Oxygen Isotopes in Bioarchaeology: Principles and Applications, Challenges and Opportunities

Sarah Pederzani[1,2*] and Kate Britton[2,1]

[1] Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, 04103 Leipzig, Germany
[2] Department of Archaeology, University of Aberdeen, Aberdeen, Scotland, United Kingdom AB24 3UF
*Corresponding Author: sarah_pederzani@eva.mpg.de

Abstract

Oxygen isotope analyses of skeletal remains ($^{18}O/^{16}O$, $\delta^{18}O$) are a powerful tool for exploring major themes in bioarchaeology (the study of biological archaeological remains) and can aid in the reconstruction of past human-environment interactions, socio-cultural decisions and individual life histories. Making use of the preserved animal and human tooth and bone commonly found at archaeological sites, applications include the reconstruction of palaeoclimate and palaeoseasonality; animal husbandry and management practices; human and animal lifetime mobility and provenance; and cultural practices such as breastfeeding, weaning and even past culinary preparation techniques. With a range of other uses across the natural, physical, chemical and biological sciences, oxygen isotope analyses are also highly cross-disciplinary, with developments in the field of isotope bioarchaeology potentially feeding into other fields and *vice-versa*. The purpose of this paper is to provide a summary of the biogeochemical background of oxygen isotope systematics from the water cycle to human and animal skeletal tissues for archaeologists and other scientists, and to explore how these have been utilised in terrestrial bioarchaeological research. In this way, we aim to provide an overview resource for stable isotope analysts in archaeology and the wider earth science community, as well as for archaeological practitioners and consumers interested in specific applications. By providing a summary of fundamental isotope mechanics alongside a review of recent developments in the field, we hope to highlight the potential of oxygen isotope bioarchaeology to not only reveal environmental and ecological aspects of the past relevant to human groups using archaeological materials, but also to illuminate past human decisions and behaviours. Current limitations and caveats of the approaches used are also explored.

Keywords: $\delta^{18}O$; bioapatite; carbonate, phosphate; archaeology; climate; mobility; zooarchaeology

1 Overview

From dating techniques to dietary reconstruction, isotope analyses play a key role in the modern field of archaeological science. Including stable light, heavy and radiogenic isotopes, a range of isotope systems have been exploited by archaeologists in order to study archaeological artefacts and ‘ecofacts’, and to better understand past human lives and societies. Oxygen isotope analysis forms one of the largest and most established areas of stable isotope bioarchaeology, second only perhaps to the carbon and nitrogen isotope analysis of bone collagen. Bioarchaeology[1] itself is a well-developed sub-field of archaeology that commonly incorporates techniques from the biological, (geo)chemical, physical and earth sciences into the analysis of biological remains from archaeological sites. Initially adopted from the climate sciences for investigating past environments, oxygen isotope approaches in bioarchaeology are now used to address a variety of archaeological queries, from trade to transhumance, birth seasonality to breastfeeding. In this review we seek to make this large and diverse field more accessible to practitioners and consumers alike, in both the archaeological sciences and wider earth sciences communities. We provide an overview of research in the current major areas of application alongside a summary of their underlying fundamental isotopic systematics and principles. By following the principles of isotopic change from the water cycle to the incorporation and modification of oxygenous compounds in animal biological tissues, we hope to foster a greater understanding of the complexity of oxygen stable isotopes in biological tissues and to illustrate the caution and nuance that must be involved in the interpretation of such data. Through pointing out key applications and case studies in the reconstruction of past climate, animal husbandry, movement, provenance, weaning and culinary practices, we present both the potential of oxygen isotopes and the challenges of disentangling a complex isotopic system in biological materials from anthropogenically-derived assemblages. Finally, we highlight possible developments for the

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[1] Defined here in the UK/European sense after Clark (1972); the study of biological remains from archaeological sites, specifically preserved human and animal tissues.

future of this field and explore methodological advances and approaches that could be utilised to overcome technique limitations.

1.1 Oxygen and its isotopes

By mass, oxygen (O) is Earth's most abundant element, forming the most common components of the hydrosphere, biosphere and lithosphere (Cook and Lauer, 1968; Emsley, 2011). Oxygen naturally occurs, with decreasing abundance, as one of three stable isotopes: ^{16}O (99.755%), ^{18}O (0.206%) and ^{17}O (0.039%) (Rundel et al., 1989; Schoeller, 1999). Across the life and earth sciences, the ratio between ^{16}O and ^{18}O is most typically analysed, although more recently developed approaches, such as triple oxygen isotopic analysis (Δ^{17}O) and clumped isotope analysis (Δ_{47}), represent a growing field particularly in palaeoclimate science (Affek, 2012; Eagle et al., 2010; Gehler et al., 2011; Suarez and Passey, 2014).

1.2 Notations and standards

The relative abundance of ^{18}O to ^{16}O of a particular material or compound is most commonly expressed in per mil (‰) relative to an international primary reference material (R) of assigned value using the delta notation (see equation 1), where ^{18}O/^{16}O is the isotope ratio of ^{18}O to ^{16}O [R(^{18}O)] (Coplen, 1995; Craig, 1961):

$$\delta = \frac{\left({}^{18}\mathrm{O}_{sample}/{}^{16}\mathrm{O}_{sample}\right)}{\left({}^{18}\mathrm{O}_{standard}/{}^{16}\mathrm{O}_{standard}\right)} - 1 \qquad (1)$$

According to IUPAC (International Union of Pure and Applied Chemistry) guidelines, relative oxygen isotope abundances should be normalised using both VSMOW (Vienna Standard Mean Ocean Water) and SLAP (Standard Light Antarctic Precipitation) standards on the VSMOW/SLAP scale, where the difference between $\delta^{18}\mathrm{O}_{\mathrm{VSMOW}}$ and $\delta^{18}\mathrm{O}_{\mathrm{SLAP}}$ is exactly 55.5 ‰ (Coplen, 2011, 1996, 1995; Craig, 1961; Gonfiantini, 1978). The use of the VSMOW/SLAP scale is recommended and has been widely adopted; however, particularly for carbonates, δ^{18}O values are often also reported on the VPDB (Vienna Pee Dee Belemnite) scale. The two scales can be related to each other through VSMOW using a conversion established by Coplen et al. (1983) (see equation 2):

$$\delta^{18}O_{VSMOW} = 1.03091\,\delta^{18}O_{VPDB} + 30.91 \qquad (2)$$

The IAEA (International Atomic Energy Agency) distributes a variety of international reference materials calibrated to the VSMOW/SLAP scale for use in oxygen isotope analysis of different compounds. As archaeological analytes are primarily solid materials derived from skeletal remains (such as bioapatite phosphate, bioapatite carbonate or collagen), solid standard materials, preferably matrix-matched ones, are usually preferred for calibration and normalisation purposes. Examples of international reference materials commonly used during analyses of phosphates, carbonates and collagen can be found in Brand et al. (2014, 2009), Coplen et al. (2006, 1983) and Hunsinger and Stern (2012). To prevent early exhaustion of international reference materials, reduce costs and ensure availability over several years, laboratories also commonly make up batches of in-house standards that are calibrated to international reference materials. As long as such secondary reference materials have been scale normalised on the VSMOW/SLAP scale, they can then be used in day-to-day sample analysis for quality control, as well as to normalise data to the VSMOW/SLAP scale (Coplen, 2011). Non-international reference materials are often also used by laboratories and analysed in cross-laboratory studies, with the accepted value ranges then being published (for examples, see Brand et al., 2009 and Halas et al., 2011). This practice has been particularly important for the analysis of silver phosphate precipitates (commonly used in phosphate oxygen isotope analysis), for which no international reference materials are available for two-point scale normalisation of data. Examples of a number of commonly used secondary reference materials, often used as intra-/inter- laboratory quality control checks or in place of international standards during routine analysis, can be found in the literature (e.g. Halas et al., 2011; LaPorte et al., 2009; Munro et al., 2007; Tian et al., 2016; Vennemann et al., 2002; Webb et al., 2014). Despite being essential for producing comparable isotopic data and providing quality control checks, many archaeological science research articles fail to report normalisation and quality control procedures (Szpak et al., 2017). Best practice articles reiterating established guidelines for measurement calibration and reporting of results have been published and may help to remedy this (see Roberts et al., 2017; Szpak et al., 2017 for recent examples).

2 Baseline variation in water sources for animals and humans

Variation in the oxygen isotope composition of mammalian skeletal tissues is driven by the isotopic composition of body water which, in turn, is determined by the oxygen isotopic composition of ingested sources of oxygen, such as water, and the oxygen structurally bound in food. As the largest oxygen contributor to body water, consumed water is the most important driver of mammal skeletal tissue δ^{18}O (Bryant and Froelich, 1995; Kohn, 1996; Podlesak et al., 2008). While the oxygen isotopic composition of skeletal tissues represents a mixture of sources that is subject to physiological and metabolic modifications, the influence of consumed water is particularly pronounced and baseline variability is often reflected in tissue δ^{18}O. The following sections will give a brief overview of baseline oxygen isotopic variability in water sources to highlight underlying mechanisms driving mammalian tissue δ^{18}O. For more detailed information of δ^{18}O in the hydrological cycle, readers can refer to excellent overview works such as Gat (2010) and Mook (2006).

