mean population bone collagen $\delta^{13}\text{C}$ (error bars=SD) versus mean annual temperature for each deer population habitat

low $\delta^{13}\text{C}$ values can be passed along the food chain. Several modern and archaeological studies have inferred the occupancy of a forested habitat based on low faunal $\delta^{13}\text{C}$ values and a selection of these have focused on deer. Rodiere et al. (1996) measured bone collagen $\delta^{13}\text{C}$ of roe deer from the Dourdan Forest in France and suggested that the values were depleted due to the canopy effect. Comparison of $\delta^{13}\text{C}$ was made with herbivores in general rather than specifically roe deer occupying other envi-

ronments, so it is unclear whether the values were depleted relative to roe deer from open environments. Yet, using this limited modern data set, Drucker et al. (2003) determined a $\delta^{13}\text{C}$ value of -23.4‰ (-22.5‰ in archaeological populations accounting for fossil fuel effect) below which red deer could be considered to have only eaten plants from within a closed canopy. The result of this calculation was considered acceptable as it was comparable to the average collagen $\delta^{13}\text{C}$ of -23.1‰ (-22.2‰ when accounting for fossil fuel effect) observed for red deer ($n=\text{unknown}$) from the Bialowieza Forest (Poland). However, the results from our study show that red deer $\delta^{13}\text{C}$ from forested environments (e.g. Duror) are not necessarily ^{13}C depleted and that red deer from open environments can have $\delta^{13}\text{C}$ values that are lower than deer occupying other open and closed habitats. Contrary to Drucker et al.'s conclusion, the Bialowieza Forest red deer $\delta^{13}\text{C}$ values are not unusually low compare to those of red deer from other environments as their mean $\delta^{13}\text{C}$ isotope value of -23.1‰ ($n=\text{unknown}$) is almost identical to the mean $\delta^{13}\text{C}$ value of -23.0‰ for our mean for all five populations of deer ($n=154$). Furthermore, the absence of a canopy effect signal being passed on to red deer from the plants is not totally unexpected, as although deer live both in open and closed environments, counts of faecal pellet groups have shown that red deer have a strong preference for open thicket habitats within forests and avoid closed dense canopy areas (Latham et al. 1999; Latham 2000). Thus, the plants they consume are less likely to be subject to a strong canopy effect. Where the presence or absence of a canopy effect has been inferred in an archaeological context based on faunal $\delta^{13}\text{C}$ values it has often been made using limited data (e.g. Bocherens et al. 1995; Fizet et al. 1995; Iacumin et al. 1997; Bocherens et al. 1999; Stewart and Lister 2001) and in the absence of a good understanding of modern species' specific isotopic variability. There is no doubt that the canopy effect can potentially result in depleted faunal $\delta^{13}\text{C}$ in certain contexts, particularly in very dense tropical rainforest (e.g. Froment and Ambrose 1995). However, there is a difference between living in a forest and feeding in a forest, thus occupancy

within a forest habitat does not necessarily result in low faunal $\delta^{13}\text{C}$. Similarly, low faunal $\delta^{13}\text{C}$ (both modern and archaeological) does not necessarily imply inhabitation of a forested environment. With the canopy effect discounted other parameters that could result in inter-population isotopic variability were considered.

Marine inputs

Although grass is the primary food for all of the populations in nutritionally poor environments, such as the Isle of Rum, deer may consume some seaweed in order to gain essential minerals (Furness 1988; Conradt 2000). Marine plant and faunal isotope signatures are generally higher in $\delta^{13}\text{C}$, due to the $\delta^{13}\text{C}$ composition of the oceans. As a primary producer seaweed has relatively low $\delta^{15}\text{N}$ values. Seaweed is rich in protein, so consuming even small quantities could potentially affect the deer $\delta^{13}\text{C}$ signatures. The Rum deer generally have higher $\delta^{13}\text{C}$ values relative to the other populations whereas their $\delta^{15}\text{N}$ values are similar to the other populations, thus indicating the unusual $\delta^{13}\text{C}$ values of the Rum population may be due to consumption of seaweed.

