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Stable isotope analysis of well-preserved 120,000-year-old herbivore bone collagen from the Middle Palaeolithic site of Neumark-Nord 2, Germany reveals niche separation between bovids and equids

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ABSTRACT

Herbivores from the Neumark-Nord 2 archaeological site, Germany, were analysed for bone collagen stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios in order to investigate feeding ecology at this early Last Interglacial (Eemian) shallow-lake site. Of 42 faunal samples selected, 23 yielded collagen, demonstrating remarkable preservation for material of this age. The results indicate clear inter-specific differences in $\delta^{15}N$ and $\delta^{13}C$ values, notably between equids (*Equus*) and bovids (*Bos*/*Bison*), with mean difference $\Delta^{15}N$ of +2‰ measured in the bovids compared to the equids. The potential reasons for these differences are explored, including physiology, herbivore feeding ecology, biogeography and resource partitioning within the local environment. The data are compared to previously published archaeological data, and modern experimental and ecological data, suggesting that these inter-specific differences are not consistent and therefore unlikely to be solely the product of physiology or habitual forage preference. Data from this study are compared to the local vegetation (as reconstructed from pollen profiles), and it is suggested that these trends are likely the result of niche partitioning at the shallow lake site, reflecting the local diversity in vegetational zones. The evidence for resource partitioning amongst Pleistocene herbivore communities at Neumark-Nord 2 and elsewhere is discussed. This study represents one of the largest data sets for collagen of this age, and the implications for our understanding of Late Pleistocene herbivore ecology, local herbivore community behaviour and hominin palaeodietary studies are explored.

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1. Introduction

The landscapes of Mid- and Late Pleistocene Europe were dominated by large herbivores, including pachyderms (e.g. *Mammuthus*, *Elephas*), equids (*Equus*), cervids (*Cervus*), and bovids such as bison (*Bison*) and aurochs (*Bos*). The mechanisms that allow for the co-existence of different modern mid- and large-sized grazing herbivore guilds have been debated, but are largely thought to lie in their different digestive systems that permit them to adopt alternative foraging strategies where ranges overlap (Janis, 1976), and/or through the selective feeding on different plant communities or portions of plants within the same biome—known as resource partitioning (Krysl et al., 1984; Menard et al., 2002). These mechanisms lead to niche separation, through the occupation of different sub-habitats by the selection of different plants within the same habitat, or different parts of the same plant; and therefore facilitating biodiversity in herbivore species (Janis, 1976). It has previously been suggested that the high diversity of herbivore taxa living in the steppic biomes of Pleistocene North Europe can be explained by such dietary specialisation (Guthrie, 1982), with a proposed high floral biodiversity allowing niche separation and the avoidance of direct inter-specific competition (Drucker et al., 2003). In this study, we investigate the feeding palaeoecology of equids (*Equus*) and bovids (*Bos*/*Bison*) through stable isotope data, and explore the possibility (and nature) of such niche separation in Late Pleistocene Europe. The stable isotope analysis of fossil animal remains is a powerful tool for investigating ancient environments, ecosystems and feeding behaviours, and is a method that can be used to directly investigate differences in herbivore dietary specialisation. Stable isotope techniques

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are based on the principle that an organism's tissues will reflect the chemical composition of food and water ingested during life (Kohn, 1999). Isotopic methods have been used extensively in recent years to explore the palaeobiology of different species, including predator–prey relationships (Richards et al., 2000; Bocherens, 2003); niche feeding behaviours/resource partitioning (Feranec, 2007; Feranec et al., 2010); and seasonal biogeography and range size (Hoppe et al., 1999; Feranec et al., 2007; Britton et al., 2011). Diachronic and spatial studies allow the assessment of niche conservation and the stability of animal feeding behaviours and biogeography through time (Feranec et al., 2007) and across different geographical regions (Szpak et al., 2010).

In modern case studies, numerous tissues can be used in stable isotope studies, including soft tissues sampled *in vivo* such as blood, hoof/nail, fur/wool/hair, horn and breath, as well as hard and soft tissues *post-mortem* such as bone, tooth and muscle. Except in rare cases of good preservation (such as permafrost environments), stable isotope investigations of archaeological and palaeontological materials are normally restricted to skeletal materials, including the inorganic fraction of bone and tooth (so called 'bioapatite'), and preserved proteins that may be extracted from these mineral matrices such as bone collagen. Collagen is often the favoured analyte for stable isotope studies on archaeological human and animal remains as modern experimental data and published quality control criteria can be used to evaluate extracted 'collagen' and assess its integrity prior to data interpretation (Ambrose, 1990; van Klinken, 1999). Collagen molecules break-down through time in the burial environment, and the processes of diagenesis, hydrolysis and microbial attack can serve to degrade collagen, resulting in its loss or in the alteration of *in vivo* stable isotope signatures (Ambrose, 1990; van Klinken, 1999; Collins et al., 2002; Nielsen-Marsh et al., 2007; Smith et al., 2007; Dobberstein et al., 2009). Although the age of deposits can greatly influence the chances of collagen preservation, the rate of protein breakdown largely depends on conditions within the local burial environment (Nielsen-Marsh et al., 2007; Smith et al., 2007) and, where conditions are favourable, well-preserved collagen can be extracted and analysed from Late Pleistocene samples dating to older than 50,000 yr BP (Fizet et al., 1995; Bocherens et al., 1997, 1999, 2001; Jones et al., 2001).