2.1 Geospatial and climatic variation in precipitation oxygen isotope ratios ($\delta^{18}O_{precip}$)

Precipitation is the original water source of most terrestrial water bodies and varies widely in oxygen isotopic composition due to mechanisms of isotopic change involved in evaporation, condensation events during moisture transport and the precipitation event itself. During phase transitions, fractionation effects occur that manifest in the preferential accumulation of the lighter isotopologue (as $H_2{}^{16}O$) in the vapour phase during evaporation, leaving the liquid phase increasingly ^{18}O-enriched (Dansgaard, 1964; Rundel et al., 1989) (Figure 1). Conversely, $H_2{}^{18}O$ tends to accumulate in condensation phases, such as precipitation, leaving cloud moisture masses comparatively depleted in ^{18}O compared to their previous state as rainout occurs. Due to these modifying phase transitions, the $\delta^{18}O$ 'signature' of any particular precipitation event can be thought of as reflecting the cumulative 'history' of the moisture and air masses the precipitation falls from, including moisture source, transport processes, conditions at the precipitation site and the characteristics of the precipitation event (Araguás-Araguás et al., 2000; Gonfiantini, 1985; Läderach and Sodemann, 2016; Rozanski et al., 1993; Yurtsever and Gat, 1981). Many aspects of moisture mass history can be summarised in a number of predictable effects related to continentality, altitude, latitude, temperature, precipitation amount, relative humidity and seasonality (Craig, 1961; Dansgaard, 1964; Gat, 1996; Gonfiantini, 1985; Rozanski et al., 1993; Yurtsever and Gat, 1981).

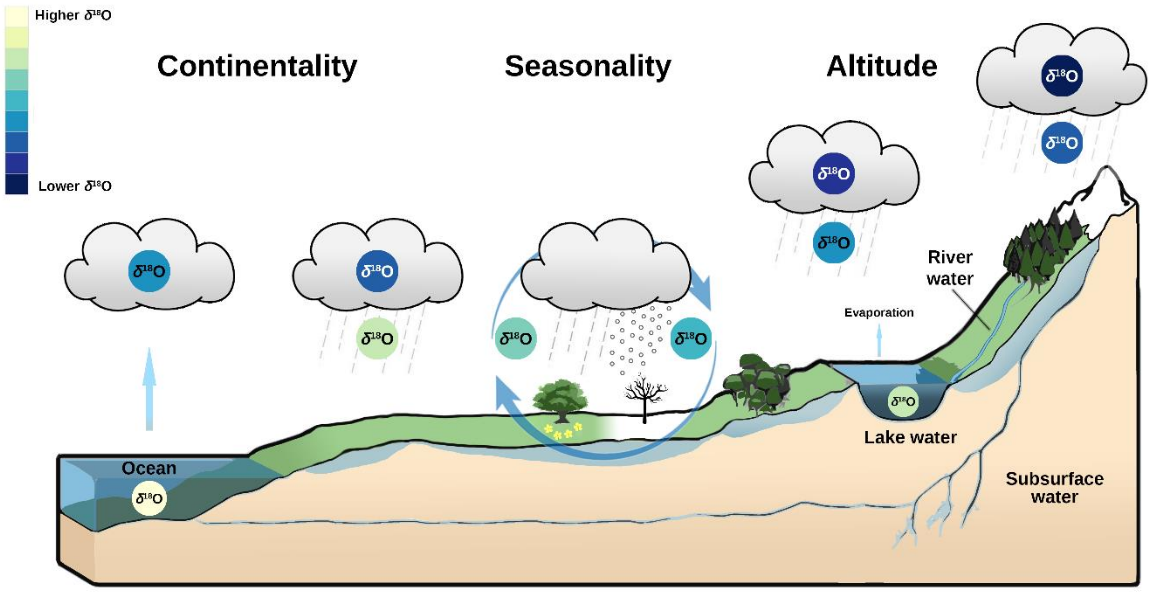

Figure 1: Isotopic baseline variation is introduced in the hydrological cycle as water $\delta^{18}O$ is changed by rainout and evaporation processes, that results in large scale effects of continentality, seasonality and altitude, as well as temperature, rainfall amount and relative humidity.

Progressive rainout: continentality, latitude, altitude

The progressive rainout of ^{18}O-rich water from moisture masses as they travel from their source area, typically the tropical oceans, causes a pattern of lower $\delta^{18}O_{precip}$ values at increasing distance from the coast and at higher latitudes compared to near shore and/or low-latitude precipitation (Araguás-Araguás et al., 2000; Dansgaard, 1964; Yurtsever, 1975). Analogously, the altitude effect is related to progressive rainout along a mountain slope, which preferentially removes $H_2{}^{18}O$ in the form of rain from cloud moisture as clouds rise (Gonfiantini et al., 2001; Poage and Chamberlain, 2001). This results in comparatively low $\delta^{18}O$ values in high-altitude precipitation and higher $\delta^{18}O$ values in low-altitude precipitation. This altitude effect is strengthened by the temperature difference between low and high elevation sites (see below for effects of temperature on precipitation $\delta^{18}O$). The overall principle of these effects is globally consistent, but their magnitude is modulated by geography and topography (Holdsworth et al., 1991; Holko et al., 2012; Ichiyanagi et al., 2016; Ingraham and Taylor, 1986; Kern et al., 2014; Liu et al., 2014; Moser and Stichler, 1974; Poage and Chamberlain, 2001; Rozanski et al., 1993; Siegenthaler and Oeschger, 1980; Yonge et al., 1989); the speed of moving moisture masses and the amount of precipitation falling from them (Chizhova et al., 2017; Gat, 2010); re-evaporation and recycling of moisture (Delavau et al., 2011; Eichler, 1965; Garcia et al., 1998; Gat and Matsui, 1991; Ingraham and Craig, 1993; Kong and Pang, 2016; Koster et al., 1993; Njitchoua et al., 1999; Salati et al., 1979; Vuille et al., 2003); and sub-cloud conditions (Ait Brahim et al., 2016; Blisniuk and Stern, 2005; Dray et al., 1998; Ren et al., 2017; Siegenthaler and Oeschger, 1980; Stern and Blisniuk, 2002). Due to the predictable influence of continentality, latitude and altitude on $\delta^{18}O_{precip}$, large scale spatial patterns can be predicted and interpolated using geospatial tools to calculate $\delta^{18}O_{precip}$ at a specified location (i.e. the Online Isotopes in Precipitation Calculator – OIPC, Bowen, 2006) or to create isotopic maps, called 'isoscapes' (Figure 2) (Bowen, 2010; Bowen and Revenaugh, 2003; Bowen and Wilkinson, 2002; West et al., 2014).

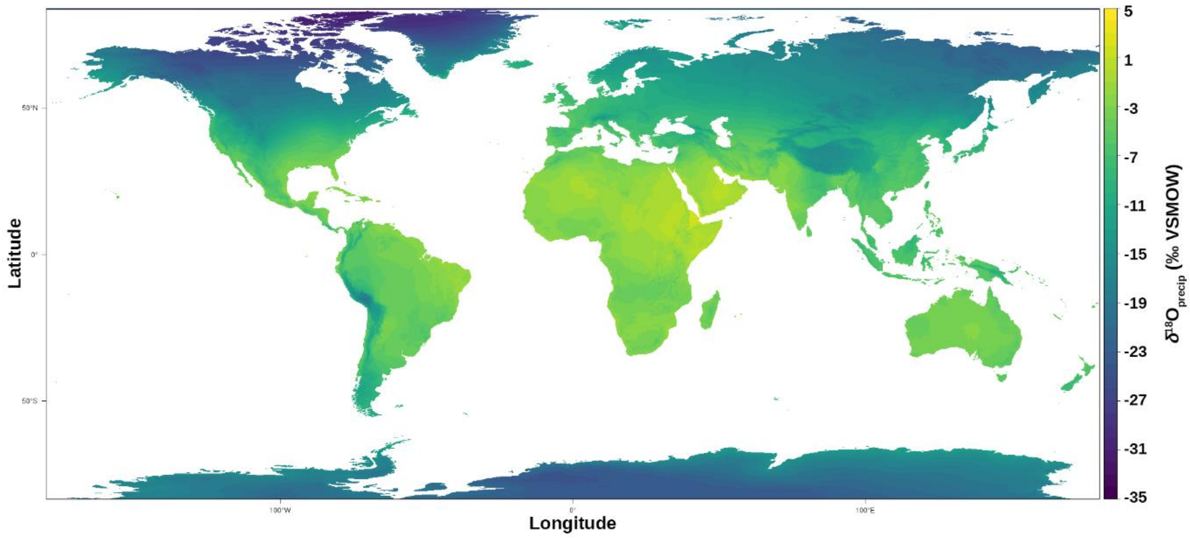

Figure 2: Isoscape of global patterns in d18O in precipitation modelled from GNIP station data (includes all GNIP monthly data sets available in the GNIP database on 05.10.2017)(IAEA/WMO, 2018). Isoscape modelling was performed using the IsoriX package (Courtiol, 2017).