Precipitation

Studies of plant $\delta^{13}\text{C}$ values consistently report negative correlations with water availability (Heaton 1999), and negative correlations have also been described between quantity of precipitation and modern faunal $\delta^{15}\text{N}$ values in South Africa, Namibia, Kenya and Australia (Heaton et al. 1986, Sealy et al. 1987, Ambrose 1991, Gröcke et al. 1997). Nevertheless, the relationship between faunal $\delta^{15}\text{N}$ and precipitation only seems to hold up in areas with <400 mm rainfall per year (Sealy et al. 1987). The annual precipitation at each of the sites in this study exceeds 400 mm per year (Table 1). Observed variations in deer bone $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ do not correlate with rainfall. Slowinski $\delta^{13}\text{C}$ values overlap with the range in $\delta^{13}\text{C}$ values of all the other deer populations yet Slowinski has a low average annual rainfall in comparison to the other areas. The Rum and Sutherland populations have relatively similar mean $\delta^{15}\text{N}$ of 3.8‰ and 4.2‰, respectively, but the average annual rainfall at the two locations is different.

Altitude

Altitudinal gradients in $\delta^{13}\text{C}$ of 1.3–1.5‰ increase per 1,000 m elevation observed in bird feather keratin are thought to be due to consumption of plants with elevation-dependent $\delta^{13}\text{C}$ as a result of physiological adaptation to changes in growing conditions and partial pressure of atmospheric CO_2 (Sparks and Ehleringer 1997; Hultine and Marshall 2000; Graves et al. 2002; Hobson et al. 2003). Limited evidence suggests $\delta^{15}\text{N}$ may also correlate weakly with elevation, but converse trends are observed in soil $\delta^{15}\text{N}$ values (negative trend) (Mariotti et al. 1980) and in feather $\delta^{15}\text{N}$ values (positive trend)

(Hobson et al. 2003). The range in elevations occupied by each deer population in this study are relatively similar (Table 1), thus diverse population mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are unlikely to be due to an altitudinal difference.

Salinity

Positive correlations have been observed between salinity and plant $\delta^{13}\text{C}$ (C3 plants) (Guy et al. 1986a, 1986b). Thus plants subject to elevated salinity in areas proximal to coastlines have more positive $\delta^{13}\text{C}$ values than plants from inland areas. The Rum population mainly graze in coastal area, and can consume seaweed. This may explain why the Rum population has the most positive $\delta^{13}\text{C}$ values. The influence of salinity on plant $\delta^{15}\text{N}$ values has not been established as both positive (Heaton 1987; Van Groenigen and Van Kessel 2002) and negative (Handley and Scrimgeour 1997; Robinson et al. 2000) correlations have been reported. Thus the effect of salinity on faunal $\delta^{15}\text{N}$ values is unclear.

Although other parameters that could result in inter-population isotopic variability were considered (such as soil acidity, nutritional stress, etc.), the primary variable influencing deer population isotope values appears to be temperature.

Temperature

Temperature seems to be the main parameter influencing population mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. A negative correlation is observed between annual maximum temperature and deer $\delta^{13}\text{C}$ ($R^2=0.5882$) (Fig. 4), whereas a weak negative correlation is observed between mean annual temperature and deer $\delta^{13}\text{C}$ ($R^2=0.3466$) (Fig. 5), with lower bone collagen $\delta^{13}\text{C}$ values in areas with higher temperatures. This is contrary to the findings of Van Klinken et al. (1994) who observed a positive correlation between temperature and faunal bone $\delta^{13}\text{C}$ over a range of Holocene species as a whole. The majority of studies of plant $\delta^{13}\text{C}$ values report positive correlations with temperature; however, there is no clear theoretical mechanism for this relationship (Heaton 1999), and growth chamber experiments in controlled conditions have shown a negative correlation between temperature and plant $\delta^{13}\text{C}$ (O'Leary 1995). Thus the global relationship between faunal bone collagen $\delta^{13}\text{C}$ and temperature is uncertain.