Here, we report the results of stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analysis of herbivore bone collagen from the site of Neumark-Nord 2, Germany (archaeological find layer NN2/2), with the aim of investigating potential differences in herbivore feeding ecology at this early Last Interglacial (Eemian) 'water-hole' site. Carbon and nitrogen composition and mass ratios of ultra filtered bone collagen show that the samples are mostly well preserved, indicating extracted proteins are useful for reconstructing diet and feeding ecology. The data are explored for inter-specific differences and compared to previously published bone collagen isotope data from a range of other Late Pleistocene sites. Issues of herbivore digestive physiology, niche separation and resource partitioning amongst Late Pleistocene equids and bovids are discussed, and the implications for hominin palaeodietary studies are addressed.

2. Reconstructing herbivore ecology using carbon and nitrogen isotope analysis

Carbon and nitrogen stable isotope techniques are based around the principle that animal body tissues (e.g. bulk bone collagen) reflect the isotopic composition of the food ingested throughout life. The relative abundance of the stable isotopes of carbon, ^{13}C and ^{12}C ($\delta^{13}C$), varies characteristically between different biological communities e.g. between plants of different photosynthetic pathway (Smith and Epstein, 1970; DeNiro and Epstein, 1978) or between terrestrial and marine ecosystems (Schoeninger and DeNiro, 1984). There is a fractionation effect between plant $\delta^{13}C$ and herbivore bone collagen $\delta^{13}C$ values of approximately +5‰ (Bocherens and Drucker, 2003). Studies of resource partitioning and niche feeding ecology in modern and ancient ecosystems have generally focused on environments where both C_3 and C_4 plants can be found, such as sub-tropical Africa (Koch et al., 1995; Cerling et al., 1999) and North America (Gadbury et al., 2000; MacFadden, 2008). These plants have different photosynthetic pathways, selecting against ^{13}C to different degrees, and therefore display large differences in their $\delta^{13}C$. These variations are then expressed further up the food chain in herbivore tissues and, in turn, even in carnivores and humans, revealing resource partitioning in mixed C_3/C_4 environments. However, recent studies have also demonstrated the usefulness of carbon isotope analysis to reveal resource partitioning among modern ungulates in purely C_3 environments (Feranec, 2007). Such variations stem from intra-ecosystem variations in carbon and nitrogen isotope values of different plant communities and also reflect dietary choices of herbivores living within C_3 environments. For example, lichens exhibit higher $\delta^{13}C$ values than other terrestrial C_3 plants (Park and Epstein, 1960; Teeri, 1981; Maguas and Brugnoli, 1996) and these less negative values can be exhibited in the tissues of specialist lichen feeders such as modern barren ground caribou (Ben-David et al., 2001; Drucker et al., 2010, 2001). Other carbon isotope studies of modern ecosystems have demonstrated that vegetation in densely forested areas has characteristically-low $\delta^{13}C$ values compared to those from more open areas (van der Merwe and Medina, 1991; Heaton, 1999), leading to more negative $\delta^{13}C$ values in the tissues of leaf-foddered animals, due to the 'canopy effect', also observed in archaeological case studies (Cerling et al., 2004; Noe-Nygaard et al., 2005). Conversely, woody plants are typically enriched in ^{13}C compared to herbaceous plants growing at the same sites, varying by 2‰ or more (Heaton, 1999). These modern case studies demonstrate the potential for intra-ecosystem variations in carbon isotope values of different plant communities within purely C_3 environments. Where these are pronounced, differences in feeding behaviours (resource partitioning) amongst different animals in the same habitat can result in differences in the carbon isotope composition of tooth enamel and bone collagen (Feranec, 2007).

The nitrogen isotope composition of animal collagen largely reflects the animal's position within food webs, with the ratio of ^{15}N and ^{14}N ($\delta^{15}N$) increasing by 3–5‰ with each trophic step (Bocherens and Drucker, 2003). However, although occupying the same trophic level, absolute $\delta^{15}N$ values of herbivore tissues depend on a number of factors, most notably on the varying ^{15}N levels of the plants they consume (and ultimately the soils) at the base of the food chain. Nitrogen metabolism in certain animal species may also influence the $\delta^{15}N$ of their tissues, although this has been poorly characterized to date. The majority of terrestrial plants obtain their nitrogen from soil ammonium (NH_4^+) or nitrate (NO_3^-), and therefore the abundance of ^{15}N in their vegetation reflects the ^{15}N abundance of nitrogen sources in the soils (Shearer and Kohl, 1986). A range of variables can lead to depletion or enrichment in soil and therefore plant ^{15}N, which, in turn affects the tissue $\delta^{15}N$ values of animal feeders—even herbivores at the same trophic level. One major influence is that of local temperatures and water availability, which is inversely correlated with plant $\delta^{15}N$ values in modern studies (Heaton et al., 1986; Schwarcz et al., 1999). The relationship between long-term climatic changes and $\delta^{15}N$ of archaeological herbivore collagen has been established in archaeological studies (van Klinken et al., 2000; Richards and Hedges, 2003; Hedges et al., 2004; Stevens and Hedges, 2004; Stevens et al., 2008), likely due to soil water availability being reduced during cooler, drier climatic phases. Salinity has also been demonstrated to positively correlate with $\delta^{15}N$ values in studies on modern plants (Heaton, 1987; van Groenigen and van Kessel, 2002), possibly inducing a form of 'pseudo-aridity'. Variation in plant $\delta^{15}N$ values in modern studies has also been demonstrated to vary with soil type (Schwertl et al., 2005) and proximity to coast (Virginia and Delwiche, 1982; Heaton, 1987; Hicks et al., 2005); fire regime (Grogan et al., 2000); nitrogen availability (Hobbie et al., 2000);and the addition of modern and ancient fertilizers organic and inorganic (Choi et al., 2003; Bogaard et al., 2007), amongst other factors including

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