Temperature, precipitation amount and seasonality

A prominent relationship between surface air temperature and local $\delta^{18}O_{precip}$ can be observed in mid- and high-latitude regions. This close relationship is present on both a seasonal scale (e.g. Müller et al., 2017a), as well as through time if decades of water isotope and temperature data are compared (e.g. Stumpp et al., 2014). Such effects are far less pronounced in tropical regions, where the rainfall amount effect is usually a stronger driver of seasonal changes in $\delta^{18}O_{precip}$ (Bowen, 2008; Dansgaard, 1964; Gat, 2010; Müller et al., 2017; Rozanski et al., 1992; Yurtsever, 1975). These two effects form the basis of many isotope based palaeoclimate reconstruction approaches (Johnsen et al., 1995; Jouzel et al., 2000; Longinelli, 1984; Luz et al., 1984; Rozanski et al., 1992; Straaten and Mook, 1983).

The temperature effect is predominantly rooted in the temperature dependence of isotopic fractionation during the condensation of precipitation and causes, for example, summer precipitation to exhibit higher $\delta^{18}O$ values than winter precipitation (Clark and Fritz, 1997; Craig, 1961; Dansgaard, 1964; Kohn and Welker, 2005; Lee and Fung, 2008; Mook, 2006; Rozanski et al., 1993). The slope of the temperature effect varies geographically (Aggarwal et al., 2012; Akers et al., 2017; Dayem et al., 2010; Gat, 2010; Gourcy et al., 2005; Sime et al., 2009) and seasonally (Akers et al., 2017; Field, 2010; Jacob and Sonntag, 1991; Schmidt et al., 2005), but strong temperature effects and relatively consistent slopes are observed in many regions (Bowen, 2008; Cole et al., 1999; Field, 2010; Kohn and Welker, 2005; Noone et al., 2002; Schmidt et al., 2005). At tropical latitudes, or other areas with temperatures consistently above 20°C, $\delta^{18}O$ of precipitation decreases with increasing amounts of precipitation or high humidity at a set location (Dansgaard, 1964; Rozanski et al., 1993). The amount effect is thought to be caused by reduced evaporation and equilibration in larger raindrops (Bony et al., 2008; Dansgaard, 1964; Risi et al., 2008; Rozanski et al., 1993), increased relative humidity at the precipitation site (Araguás-Araguás et al., 2000; Rozanski et al., 1993; Salamalikis et al., 2016a) and recycling of re-evaporated moisture (Bony et al., 2008; Cai et al., 2016; Moore et al., 2014; Risi et al., 2008). In monsoon regions, the amount effect may also partially be related to organised convection effects (Kurita, 2013; Lekshmy et al., 2014; Tharammal et al., 2017). The amount effect is most pronounced in coastal and island locations (Rozanski et al., 1993), in tropical regions and in areas characterised by monsoon activity, which creates a marked seasonal $\delta^{18}O_{precip}$ pattern (Aizen et al., 1996; Araguás Araguás and Froehlich, 1998; Liu et al., 2014; Posmentier et al., 2004; Vuille et al., 2005). Both temperature and amount effects are moderated by moisture source effects and by changes in atmospheric cycling (Aggarwal et al., 2012; Cai et al., 2016; Cole et al., 1999; Dayem et al., 2010; Gat, 2010; Lee et al., 2007; Sime et al., 2009).

Both temperature and rainfall amount vary substantially on a seasonal basis in many locations, creating a predictable seasonal pattern of $\delta^{18}O_{precip}$ based on the temperature effect (Clark and Fritz, 1997; Feng et al., 2009; Field, 2010; Jacob and Sonntag, 1991; Klaus et al., 2015; Rozanski et al., 1993; Salamalikis et al., 2016b) and/or amount effect (Araguás Araguás and Froehlich, 1998; Garcia et al., 1998; Rozanski and Araguás-Araguás, 1995; Vuille et al., 2003). Seasonal $\delta^{18}O_{precip}$ patterns can also be created or modulated by shifting moisture sources and transport processes (Deininger et al., 2016; Feng et al., 2009; Field, 2010; Puntsag et al., 2016). Such sub-annual patterns in environmental $\delta^{18}O$ are particularly important for understanding seasonal changes of $\delta^{18}O$ recorded in incrementally forming tissues, such as tooth enamel, which underlie many important bioarchaeological applications such as the investigation of seasonal mobility, birth seasonality and the reconstruction of past seasonal climatic conditions.

2.2 Isotopic variation in water bodies

Isotopic variation in precipitation dominates large parts of the hydrological cycle, and precipitation $\delta^{18}O$ values are often used as a proxy for predicting animal drinking water. However, humans and animals often source their drinking water from water bodies such as rivers, lakes, springs or wells, the $\delta^{18}O$ values of which may depart from local $\delta^{18}O_{precip}$ values. The individual isotopic characteristics of source water, water influxes and outfluxes, and mixing during water residence determine if and how water bodies deviate in $\delta^{18}O$ from local precipitation. In general, rivers and groundwater have been shown to closely reflect local $\delta^{18}O_{precip}$ values (Darling et al., 2003; Gat, 1995; Gibson et al., 2016; Kendall and Coplen, 2001; Rozanski, 1985; Tian et al., 2001; Van Geldern et al., 2014b; Van Geldern and Barth, 2016), and rivers, lakes and groundwater generally represent an amount-weighted isotopic average of the precipitation falling in their broader catchment area (Darling et al., 2006, 2003; Gat, 1995; Gibson and Edwards, 2002; Gonfiantini, 1986; Halder et al., 2015; Kendall and Coplen, 2001; Rank et al., 2017; Rozanski, 1985; Van Geldern et al., 2014a). A prominent driver that can cause rivers, groundwater or lakes to deviate from local precipitation is the influx or transport of 'non-local' waters (Datta et al., 1996; Gibson and Edwards, 2002; Ingraham et al., 1998; Krabbenhoft et al., 1990; Meier et al., 2013; Musgrove and Banner, 1993; Ramesh and Sarin, 1992; Seiler and Gat, 2007; Siegenthaler and Oeschger, 1980; Weyhenmeyer, 2002), which are often low $\delta^{18}O$ water from higher elevations. Evaporative enrichment can also induce considerable isotopic deviations from local precipitation and is especially pronounced in standing water bodies, such as lakes, due to long water residence times (Craig and Gordon, 1965; Fontes et al., 1986; Gibson et al., 2016; Gonfiantini, 1986; Ingraham et al., 1998; Jasechko et al., 2014; Martinelli et al., 1996; Tsujimura et al., 2007).

In addition, due to the nature of their formation (accumulating various sources) and larger volume, bodies of water, such as lakes, are commonly more isotopically stable through time. In light of this, seasonal shifts in $\delta^{18}O$ are often dampened (i.e. of reduced magnitude) in water bodies compared to precipitation and/or may be visible with a significant time lag at downstream river sites (Frederickson and Criss, 1999; Halder et al., 2015; Jasechko et al., 2016; Kendall and McDonnell, 1998; Rank et al., 2017). Furthermore, lakes and rivers in arid environments can commonly exhibit seasonal isotopic patterns driven by evaporative enrichment, with maximum $\delta^{18}O$ values in summer months (Gonfiantini, 1986; Gonfiantini et al., 1998; Kattan, 2012, 2008; Pham et al., 2009; Tyler et al., 2007; Wen et al., 2016). On the other hand, rivers with high elevation water influxes are often characterised by snowmelt-dominated seasonal changes, with resulting low summer $\delta^{18}O$ values (Congjian et al., 2016; Halder et al., 2015; Jeelani et al., 2017; Meier et al., 2013; Müldner et al., 2009; Rank et al., 2017, 2012, 1998).

In most surface and subsurface water bodies, seasonal isotopic shifts are small (often <2 ‰) because water residence buffers isotopic changes and evaporative enrichment and low $\delta^{18}O$ water influxes sometimes cancel each other out (Frederickson and Criss, 1999; Gat, 2010; Gonfiantini, 1986; Halder et al., 2015; Jasechko et al., 2016; Jones et al., 2005; Jones and Imbers, 2010; Kattan, 2012, 2008; Kendall and McDonnell, 1998; Kortelainen and Karhu, 2004; Paternoster et al., 2008; Pham et al., 2009; Rank et al., 2017; Reddy et al., 2006; Tyler et al., 2007; Wassenaar et al., 2009; Wen et al., 2016). Long-term averaging and strongly reduced seasonal effects are also often a main driver of $\delta^{18}O$ in groundwater that, in turn, feeds springs or wells, leading to these bodies generally being very stable over time (Darling et al., 2006, 2003; Kortelainen and Karhu, 2004; Rozanski, 1985; Van Geldern et al., 2014a; West et al., 2014).