A positive correlation ($R^2=0.6563$) (Fig. 6) is observed between mean annual temperature of the habitat occupied by each population and mean population $\delta^{15}\text{N}$. Soil and plant $\delta^{15}\text{N}$ systematically decrease with decreasing mean annual temperature and increasing mean annual precipitation (Amundson et al. 2003). Based on global mean annual temperature and precipitation data, Amundson et al. (2003) mapped the estimated geographical distribution of soil $\delta^{15}\text{N}$ values. Soils in Scotland typically have estimated $\delta^{15}\text{N}$ values between 2.1 and 4.8‰, whereas soils in southern England and northern Poland typically have estimated $\delta^{15}\text{N}$ of 4.8–6.2‰. Plant $\delta^{15}\text{N}$ is influenced by soil $\delta^{15}\text{N}$ but globally is

more negative due to the way they take up N. The observed higher $\delta^{15}\text{N}$ values in the Exmoor and Slowinski deer populations compared to the lower $\delta^{15}\text{N}$ values in the three Scottish populations suggest that isotopic variability between the deer populations may reflect temperature-dependent differences in soil $\delta^{15}\text{N}$.

Plotting the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for each population results in graphs that contain just five points. Although this is not a large enough sample set to conclusively confirm the correlations, it gives a clear indication that variations in mean population bone collagen $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values relate to temperature ($R^2=0.66$).

Intra-population variability

The results show that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of red deer collagen vary considerably within a population. The Sutherland population has the least variable $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The most variable $\delta^{13}\text{C}$ values are seen in the Rum population, whereas for N this is seen in the Exmoor population (Table 2). Several factors that could potentially cause this intra-population isotopic variability are discussed below.

Physiological parameters

Weaning

Enriched $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in human and other mammalian infants have been attributed to trophic level enrichment due to the consumption of their mother's milk (Fogel et al. 1989; Jenkins et al. 2001; Polischuk et al. 2001). Only five pre-weaned deer (Rum population) were analysed in this study and no significant difference between pre-weaned and weaned deer was observed. Red deer are weaned off their mother's milk by 8 months (Mammal Society red deer fact sheet <http://www.mammal.org.uk/reddeer.htm>). The pre-weaned deer in this study are 6 or 7 months old, and thus we would expect their isotope values to be close to the adult values due to lesser intake of milk and a greater intake of solid foods. Therefore the isotopic variability observed within the deer populations is not due to weaning.

Age

A weak, but significant, positive correlation ($R^2=0.2318$, $P<0.001$) is observed between age and $\delta^{13}\text{C}$ of the Rum population (Fig. 3). This correlation may just be due to the sample selection as no other study has observed a correlation with age (for weaned animals) even when the study set out specifically to search for it (e.g. Lovell et al. 1986). No correlation between $\delta^{13}\text{C}$ and age is observed for the Exmoor and Sutherland deer populations. This may be due to the inaccurate estimates of age based on molar eruption and tooth wear (see [Methods](#)). All populations potentially may show an age correlation, but only the age data from Rum are accurate enough for the correlations to be detected.

Sex

Although sexual segregation of grazing areas is observed at many sites on the Isle of Rum, neither $\delta^{13}\text{C}$ nor $\delta^{15}\text{N}$ correlate with sex. This agrees with the observations of Conradt et al. (2001) that male and female deer on Rum consume forage of equal quality.

Nutritional stress

Feeding experiments have shown that nutritional stress can result in approximately 1‰ enrichment in body tissue $\delta^{15}\text{N}$ in birds (Hobson et al. 1993). The Rum deer are thought to be nutritionally stressed as they live on the margins of the natural habitat range for this species. However, their $\delta^{15}\text{N}$ values are less variable than those of the Slowinski and Exmoor populations and are comparable to those of the Duror population (Table 2), suggesting that differential nutritional stress is not the primary variable causing the intra-population $\delta^{15}\text{N}$ variability.

Environmental parameters

Soil development

The variation in Slowinski deer $\delta^{15}\text{N}$ may reflect differential soil development in the micro-habitats occupied by the individual deer within the Slowinski National Park as differential N cycling in the soils has been shown to affect plant $\delta^{15}\text{N}$ (Handley et al. 1999). Soil development is less variable at the other locations.

Altitude

If using the calculation of 1.5‰ increase in $\delta^{13}\text{C}$ per 1,000 m as observed for feather keratin of humming birds (Hobson et al. 2003), the range in elevation at each of the sites is not great enough for the observed $\delta^{13}\text{C}$ variability to be primarily due to altitude of grazing area (Table 1).