Despite the isotopic diversity in water sources used by humans and animals, and the isotopic variation that can exist within those sources, mammalian skeletal δ^{18}O data have consistently been shown to relatively closely align with local precipitation δ^{18}O, particularly in obligate-drinking species (Bryant et al., 1994; Bryant and Froelich, 1995; Daux et al., 2008; Delgado Huertas et al., 1995; Ehleringer et al., 2010; Hoppe et al., 2004a; Hoppe, 2006; Kohn, 1996; Kohn et al., 1996; Longinelli, 1984). However, in archaeological case studies where dominant consumption of a particular water source is suspected, or otherwise evidenced, baseline isotope variation in environmental water could be an important consideration for the interpretation of bioarchaeological oxygen isotope data.

2.3 Water in plant foods: leaf water

For most commonly analysed fauna in archaeological contexts, tissue δ^{18}O has been shown to be closely related to the isotopic composition of environmental water ($\delta^{18}O_{ew}$) (Bryant et al., 1994; Bryant and Froelich, 1995; Delgado Huertas et al., 1995; Hoppe et al., 2004a; Hoppe, 2006; Kohn, 1996; Kohn et al., 1996; Longinelli, 1984) because this reflects the dominant source of water (and therefore oxygen) of animals that drink regularly, including humans. However, some non-obligate drinking animals, such as drought-adapted herbivores, can obtain large proportions of (or even all) their water from water contained within the plant foods they consume (Brown and Lynch, 1972; Cain et al., 2006; Dunson, 1974; Ealey et al., 1965; Maloiy, 1973; Nicholson, 1985; Schmidt-Nielsen and Schmidt-Nielsen, 1952). Leaf water δ^{18}O values are substantially higher than those of local precipitation due to strong evaporative enrichment caused by evapotranspiration through leaf stomata (Barbour et al., 2004; Cernusak et al., 2016; Farquhar et al., 1989; Luz et al., 2009; Merlivat, 1978). The magnitude of ^{18}O-enrichment above source water correlates strongly with environmental factors, such as leaf temperature and relative humidity, with leaf water enrichment strongest in warm, arid conditions (Barbour et al., 2017; Cernusak et al., 2016; Craig and Gordon, 1965; Cuntz et al., 2007; Dongmann et al., 1974; Farquhar et al., 1989; Farquhar and Cernusak, 2005; Farris and

Strain, 1978; Flanagan et al., 1991; Kahmen et al., 2013; Luz et al., 2009; Merlivat, 1978). This enrichment can vary widely: up to 20 ‰ or even 40 ‰ (Cernusak et al., 2016). Additionally, different plant types can vary in leaf water δ^{18}O due to influences of leaf anatomy. Leaf water in grasses, for example, becomes progressively more ^{18}O-enriched (compared to source water) towards the leaf tip, as water with already high δ^{18}O values travels up the leaf to serve as 'source' water for following evaporation sites (Gan et al., 2003, 2002; Gat and Bowser, 1991; Helliker and Ehleringer, 2000; Ogée et al., 2007; Wang and Yakir, 1995). This leads to an overall stronger leaf water enrichment in grasses than is exhibited in leafy dicotyledonous plants. The oxygen isotopic composition of source water for plants also plays an important role in determining leaf water δ^{18}O values (Dawson, 1993; Dawson and Ehleringer, 1991; Ehleringer and Dawson, 1992; Wershaw et al., 1966). For example, some plants, such as grasses or shrubs and trees with shallow roots, predominantly take up water from the upper soil layer, where it has already undergone significant evaporative enrichment (Cook and O'Grady, 2006; Dodd et al., 1998; Snyder and Williams, 2000; Tang and Feng, 2001). Plants with deep roots, however, may access lower subsurface waters that are isotopically more closely aligned to local precipitation (Adams and Grierson, 2001; Barbour, 2007; Brunel et al., 1991; Busch et al., 1992; Cook and O'Grady, 2006; Drake and Franks, 2003). This effect may be relevant when interpreting data from herbivores with different dietary preferences and foraging behaviours, for example browsers and grazers. While these niche feeding behaviours need not be conservative, and could therefore pose a problem for archaeological studies (where feeding behaviour should not be assumed), substantial effects on tissue δ^{18}O are likely to only occur in non-obligate drinkers, and especially in those from arid environments (see more detail in section 4.2). Some researchers have exploited the influence of leaf water values on tissue δ^{18}O to explore different feeding behaviours amongst herbivores in the past, as well as to reconstruct relative humidity through the analysis of obligate and non-obligate drinkers (e.g. Blumenthal et al., 2017; Faith, 2017; Franz-Odendaal et al., 2002; Levin et al., 2006) (see section 4.2). Carnivorous animals are often non-obligate drinkers and obtain most of their water from their prey or as metabolic water from food macronutrients. While this would theoretically lead to an impact of prey choice on tissue δ^{18}O, carnivores have so far shown tissue δ^{18}O values that are almost completely decoupled from prey δ^{18}O or environmental water, likely due to metabolic effects (Pietsch et al., 2011; Pietsch and Tütken, 2015). For most purposes, the selection of likely obligate drinkers, including humans, in archaeological studies should mediate the effects of food, water and dietary preference on tissue δ^{18}O (although see section 4.6 for the potential influence of culinary processes in humans).

3 Mammalian skeletal remains

3.1 Isotopic composition of bones and dental tissues

The oxygen isotopic composition of components of skeletal tissues, such as bioapatite or collagen, is a function of the isotopic signature of oxygen influxes into the body of an animal during the period of tissue formation, as well as the fractionating processes that occur during metabolic routing and tissue formation (Figure 3). Both the phosphate and structural carbonate components of bioapatite[2] form in isotopic equilibrium with body water, albeit with a temperature-dependent fractionation (Daux et al., 2008; Iacumin et al., 1996; Longinelli, 1984; Luz et al., 1984). As body temperature in mammals is metabolically controlled to be constant, the oxygen isotopic composition of bioapatite ($\delta^{18}O_{bioapatite}$) effectively exhibits a species-specific, constant relationship with body water (Iacumin et al., 1996; Kohn, 1996; Kohn and Cerling, 2002; Longinelli, 1984; Luz et al., 1984). Due to differences in fractionation, the δ^{18}O values of the carbonate ($\delta^{18}O_{carb}$) and phosphate ($\delta^{18}O_{phos}$) groups of bioapatite, although both formed in equilibrium with body water, are offset from each other by a relatively constant, but apparently species-specific, spacing of between ~8 and 12 ‰ (Bryant et al., 1996c; Chenery

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[2] Bioapatite refers to the mineral portion of skeletal tissues, which has a variable chemical stoichiometry, but can be approximated as a carbonate-rich, hydroxyl-deficient apatite (Driessens, 1980; Elliott, 2002; Wopenka and Pasteris, 2005).

et al., 2012; France and Owsley, 2015; Iacumin et al., 1996; Longinelli and Nuti, 1973; Martin et al., 2008; Pellegrini et al., 2011). The isotopic composition of body water, in turn, is governed by the isotopic characteristics and mass balance of oxygen fluxes entering and leaving the body, as well as isotopic fractionation associated with oxygen uptake and outflux (Bowen et al., 2009; Bryant and Froelich, 1995; Kohn, 1996; Podlesak et al., 2008). Both the magnitude and nature of oxygen fluxes, as well as the associated fractionations, are strongly driven by physiology and metabolism, which leads to marked species specificity in the relationship between drinking water and body water (Bryant and Froelich, 1995; Kohn, 1996; Kohn et al., 1996; Luz et al., 1984). As mentioned previously, the main oxygen influx into body water in mammals comes from fluids consumed through drinking and eating (~56%), although there are contributions from other oxygen sources, such as structural oxygen in solid foods and atmospheric O_2 taken into the body during respiration (Bryant and Froelich, 1995; Kohn, 1996; Podlesak et al., 2008).

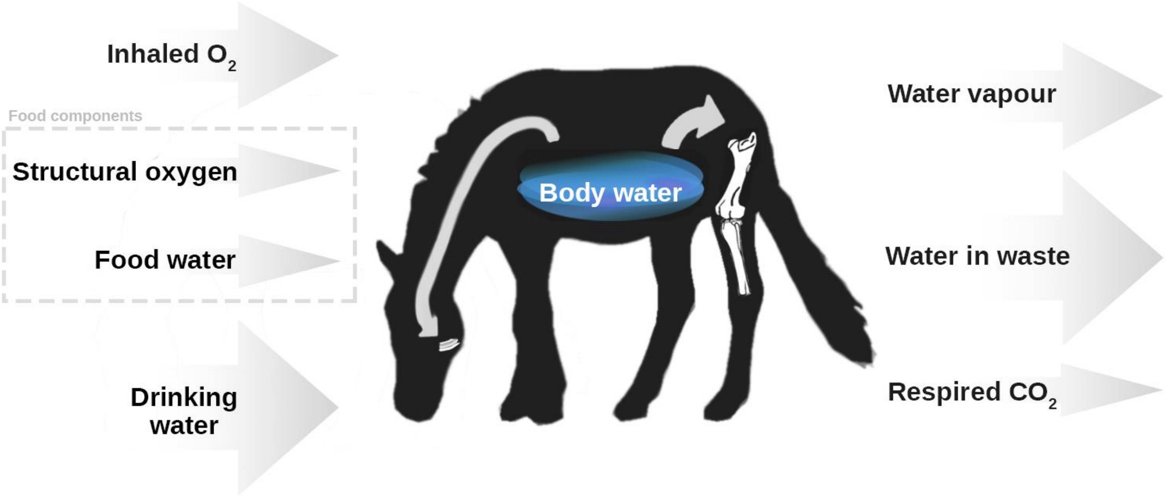

Figure 3: The oxygen isotopic composition of mammalian bone and tooth bioapatite is determined by the isotopic composition of body water which, in turn, is strongly related to the isotopic composition of consumed sources of oxygen as well as the mass balance of oxygen influxes and outfluxes.

In animals that ingest large amounts of water through drinking (i.e. obligate drinkers), the linear relationship between body water and ingested water extends to local environmental water and, often, precipitation (Ehleringer et al., 2010; Longinelli, 1984; Luz et al., 1984). However, as noted above, this relationship can be much weaker in drought-adapted animals (see sections

2.3 and 4.2) or carnivorous animals (e.g. Pietsch et al., 2011; Pietsch and Tütken, 2015). A number of studies have investigated the relationship between local water $\delta^{18}O$ and that of mammalian biogenic apatite phosphate or carbonate through experimental or observational studies on modern specimens (see Table 1 in the Appendix for an overview).

Oxygen in collagen ($\delta^{18}O_{coll}$) is not solely directly derived from body water in the way that it is in bioapatite; the oxygen in bone and dentinal collagen appears to derive from both structural oxygen in food as well as food water and drinking water, while also undergoing more extensive and complex modification due to the impact of collagen synthesis and metabolic and physiological processes (Kirsanow et al., 2008; Kirsanow and Tuross, 2011; Tuross et al., 2008). These factors lead to a weaker relationship between environmental water and $\delta^{18}O_{coll}$ compared with bioapatite (Kirsanow et al., 2008; Kirsanow and Tuross, 2011; Tuross et al., 2008).

Due to their different formation characteristics, different tissues of the same animal will exhibit different $\delta^{18}O$ values. As already discussed above, the mineral and proteinaceous components of skeletal tissues differ isotopically due to variation in isotopic fractionation and routing. Additionally, the type of skeletal tissue (e.g. bone, dentine and enamel) will determine its isotopic composition; each tissue has different characteristics, for example formation time and remodelling, that can impact the recording of isotopic information. Dental enamel forms during the first years of life, after which it is biologically inert and does not undergo remodelling (Dean, 1987; Hillson, 2005); therefore, it records isotopic input experienced by the animal during the time of formation in early life (Balasse, 2002; Fricke et al., 1998; Fricke and O'Neil, 1996; Passey and Cerling, 2002; Sharp and Cerling, 1998). Tooth dentine exhibits similar behaviour, growing incrementally during tooth formation with negligible remodelling later in life (Dean, 1995; Hillson, 2005; Kuttler, 1959; Nanci, 2017). However, secondary and tertiary dentine keep forming after tooth formation is complete, and dentine is not considered completely biologically inert due to the presence of dentinal tubules that continue to provide nutrients (Dean, 1995; Hillson, 2005; Kuttler, 1959; Nanci, 2017). Conversely, bone continuously and extensively remodels over time through bone removal and regrowth during life (Martin and Burr, 1989; Meghji, 1992; Walsh et al., 2003) and represents an amalgamated isotopic input averaged over the time of turnover. Bone remodelling varies by skeletal element, bone region, and with physical activity and age (Eriksen, 2010; Fahy et al., 2017; Hedges et al., 2007; Martin and Seeman, 2008; McNamara and Prendergast, 2007). Turnover times (the time taken for a volume of tissue to be completely replaced) are commonly in the order of several years to decades (Copley et al., 2004; Dupras and Schwarcz, 2001; Hedges et al., 2007; Libby et al., 1964; Manolagas, 2000; Meier-Augenstein and Fraser, 2008; Pearson and Lieberman, 2004; Stenhouse and Baxter, 1979, 1977). Bone mineral or collagen δ^{18}O values therefore give an isotopic signal that is averaged over many years before death.

The three analytic 'fractions' commonly exploited in the mammalian skeleton – bioapatite phosphate, bioapatite carbonate and collagen – exhibit other differences in their characteristics. As already outlined above, collagen oxygen is routed differently than bioapatite oxygen and the connection to body water is weaker (Kirsanow and Tuross, 2011; Tuross et al., 2008). For bioapatite, tooth enamel is commonly preferred over dentine or bone due to its higher crystallinity and resistance to diagenesis (Fricke and O'Neil, 1996; Iacumin et al., 1996; Koch et al., 1997; Kohn et al., 1999; Lee-Thorp and Van der Merwe, 1991; Wang and Cerling, 1994; Zazzo et al., 2004). In addition, the organic content of enamel is very low (<1%) (Eastoe, 1979; Hillson, 2005; Williams and Elliott, 1989), thus circumventing problems that might arise from the inclusion of high amounts of isotopically distinct organics in samples (see Balasse, 2002; Chenery et al., 2012; Crowley and Wheatley, 2014; Crowson and Showers, 1991; Grimes and Pellegrini, 2013; Koch et al., 1997; O'Neil et al., 1994; Pellegrini and Snoeck, 2016; Stephan, 2000; Wiedemann-Bidlack et al., 2008 for discussion of this issue). In general, tooth enamel carbonate is much more frequently analysed than enamel phosphate due to the relative ease of sample preparation and analysis, as well as greater measurement precision (Balasse et al., 2002; Chenery et al., 2012; Crowley and Wheatley, 2014; Koch et al., 1997; LaPorte et al., 2009; Passey et al., 2007; Pellegrini and Snoeck, 2016;

Snoeck and Pellegrini, 2015; Vennemann et al., 2002; Zazzo et al., 2006). However, bioapatite phosphate has been shown to be much more resistant to diagenetic change (Iacumin et al., 1996; Lee-Thorp, 2008; Zazzo et al., 2004) and is therefore preferred over carbonate for deep time applications (e.g. Amiot et al., 2006; Fricke and Rogers, 2000; Straight et al., 2004) or when analysing archaeological dentine or bone bioapatite (e.g. Britton et al., 2015a; Fisher et al., 2003; Fisher and Fox, 1998; White et al., 2004). Bioapatite phosphate is also often used in palaeoclimate reconstructions as early foundational work on the bioapatite δ^{18}O palaeothermometer was based on phosphate analyses (e.g. Bryant et al., 1994; Cormie et al., 1994; Fricke et al., 1995; Longinelli, 1984; Luz et al., 1990, 1984; Sánchez Chillón et al., 1994). Currently, bone or dentinal collagen are not routinely used for oxygen isotope analysis; although collagen may offer a more diagenetically robust substrate for δ^{18}O measurements of bone tissue compared to bioapatite carbonate, to date there is no consensus quality controls to assess diagenetic alteration in $\delta^{18}O_{coll}$ data (Crowley, 2015, 2014; Kirsanow et al., 2008; Tuross et al., 2008; von Holstein et al., 2013). Furthermore, concerns have been raised about isotopic alteration of collagen during collagen extraction and burial (von Holstein et al., 2018).

3.2 Sampling and analysis

For the incrementally forming dental tissues, analyses can be conducted on either a ‘bulk’ sample (yielding a single value) or on a series of sequential samples (producing multiple values). Bulk samples represent an amalgamation of isotopic input over a long period of time. Samples taken from the complete tooth length, for example, incorporate tissue and, therefore, isotopic input over the complete period of tooth formation. Researchers undertaking bulk samples are often seeking a long-term averaged value, perhaps representative of an annual average of inputs. However, samples of the complete tooth length can instead correspond to a time span of anywhere between a few months and a few years depending on the species and tooth selected and the extent of tooth wear (Brown et al., 1960; Hillson, 2005; Passey and

Cerling, 2002; Silver, 1963; Smith, 2000). Therefore, bulk sampling of dental tissues can easily create a seasonal bias in data depending on which portions of the tooth are sampled. Variations in ontogenesis, birth seasonality, tooth formation timing and tooth wear can all lead to certain seasons being over-represented in such samples. Sampling should therefore be undertaken in a way that ensures that isotopic inputs (and thus measurements) originate from either the same season, a complete year or multiple complete years (Hoppe et al., 2004b). This can usually be accomplished by sampling a fixed distance on a tooth in a consistent manner, informed by dental growth/mineralisation in the particular species in question (Britton et al., 2015b; Hoppe et al., 2004b).