Salinity

As previously mentioned, salinity can influence plant $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Intra-population variability of deer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ at Rum, Exmoor and Slowinski may be due to consumption of plants from different areas, with plants subject to elevated salinity in areas proximal to coastlines having different isotope values to plants from inland areas. Further information on the grazing patterns of individual deer would be required in order to test the influence of salinity in these habitats.

Marine isotope signatures

As previously mentioned marine faunal isotope signatures are generally more enriched in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Terrestrial plants collected near seabird colonies have elevated $\delta^{15}\text{N}$ values (11‰ higher than plants outside the colonies) due to the uptake of ornithogenic N (Wainright et al. 1998). In

gull colonies on the Isle of Rum local enrichment of soil and plant N content due to gull droppings has been observed (Iason et al. 1986). Intermittent grazing in the gull colony areas by some of the Rum deer could result in a small change of a few ‰ in the deer isotope values, which would be consistent with observed results, but extensive grazing in the gull colonies is unlikely as the magnitude of deer $\delta^{15}\text{N}$ variation is not as great as that observed in the aforementioned study (although plant and collagen isotope values are not directly comparable).

Size of area occupied and diversity of habitats

The Rum population occupies a 5 square mile area, thus the deer are subject to similar climatic, environmental, and habitat conditions. Due to the lack of a large environmental or vegetation gradient, and limited human impact within the study area, the observed intra-population isotopic variability might be expected to be small. The Duror and the Sutherland populations occupy areas that are larger than that of the Rum population, yet their $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ are less variable. It appears that the amount of isotopic variability within a population is not consistent. Both Slowinski National Park and Exmoor cover large areas, 70 square miles and 267 square miles, respectively. Slowinski includes pine forests, reed and lakeshore shrublands, and bogs, meadow and dunes, and Exmoor includes areas of open forest, moorland and heath. Although all the deer primarily eat grass, isotopic variability within these deer population might be due to different microclimate or microhabitats, or [as at Exmoor (Langbein 1997)] might be due to consumption of grass from improved pasture. It is extremely hard however, to distinguish the genetic variability from environmentally induced variability.

Conclusions

Our attempts to understand variation in modern deer bone collagen isotope values are limited by the material available for analyses at the time of study. The study could be enhanced with complete data for age and sex of individual deer and with information on grazing patterns for individual deer. The data presented here suggest that a $\delta^{13}\text{C}$ canopy effect is not observed in modern European red deer when it might be expected. Mean population $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values appear to relate to temperature, with a negative correlation between $\delta^{13}\text{C}$ and annual maximum temperature, and a positive correlation between $\delta^{15}\text{N}$ and mean annual temperature. However, further isotopic investigation of more populations is required to statistically validate these correlations in order to allow us to use them for palaeoenvironmental reconstructions. The amount of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variation within a population is not constant. Deer isotope values can be highly variable in some populations, in others less so. In modern environments we can attempt to account for this variability based on our knowledge of habitat, but in an archaeological context it is difficult to infer environmental differences

from the isotope values as variation of several parameters can result in similar isotopic results. If we cannot fully explain modern isotopic differences, even less can we explain ancient ones. One question that arises from these data is whether isotopic variability within a population is purely due to differential dietary intake and environment, or due to varying amount of enrichment at each trophic level. If the amount of trophic level enrichment is variable [as suggested by Hobson et al. (1993) and Sponheimer et al. (2003)] it would seriously complicate the mapping of modern and archaeological food webs. The intra-population variability also creates problems when using stable isotope mixing models. Some mixing models attempt to determine the amount of different foods (or prey) consumed by an animal based on the isotope value of the consumer and on the mean isotope values of the possible source foods. With considerable isotopic variability in the source food, any calculations of quantity of different foods consumed based on mean isotope values may be subject to considerable error. Statistical techniques such as power analysis can be used on pilot data to calculate the minimum number of samples required to get a good representation of the typical values for a population. Where populations' isotope results are divergent and SDs small, low numbers of samples are necessary to show that one population is significantly different from another [e.g. ten and seven samples per population (respectively) are required to differentiate the $\delta^{13}\text{C}$ of the Exmoor population from the Duror population ($P=0.001$, power=0.95)]. However, where populations' isotope results are similar and SDs larger, greater numbers of samples are sufficient to show one population is significantly different from another [e.g. 102 and 16 samples per population (respectively) are required to differentiate the $\delta^{13}\text{C}$ of the Rum population from the Sutherland population ($P=0.001$, power=0.95)]. Thus in both modern and archaeological cases, a considerable number of individuals from each species must be analysed so that realistic food web, palaeodietary, and palaeoecological reconstructions can be made. Published studies which reconstruct palaeodiets and palaeoenvironments based on a limited number of faunal isotope values should be considered with caution. Even greater caution should be taken when considering studies that have reconstructed human palaeodiet from human isotope values, without sufficient analysis of associated fauna.