Sub-samples taken as powder or cut strips along the growth axis of dental tissues yield a time series of δ^{18}O measurements that span the period of individual tooth formation or even across multiple successively growing teeth in the same individual (Balasse, 2002; Fricke et al., 1998; Fricke and O'Neil, 1996; Passey and Cerling, 2002; Sharp and Cerling, 1998). Sampling in this way invariably crosscuts incrementally formed and mineralised structures in both enamel and dentine; thus, single samples do not represent true biological increments (or isotopic 'events'), but should instead be considered arbitrary units in which a loosely known (and at least partially homogenised) amount of isotopic input signal is contained (Balasse, 2003; Zazzo et al., 2006, 2005). Due to the complex and discontinuous nature of amelogenesis, δ^{18}O values of sub-samples of enamel represent isotopic input that is both temporally offset and significantly time averaged compared to inputs during initial tooth growth (Balasse, 2002; Balasse et al., 2012b; Bendrey et al., 2015; Blaise and Balasse, 2011; Blumenthal et al., 2014; Green et al., 2017; Hoppe et al., 2004b; Montgomery et al., 2010; Passey and Cerling, 2002; Zazzo et al., 2005, 2010, 2012). Time averaging and temporal offsets are known to impact the amplitude of seasonal δ^{18}O time series and the position of isotopic 'peaks' and 'troughs' relative to the enamel root junction (ERJ) (Balasse, 2002; Balasse et al., 2002, 2012b; Bendrey et al., 2015; Green et al., 2018; Kohn et al., 1996; Kohn, 1996, 2004; Kohn and Cerling, 2002; Passey et al., 2002; Zazzo et al., 2005, 2010). This impacts the recovery of isotope data from teeth, and there has been extensive discussion of methodological approaches that could mediate these effects, including alternative sampling strategies and mathematical corrections (Bendrey et al., 2015; Blumenthal et al., 2014; Green et al., 2018; Hoppe et al., 2004b; Kohn, 2004; Passey et al., 2005a; Trayler and Kohn, 2016; Zazzo et al., 2005, 2012). In bone, while serial sampling is not possible due to remodelling (see section 3.1), differences in remodelling rates in different skeletal elements and/or bone regions have been exploited to access seasonality or mobility information, along with the sampling of individual osteons (Koon and Tuross, 2013; Lamb et al., 2014; Meier-Augenstein and Fraser, 2008; Tütken et al., 2004).

4 Applications to mammalian skeletal remains

From palaeoclimatic reconstruction to the inference of drinking habits of medieval kings, oxygen isotope analysis of human and animal remains is becoming increasingly common in the fields of archaeology and palaeoanthropology. Arising from seminal studies demonstrating the relationship between environmental (and thus drinking) water and mammalian tissues (see section 3.1), the determination of oxygen isotope values from bone and tooth found at archaeological sites is now one of the most commonly employed approaches in isotope bioarchaeology[3]. Although increasing cost-effectiveness has certainly enabled the expansion of the field (particularly in the case of the analysis of the carbonate component), the root of the increasingly widespread use of these approaches more likely lies in the diverse range of archaeological queries for which oxygen isotope data can be useful. Beyond their origin in palaeoclimatic investigations (perhaps the most literal relating of environmental conditions to animal tissue), oxygen isotope determinations can provide evidence for wild animal palaeoecology, past animal husbandry practices, human and animal movements, breastfeeding and other bio-cultural processes, and potentially even culinary practices. The

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[3] While common, oxygen isotope applications in bioarchaeology are still significantly dwarfed by carbon and nitrogen analyses of bone collagen for dietary reconstruction in terms of the sheer number of studies undertaken.

following sections of this review will explore the applications of oxygen isotope analysis to archaeological materials. Here, we explain the rationale behind the use of these approaches in these diverse contexts, explore the main methods (and materials) employed, highlight current trends and developments in each topic, and present example case studies. Oxygen isotope approaches intercept the environmental and the biological, the behavioural and the cultural, and the oxygen isotopic composition of archaeological human and animal remains is shaped by isotopic systems in all of these spheres. Through this, $\delta^{18}O$ values of human and animal tissues simultaneously have the potential to both illuminate and obfuscate these different aspects of the past, as their impacts are condensed into a single variable. These challenges, and others, and potential future developments are touched upon for each research area in turn and are further discussed in section 5.

4.1 Palaeoclimate

Environmental studies provide a pivotal framework for the exploration and contextualisation of human culture and behaviour in the past, and reconstructions of palaeoclimate and palaeotemperature have been a central theme in oxygen isotope analyses in bioarchaeology since the early days of the field. Given the relationship between local climate and the $\delta^{18}O$ of mammalian body water/bodily tissues via drinking water (see sections 3.1 and 2.1), the oxygen isotope analysis of mammalian bioapatite can serve as a powerful proxy for past palaeoclimatic conditions. At a single locality, the $\delta^{18}O_{bioapatite}$ of obligate drinking non-migratory animals can reflect the dominant climatic influence acting on $\delta^{18}O_{ew}$ at that place, including seasonal (enamel serial samples) and mean annual or supra-annual (bone or enamel bulk samples) conditions. In temperate environments at mid or high latitudes, the most common climatic influence is ambient air temperature (see section 2.1), and empirical regression formulae have been established to estimate air temperature from environmental water values (i.e. predicted drinking water values) for a number of regions, particularly in Europe (Arppe and Karhu, 2010; Lucy et al., 2008; Pryor et al., 2014; Rozanski et al., 1992; Skrzypek et al., 2016, 2011; Tütken et al., 2007). In an environment where $\delta^{18}O_{ew}$ is mostly temperature controlled, a positive correlation exists between the two, resulting in higher $\delta^{18}O_{ew}$ and (therefore higher $\delta^{18}O_{bioapatite}$) in warmer periods. In this way, faunal $\delta^{18}O$ values can be a very valuable tool for the reconstruction of terrestrial climatic conditions. By using non-migratory taxa, a distinctly local environmental signal can be obtained that contrasts with broader regional or global proxy climatic records, such as lake, marine or ice cores. Most importantly, by utilising anthropogenically modified faunal remains from archaeological sites, a direct temporal and spatial relationship with human activity is established – an advantage over almost all other available climate archives. Uncertainties associated with the cross-dating of archaeological sites and climate records is a challenge that is notoriously hard to overcome in climate reconstruction studies, but these issues are circumvented in the fauna-based isotope zooarchaeology approach. This approach allows the application of bioarchaeological climate research to questions about the environmental context of human activities and behaviours at specific archaeological sites and permits insight into high-resolution diachronic changes at those locales.

Bulk samples of faunal bioapatite (e.g. bones and bulk sampled teeth) represent multiple seasons/years of isotopic inputs and can therefore be used to reconstruct general and/or mean annual climatic conditions (see section 3.2). Bulk samples of faunal bioapatite have, for instance, been used to provide a framework for the exploration of human evolution and climate adaptations of Neanderthals and modern humans during the Late Pleistocene (Arppe and Karhu, 2010, 2006; Delgado Huertas et al., 1997; Fabre et al., 2011; Kovács et al., 2012; Richards et al., 2017; Skrzypek et al., 2011; Tütken et al., 2007). For example, using temperature reconstructions in conjunction with the analyses of archaeological material enabled Fabre and colleagues (2011) to show that a decrease in mean annual temperature (MAT) at La Baume de Gigny cave, France, during MIS 4 corresponded with decreased Neanderthal activity at the site, likely related to intermittent seasonal site use as a response to a more hostile environment. Similarly, $\delta^{18}O_{bioapatite}$-based temperature estimates for Upper Pleistocene Central Europe may show that Neanderthal migrations along the Odra occurred only during warmer periods of MIS 3 and MIS 5 (Skrzypek et al., 2011). This suggests a preference by Neanderthals for warmer climate zones, which is also indicated by some studies of site distribution patterns (e.g. Benito et al., 2017; Finlayson, 2008; Nicholson, 2017) although some studies have also produced results that indicate this may not always be the case (e.g. Nielsen et al., 2017). In this way, oxygen isotope climate reconstructions based on zooarchaeological remains (with their direct relationship to hominin activity) can shed light on the debate around the climatic resilience of Neanderthals and anatomically modern humans. Late Pleistocene palaeoclimate has also been explored using the oxygen isotope analysis of faunal remains in other contexts and regions. For example, in a study of marsupial tooth enamel from South Australia, $\delta^{18}O$ values demonstrated both lower temperatures and low humidity in the period between 100 and 50 ka BP than today (Forbes et al., 2010). In older palaeoanthropological contexts, other topics have been explored using these techniques. For instance, in deeper time, oxygen isotopes of non-anthropogenic faunal remains have been used to show that the temporary replacement of hominoid apes by cercopithecid monkeys in Europe during the late Miocene Vallesian-Turolian faunal turnover was likely not related to climatic change (Rey et al., 2013). Several studies of faunal tooth enamel $\delta^{18}O$, also from non-anthropogenic contexts, have also been devoted to exploring the Eocene-Oligocene transition in North America and demonstrate a pronounced temperature drop and increase in seasonality around 400,000 years ago (D'Ambrosia et al., 2014; Zanazzi et al., 2015, 2007).