Acknowledgements We would like to thank Peter Ditchfield for technical assistance with isotopic analysis. We are grateful to Tim Clutton-Brock and Fiona Guinness (University of Cambridge), Tim Coulson (Imperial College London) and Josephine Pemberton (University of Edinburgh) for access to long-term data for deer on Rum. Alison Donald (University of Cambridge), Sarah Collinge (University College London) and Tamsin O'Connell (University of Cambridge) are thanked for help with the collection of bone samples. The Forestry Commission, Richard Carter, and Jochen Langbein are thanked for providing samples. Hugh Rose at the British Deer Society is thanked for general advice. This project was funded by a NERC studentship (NER/S/A/2000/03522) to R. E. Stevens. Tamsin O'Connell, Jennifer Tripp and Angela Lamb are thanked for their comments on an earlier version of the manuscript. All experimental analyses were performed in compliance with the current laws of the United Kingdom.

References

- Ambrose SH (1991) Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial food webs. *J Archaeol Sci* 18:293–317
- Ambrose SH, Norr L (1993) Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbonate. In: Lambert JB, Grupe G (eds) *Prehistoric human bone—archaeology at the molecular level*. Springer, Berlin Heidelberg New York, pp 1–37
- Amundson R, Austin AT, Schuur EAG, Yoo K, Matzek V, Kendall C, Uebersax A, Brenner D, Baisden WT (2003) Global patterns of the isotopic composition of soil and plant nitrogen. *Global Biogeochem Cycles* 17(1):1031
- Bocherens H, Drucker D (2003) Trophic level isotopic enrichment of carbon and nitrogen in bone collagen: case studies from recent and ancient terrestrial ecosystems. *Int J Osteoarchaeol* 13:46–53
- Bocherens H, Fogel ML, Tuross N, Zeder M (1995) Trophic structure and climatic information from isotopic signatures in Pleistocene cave fauna of southern England. *J Archaeol Sci* 22:327–340
- Bocherens H, Billiou D, Mariotti A, Patou-Mathis M, Otte M, Bonjean D, Toussaint M (1999) Palaeoenvironmental and palaeodietary implications of isotopic biogeochemistry of last interglacial neanderthal and mammal bones in Scladina Cave (Belgium). *J Archaeol Sci* 26:599–607
- Broadmeadow MSJ, Griffiths H, Maxwell C, Borland AM (1992) The carbon isotope ratio of plant organic material reflects temporal and spatial variations in CO₂ within tropical forest formations in Trinidad. *Oecologia* 89:435–441
- Cerling TE, Harris JM (1999) Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia* 120:347–363
- Conradt L (2000) Use of a seaweed habitat by red deer (*Cervus elaphus* L.). *J Zool* 250:541–549
- Conradt L, Gordon IJ, Clutton-Brock TH, Thomson D, Guinness FE (2001) Could the indirect competition hypothesis explain inter-sexual site segregation in red deer (*Cervus elaphus* L.). *J Zool* 254:185–193
- DeNiro MJ, Epstein S (1978) Influence of diet on the distribution of carbon isotopes in animals. *Geochim Cosmochim Acta* 42:495–506
- DeNiro MJ, Epstein S (1981) Influence of diet on the distribution of nitrogen isotopes in animals. *Geochim Cosmochim Acta* 45:341–351
- Drucker D, Bocherens H, Bridault A, Billiou D (2003) Carbon and nitrogen isotopic composition of red deer (*Cervus elaphus*) collagen as a tool for tracking palaeoenvironmental change during the Late-Glacial and Early Holocene in the northern Jura (France). *Palaeogeogr Palaeoclimatol Palaeoecol* 195:375–388
- Dziedziolowski R, Goszczynski J, Wasilewski M, Babinskawerka J (1995) Numbers of red deer in the Slowinski National-Park, Poland. *Acta Theriol* 40:45–51
- Fizet M, Mariotti A, Bocherens H, Langebadre B, Vandermeersch B, Borel J P, Bellon G (1995) Effect of diet, physiology and climate on carbon and nitrogen stable isotopes of collagen in a late pleistocene anthropic palaeoecosystem Marillac, Charente, France. *J Archaeol Sci* 22:67–79
- Fogel ML, Tuross N, Owsley D (1989) Nitrogen isotope tracers of human lactation in modern and archaeological populations. In: Annual report of the director, geophysical laboratory 1988–89. Carnegie Institution of Washington, Washington, D.C.
- Fraser MD, Gordon IJ (1997) The diet of goats, red deer and South American camelids feeding on three contrasting Scottish upland vegetation communities. *J Appl Ecol* 34:668–686
- Froment A, Ambrose SH (1995) Analyses tissulaires isotopiques et reconstruction du régime alimentaire en milieu tropical: implications pour l'archéologie. *Bull Mem Soc Anthropol Paris* 7:79–98
- Furness RW (1988) Predation on ground-nesting seabirds by island populations of red deer (*Cervus elaphus*) and sheep (*Ovis*). *J Zool* 216:565–573
- Gonfiantini R, Rozanski K, Stichler W (1990) Inter-calibration of environmental isotope measurements: the program of the International Atomic Energy Agency. *Radiocarbon* 32:369–374
- Graves GR, Romanek CS, Navarro AR (2002) Stable isotope signature of philopatry and dispersal in a migratory songbird. *Proc Natl Acad Sci USA* 99:8096–8100
- Gröcke DR, Bocherens H, Mariotti A (1997) Annual rainfall and nitrogen-isotope correlation in macropod collagen: application as a palaeoprecipitation indicator. *Earth Planet Sci Lett* 153:279–285
- Guy RD, Reid DM, Krouse HR (1986a) Factors affecting C¹³/C¹² ratios of inland halophytes. 1. Controlled studies on growth and isotopic composition of *Puccinellia nuttalliana*. *Can J Bot* 64:2693–2699
- Guy RD, Reid DM, Krouse HR (1986b) Factors affecting C¹³/C¹² ratios of inland halophytes. 2. Ecophysiological interpretations of patterns in the field. *Can J Bot* 64:2700–2707
- Handley LL, Scrimgeour CM (1997) Terrestrial plant ecology and N-15 natural abundance: The present limits to interpretation for uncultivated systems with original data from a Scottish old field. *Adv Ecol Res* 27:133–212
- Handley LL, Austin AT, Robinson D, Scrimgeour CM, Raven JA, Heaton THE, Schmidt S, Stewart GR (1999) The N-15 natural abundance (δ¹⁵N) of ecosystem samples reflects measures of water availability. *Aust J Plant Physiol* 26:185–199
- Harrison RG, Katzenberg MA (2003) Paleodiet studies using stable carbon isotopes from bone apatite and collagen: examples from Southern Ontario and San Nicolas Island, California. *J Anthropol Archaeol* 22:227–244
- Heaton THE (1987) The N-15/N-14 ratios of plants in South-Africa and Namibia—relationship to climate and coastal saline environments. *Oecologia* 74:236–246
- Heaton THE (1999) Spatial, species, and temporal variations in the ¹³C/¹²C ratios of C3 plants: implications for palaeodiet studies. *J Archaeol Sci* 26:637–649
- Heaton THE, Vogel JC, von la Chevallerie G, Collett G (1986). Climatic influence on the isotopic composition of bone collagen. *Nature* 322: 822–823
- Hedges REM, Stevens RE, Koch PL (2005) Isotopes in bones and teeth. In: Leng MJ (ed) *Isotopes in palaeoenvironmental research*. Developments in palaeoenvironmental research, vol 10, pp 117–145
- Hewison AJM, Vincen JP, Angibault JM, Delorme D, Van Laere G, Gaillard JM (1999) Tests of estimation of age from tooth wear on roe deer of known age: variation within and among populations. *Can J Zool* 77:58–67
- Hobson KA, Alisauskas RT, Clark RG (1993) Stable nitrogen isotope enrichment in avian tissues due to fasting and nutritional stress—implications for isotopic analyses of diet. *Condor* 95:388–394
- Hobson KA, Wassenaar LI, Mila B, Lovette I, Dingle C, Smith TB (2003) Stable isotopes as indicators of altitudinal distributions and movements in an Ecuadorian hummingbird community. *Oecologia* 136:302–308
- Hultine KR, Marshall JD (2000) Altitude trends in conifer leaf morphology and stable carbon isotope composition. *Oecologia* 123:32–40
- Iacumin P, Bocherens H, Delgado Huertas A, Mariotti A, Longinelli A (1997) A stable isotope study of fossil mammal remains from the Paglicci cave, S. Italy: N and C as palaeoenvironmental indicators. *Earth Planet Sci Lett* 148:349–357
- Iason GR, Duck CD, Clutton-Brock TH (1986) Grazing and reproductive success of red deer—the effect of local enrichment by gull colonies. *J Anim Ecol* 55:507–515
- Jenkins SG, Partridge ST, Stephenson TR, Farley SD, Robbins CT (2001) Nitrogen and carbon isotope fractionation between mothers, neonates, and nursing offspring. *Oecologia* 129:336–341
- Katzenberg MA, Weber A (1999) Stable isotope ecology and palaeodiet in the Lake Baikal region of Siberia. *J Archaeol Sci* 26:651–659
- Krigbaum J (2003) Neolithic subsistence patterns in northern Borneo reconstructed with stable carbon isotopes of enamel. *J Anthropol Archaeol* 22:292–304