As well as faunal remains, the oxygen isotope analysis of human remains has also been employed to investigate climatic change. For example, phosphate from bulk samples of human tooth enamel has been used to explore the local impacts of more recent climatic excursions, such as the Little Ice Age (Daux et al., 2005; Fricke et al., 1995). Generally, however, in archaeological and palaeontological studies the use of ungulate remains is more common.

While functioning predominantly as a temperature proxy in mid- and high-latitude environments, mammalian bioapatite $\delta^{18}O$ has also been used to evidence rainfall amount and monsoon activity in tropical or monsoon environments (Dettman et al., 2001; Higgins and

MacFadden, 2004; Li et al., 2017; Nelson, 2005). For example, these techniques were used to indicate that changes in monsoon intensity were not responsible for the decline of the Bronze Age Harappan culture in India, as had been previously thought (Sarkar et al., 2016).

Climate data from ancient faunal remains are equally valuable in palaeoecological studies, where a direct relationship with faunal accumulations and animal dietary information can be established. Tütken and colleagues have, for example, exploited this to investigate the palaeoecology of mammoths during the Late Pleistocene (Tütken et al., 2007) and to characterise a Middle Miocene lake ecosystem (Tütken et al., 2006). Influences of monsoon activity on herbivore diet and ecosystem in the Linxia Basin during the late Cenozoic were explored by Biasatti et al. (2010). As part of a recent study, González-Guarda et al. (2017) used δ^{18}O of faunal remains from Late Pleistocene Patagonia to show that that the presence of gomphothere megafauna (elephant-like proboscideans) in this region was likely restricted to warmer periods characterised by mean annual temperatures that are close to present day conditions. The gomphotheres examined also appear to have been less climatically tolerant than previously assumed.

While isotope studies using archaeological mammalian skeletal remains (both anthropogenically derived and natural accumulations) to evidence climatic conditions can contribute to a range of archaeological and palaeoecological queries, close consideration must be given to species/skeletal components targeted and other aspects of sampling strategy. Studies of temperature and rainfall amount, for example, should utilise taxa that are obligate drinkers, as they are likely to have consumed water with an isotopic composition more closely related to that of precipitation (Kohn, 1996; Kohn et al., 1996; Luz et al., 1984). Taxa that are less dependent on water and that mostly meet their water needs through the water in plants, such as caprines or cervids, particularly in arid environments, are often unsuitable for exploration of temperatures and rainfall amount. This is because leaf water isotope signatures can superimpose and therefore obscure relationships with precipitation δ^{18}O (Ayliffe and Chivas, 1990; Cormie et al., 1994; Levin et al., 2006; Luz et al., 1990; Makarewicz and

Pederzani, 2017). However, this can also be turned to an advantage in studies wishing to investigate aridity. For instance, Levin and co-workers (2006) developed a measure of aridity from faunal oxygen isotopic data by analysing the ^{18}O-enrichment in bioapatite of evaporation sensitive taxa (ES; i.e. non-obligate drinkers) over evaporation insensitive taxa (EI; i.e. obligate drinkers), $\varepsilon_{ES\text{-}EI}$. Aridity, as represented by the water deficit metric, was then established based on a regression between $\varepsilon_{ES\text{-}EI}$ and water deficit metrics obtained from a modern comparative data set. This method was recently refined by Blumenthal and colleagues (2017) through the production of a large comparative modern data set. Additionally, a recent study has indicated that aridity indices may benefit from the inclusion of palaeodietary information from other isotope proxies, such as δ^{13}C, to account for changes in water needs related to the type of diet consumed (Faith, 2017; but see Blumenthal et al., 2018, and Faith, 2018 for discussion). Other researchers have also used investigations of leaf water reliant taxa, such as caprines, as well as comparisons between browsers and grazers to more informally explore aridity (e.g. Reade et al., 2016; Robinson et al., 2016). It should be noted, however, that some studies evaluating the sensitivity of deer δ^{18}O to aridity have returned varying results (e.g. Cormie et al., 1994; Luz et al., 1990; Stevens et al., 2011), possibly related to differences in case study location or environment and animal diet.

Although humans are obligate drinkers, they employ a range of water sourcing and culinary practices that mean liquids consumed may not wholly reflect local environmental water (see section 4.6). This, along with the unnecessary destruction of human skeletal material (where ungulates could be used instead), make the use of archaeological human skeletal materials to evidence local climate generally undesirable. Additionally, the isotopic time-averaging effects of the timing and geometry of human enamel maturation is poorly understood and varies between teeth, making it difficult to estimate if ‘bulk’ human enamel samples can give an oxygen isotope value that is representative of mean annual conditions unbiased towards a certain season (Boyde et al., 1989; Bryant et al., 1996a; Montgomery, 2010; Smith and Tafforeau, 2008). As mentioned in section 3.2, this is also a concern in hypsodont teeth, but can be circumvented by sampling a specific length of enamel known to more or less correspond with one year of growth (Britton et al., 2015b; Hoppe et al., 2004b). In human teeth, such strategies have not yet been established and, indeed, due to the more complicated enamel geometry and slow tooth development of human teeth (coupled with a lack of restricted birth seasonality often seen in other mammals), this may not prove methodologically possible. Further study and the use of consistent sampling strategies are necessary to avoid seasonally biased δ^{18}O signals derived from human tooth enamel which could influence the use of oxygen isotope analysis for other purposes, for example in mobility studies.

In addition to reconstructing mean annual conditions using bulk samples, δ^{18}O time-series data obtained through the serial sampling of teeth can be used to explore climatic fluctuations on a sub-annual scale, revealing seasonal climatic information (Figure 4). With enamel, as discussed in section 3.2, the time resolution achievable and the magnitude of signal averaging per sample taken largely depends on the speed and geometry of enamel maturation in that particular species and tooth, along with the size, shape and location of the sub-samples. However, in most herbivores a resolution in the order of weeks is commonly obtainable, albeit with some signal mixing and attenuation, allowing the study of sub-seasonal patterns of δ^{18}O change.

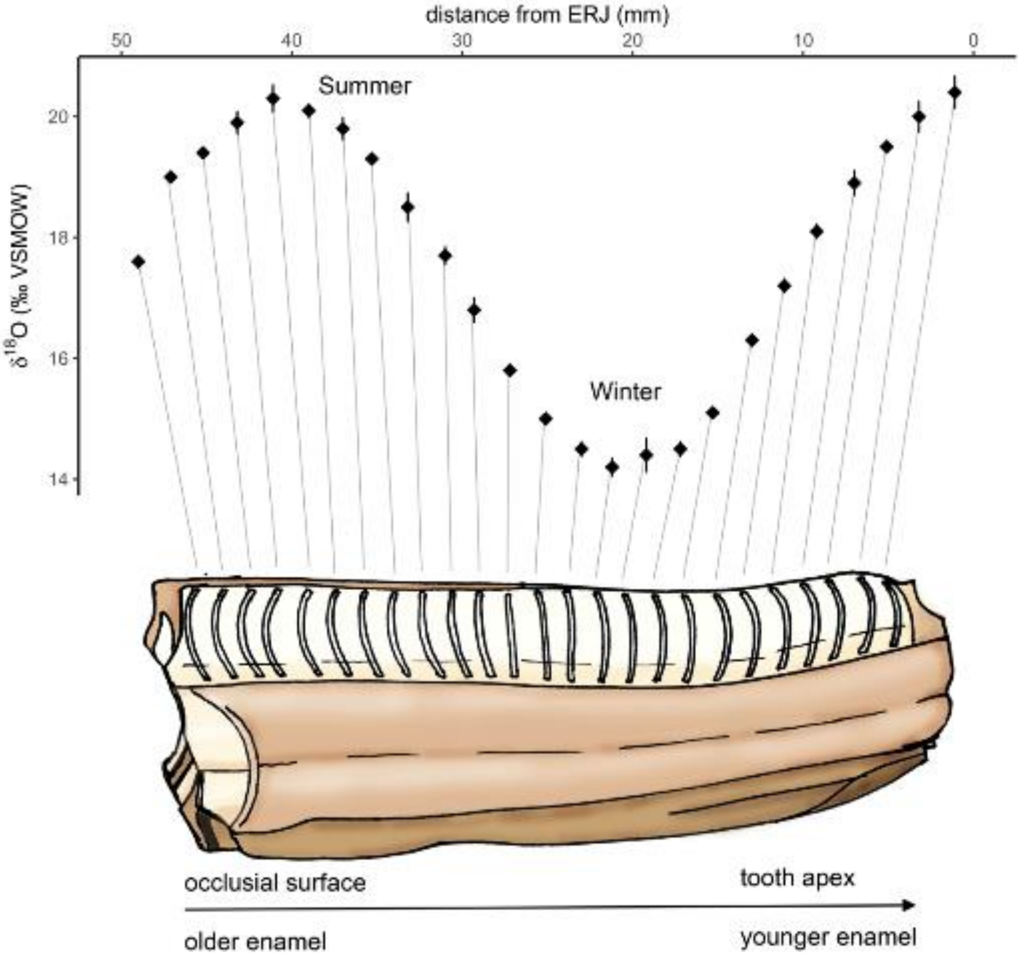

Figure 4: Series of δ^{18}O measurements (black diamonds) of serial samples taken from the occlusal surface (left) to the enamel root junction (ERJ; right) yield time-series oxygen isotopic information and record seasonal fluctuations in $\delta^{18}O_{ew}$ in obligate drinking hypsodont herbivores, such as horses. In environments dominated by the temperature effect, these fluctuations commonly present themselves as sinusoidal curves, with high δ^{18}O values corresponding to the summer months and low values to winter months.