- Langbein J (1997) The ranging behavior, habitat use and impact of deer in oak woodlands and heather moors of Exmoor and the Quantock hills. *Deer* 10: 516–521
- Latham J (2000) Use of thicket stages of Scottish conifer plantations by red and roe deer in relation to openness. *Forestry* 73:403–406
- Latham J, Staines BW, Gorman ML (1999) Comparative feeding ecology of red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) in Scottish plantation forests. *J Zool* 247:409–418
- Lovell NC, Nelson DE, Schwarcz HP (1986) Carbon isotope ratios in paleodiet, lack of age or sex effect. *Archaeometry* 28:51–55
- Lowe VPW (1967) Teeth as indicators of age with special reference to red deer (*Cervus elaphus*) of known age from Rhum. *J Zool* 152:137–153
- Mariotti A (1983) Atmospheric nitrogen is a reliable standard for natural ^{15}N measurements. *Nature* 303:685–687
- Mariotti A, Pierre D, Vedy JC, Bruckert S, Guillemot J (1980) The abundance of natural nitrogen 15 in soils along an altitudinal gradient. *Catena* 7:293–300
- Medina E, Michin P (1980) Stratification of $\delta^{13}\text{C}$ in Amazonian rainforests. *Oecologia* 45:337–378
- O'Connell TC, Hedges REM (1999) Investigations into the effect of diet on modern human hair isotopic values. *Am J Phys Anthropol* 108:409–425
- O'Connell TC, Hedges REM, Healey MA, Simpson AHRW (2001) Isotopic comparison of hair, bone and nail: modern analyses. *J Archaeol Sci* 28:1247–1255
- O'Leary MH (1995) Environmental effects on carbon isotope fractionation in terrestrial plants. In: Wada E, Yoneyama T, Minagawa M, Ando T, Fry BD (eds) *Stable isotopes in the biosphere*. Kyoto University Press, Kyoto, pp 78–91
- Polischuk SC, Hobson KA, Ramsay MA (2001) Use of stable-carbon and nitrogen isotopes to assess weaning and fasting in female polar bears and their cubs. *Can J Zool* 79:499–511
- Privat KL, O'Connell TC, Richards MP (2002) Stable isotope analysis of human and faunal remains from the Anglo-Saxon cemetery at Berinsfield, Oxfordshire: dietary and social implications. *J Archaeol Sci* 29:779–790
- Richards MP, Hedges REM (1999) Stable isotope evidence for similarities in the types of marine foods used by Late Mesolithic humans at sites along the Atlantic coast of Europe. *J Archaeol Sci* 26:717–722
- Robinson D, Handley LL, Scrimgeour CM, Gordon DC, Forster BP, Ellis RP (2000) Using stable isotope natural abundances ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) to integrate the stress responses of wild barley (*Hordeum spontaneum* C. Koch.) genotypes. *J Exp Bot* 51:41–50
- Rodiere M, Bocherens H, Angibault JM, Mariotti A (1996) Isotopic particularities of nitrogen in roe-deer (*Capreolus capreolus*): implications for palaeoenvironmental reconstructions. *C R Acad Sci Ser Ia Sci Terre Planetes* 323:179–185
- Schoeninger MJ, DeNiro MJ (1984) Nitrogen and carbon isotopic composition of bone collagen from marine and terrestrial animals. *Geochim Cosmochim Acta* 48:625–639
- Schwarcz HP, Schoeninger MJ (1991) Stable isotopic analyses in human nutritional ecology. *Yearb Phys Anthropol* 34:283–321
- Schwarcz HP, Dupras TL, Fairgrieve SI (1999) ^{15}N enrichment in the Sahara: in search of a global relationship. *J Archaeol Sci* 26:629–636
- Sealy JC, van der Merwe NJ, Lee-Thorp JA, Lanham JL (1987) Nitrogen isotopic ecology in Southern Africa: implications for environmental and dietary tracing. *Geochim Cosmochim Acta* 51:2707–2717
- Sparks JP, Ehleringer JR (1997) Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects. *Oecologia* 109:362–367
- Sponheimer M, Robinson T, Ayliffe L, Roeder B, Hammer J, Passey B, West A, Cerling TE, Dearing MD, Ehleringer JR (2003) Nitrogen isotopes in mammalian herbivores: hair delta N-15 values from a controlled feeding study. *Int J Osteoarchaeol* 13:80–87
- Stenhouse MJ, Baxter MS (1979) The uptake of bomb ^{14}C in humans. In: Berger R, Suess HE (eds) *Radiocarbon dating*. University of California Press, Berkeley, pp 324–341
- Stevens RE, Hedges REM (2004). Carbon and nitrogen stable isotope analysis of Northwest European horse bone and tooth collagen, 40,000 BP–present: palaeoclimatic interpretations. *Quat Sci Rev* 23:7–8: 977–991
- Stewart JR, Lister AM (2001) Cryptic northern refugia and the origins of the modern biota. *Trends Ecol Evol* 16:608–613
- Tieszen LL (1991) Natural variations in the carbon isotope values of plants: implications for archaeology, ecology, and paleoecology. *J Archaeol Sci* 18:227–248
- Tieszen LL, Fagre T (1993) Effect of diet quality and composition on the isotopic composition of respiratory CO_2 , bone collagen, bioapatite, and soft tissues. In: *Prehistoric human bone—archaeology at the molecular level*. Springer, Berlin Heidelberg New York, pp 121–155
- Van der Merwe NJ, Medina E (1989). Photosynthesis and $^{13}\text{C}/^{12}\text{C}$ ratios in Amazonian rain forests. *Geochim Cosmochim Acta* 53:1091–1094
- Van Klinken GJ, Van der Plicht J, Hedges REM (1994) Bone $^{13}\text{C}/^{12}\text{C}$ ratios reflect (palaeo-) climatic variations. *Geophys Res Lett* 21:445–448
- Van Groenigen JW, Van Kessel C (2002) Salinity-induced patterns of natural abundance carbon-13 and nitrogen-15 in plant and soil. *Soil Sci Soc Am J* 66:489–498
- Van der Klift MA, Ponsard S (2003) Sources of variation in consumer-diet delta N-15 enrichment: a meta-analysis. *Oecologia* 136(2):169–182
- Vogel JC (1978) Isotopic assessment of the dietary habits of ungulates. *S Afr J Sci* 74:298–301
- Vogel JC, Van der Merwe NJ (1977) Isotopic evidence for early maize cultivation in New York State. *Am Antiq* 42:238–242
- Wainright SC, Haney JC, Kerr C, Golovkin AN, Flint MV (1998) Utilization of nitrogen derived from seabird guano by terrestrial and marine plants at St. Paul, Pribilof Islands, Bering Sea, Alaska. *Mar Biol* 131:63–71