The possibility of extracting seasonal climate data was first explored in proof-of-concept studies using modern day animals from a variety of different climates (e.g. Bryant et al., 1996a; Fricke et al., 1998; Koch et al., 1989). Due to the positive relationship between air temperature and $\delta^{18}O_{ew}$ and $\delta^{18}O_{bioapatite}$, in mid- and high-latitude environments seasonal temperature fluctuations result in sinusoidal δ^{18}O time-series patterns in obligate drinkers consuming local water, with maximum values corresponding to summer months. In monsoon and tropical environments, where amount effects dominate seasonal $\delta^{18}O_{ew}$ patterns, minimum values are instead observed during the summer, when the majority of precipitation falls (Biasatti et al., 2010; Higgins and MacFadden, 2004). Information on maximum and minimum temperatures throughout the year gleaned in this way have, for instance, contributed significantly to a better understanding of the conditions faced by hominins during the last glaciation (Bernard et al., 2009; Fabre et al., 2011; Velivetskaya et al., 2016). For instance, Fabre et al. (2011) demonstrated that a decline in Neanderthal activity at a site in eastern France during MIS 4 (late Middle Palaeolithic) was related to very low winter temperatures, while summer temperatures were comparable to modern day conditions. Such approaches have also been used in palaeontology, and in deeper time, for example to highlight the role of changing seasonality in shaping the Eocene-Oligocene transition in central North America (D'Ambrosia et al., 2014; Zanazzi et al., 2015).

Due to the amount effect, seasonal rainfall patterns have been reconstructed using $\delta^{18}O$ time-series data. These have been applied in palaeoanthropological contexts, for example, to elucidate the habitat and adaptation of the Miocene hominoid *Sivapithecus* (Nelson, 2005). Seasonal rainfall amounts have also been investigated at Neanderthal and modern human sites in the Levant using these techniques in order to elucidate climatic conditions faced by hominins in this location (Hallin et al., 2012). In far more recent periods, these techniques have been employed to investigate monsoon strength in the Ganga plain, India, in the late Holocene, with results indicating that cultural changes visible in the archaeological record over the last 3600 years coincide with changes in monsoon strength (Sharma et al., 2004).

However, while seasonality information is extremely valuable, even in relative terms, the determination of absolute temperature estimates can prove challenging. The method of sampling, the buffering effect of the body water reservoir, as well as the prolonged process of enamel mineralisation, cause attenuation (dampening) of the seasonal curve, which has also been demonstrated to vary between different species (Balasse et al., 2002; Kohn, 2004, 1996; Kohn et al., 1996; Kohn and Cerling, 2002; Passey et al., 2002; Zazzo et al., 2005).

Attenuation effects can be partially corrected mathematically (Kohn, 2004; Passey et al., 2005a), although such approaches are not consistently applied across the field and attenuation estimates vary within single taxa and in different teeth of the same species. Furthermore, as constant growth rates cannot be assumed in the dental enamel of certain species (e.g. horses), it may also be necessary to rescale not only the amplitude but also the period of the sinusoidal signal of serial data using exponential models (Bendrey et al., 2015).

Whether employing bulk or sequential sampling, by far the biggest challenge facing palaeoclimate studies employing the oxygen isotope analysis of preserved mammalian skeletal remains from archaeological and palaeontological contexts, particularly those seeking to reconstruct palaeotemperatures, is the uncertainties and compound errors surrounding the conversion of bioapatite δ^{18}O data to estimated temperatures. Such conversions of tissue δ^{18}O to local air temperature rely on empirical linear regression formulae established using modern day specimens through a statistical fitting procedure. Normally, the overall regression from $\delta^{18}O_{bioapatite}$ to air temperature is achieved by combining a species-specific regression from $\delta^{18}O_{bioapatite}$ to δ^{18}O of drinking/environmental water ($\delta^{18}O_{ew}$) with a separate, regionally-specific regression from $\delta^{18}O_{precip}$ to air temperature by assuming equivalence of $\delta^{18}O_{ew}$ with $\delta^{18}O_{precip}$ (Arppe and Karhu, 2010; Fabre et al., 2011; Pryor et al., 2014; Skrzypek et al., 2016, 2011). As many drinking water conversion formulae are based on bioapatite phosphate data, an additional empirical conversion from carbonate to phosphate values is sometimes necessary when using carbonate data (Bryant et al., 1996c; Chenery et al., 2012; Iacumin et al., 1996; Lécuyer et al., 2010). There are several statistical options to conduct regression fitting, as well as to calculate the uncertainty of the final temperature estimate, the merits of which have been debated by Pryor et al. (2014) and Skrzypek et al. (2016) at length and are therefore not covered in detail here. On the basis of cross validation criteria, Skrzypek et al. (2016) recommend use of a transposed fit least squares model. Both the Pryor and Skrzypek publications highlight the effect of the propagation of errors from various sources across the temperature prediction formula. In addition to the error involved in the regression itself, measurement uncertainty and uncertainty from the normalisation procedure (as well as from differences in pretreatment and analytical methods selected, see section 1.2) will propagate to produce larger total error of the temperature prediction. It is therefore advisable to keep such procedures as consistent and transparent as possible and to follow best practice in reporting stable isotope data (see recommendations in Szpak et al., 2017). While measurements of $\delta^{18}O_{carb}$ are more precise than those of phosphate, Skrzypek et al. (2016) found that the conversion to phosphate values increases the temperature estimate error in such a way as to make up for this advantage. Use of $\delta^{18}O_{phos}$ is therefore recommended in studies that are keen to elicit palaeotemperature predictions.

In addition to aspects of statistical and laboratory procedures, there are also concerns about how applicable the species-specific drinking water conversions and the regional $\delta^{18}O_{precip}$ to temperature conversions are to archaeological studies. Firstly, as outlined in section 2.1, the slope of the linear relationship between $\delta^{18}O_{precip}$ and air temperature is not universally the same, but instead varies with region. This can be accounted for by using separate prediction equations for different locations. However, due to the influence of atmospheric circulation on this equation, the slope can also vary through time, as circulation regimes and the seasonality of precipitation change (Aggarwal et al., 2012; Akers et al., 2017; Field, 2010; Kohn and Welker, 2005). To address this, cross checks with other climate proxies, as well as with isotope circulation models, can be employed to validate the regression (see for example Sturm et al., 2010 on validation using circulation models).

Secondly, there are also some questions as to how the equations to calculate drinking water $\delta^{18}O$ may vary across populations and between individuals. Studies by Pollard et al. (2011) and Daux et al. (2008) have shown that predicted drinking water values can carry substantial error rates of 1–3.5 ‰ at 95% confidence level and, in cases where several studies have been carried out to determine the species-specific regression equation, results differ from study to study, sometimes substantially so. This not only opens up the question of which equation to use, but also indicates that some regional, population or even individual level differences determine the exact nature of the regression equation. These are likely dietary behaviours, selection of drinking water source, as well as physiological and metabolic variability within nature.

The above issues in particular highlight concerns about how researchers can make sure that conversion equations are transferable to past populations. After all, the application of conversion models assumes that past animals are physiologically and behaviourally identical to their modern counterparts, which may not be the case. Isotope zooarchaeological investigations of palaeoclimate must, for example, make assumptions concerning the growth of faunal tissues and rely on the predictability of animal behaviour within known ecological bounds. Ideally, both of these assumptions should be queried and, wherever possible, aspects of past animal behaviour, physiology and ontogeny should be substantiated with additional lines of evidence. Furthermore, given the diverse range of human subsistence behaviours and/or animal husbandry strategies employed (past and present), data from both humans and domestic fauna could be particularly prone to biases due to unpredictable or unknown dietary or drinking behaviours. Perhaps partially because of this, studies of palaeoclimate using faunal remains have largely focused on the Pleistocene where human management of animals is either non-existent or minimal compared to later time periods. It should be noted, however, that conservatism in dietary and ranging behaviour should also not be assumed in wild fauna, particularly in the context of the profound environmental fluctuations experienced globally during the Pleistocene and early Holocene, and modern analogues are insufficient for the inference of Pleistocene faunal palaeoecology (see discussion in Britton, 2018). Human management of animals, however, certainly has the potential to introduce far more extensive changes and unpredictable animal behaviours in terms of mobility, reproductive patterns, diet and drinking behaviour that prevent faithful reflection of environmental conditions. These may, however, open the door to investigations of group variability, behavioural plasticity and management practices. To alleviate such concerns in palaeoclimate research and to independently explore palaeoecological and zooarchaeological questions, studies can consult other types of stable isotope data (e.g. carbon isotope ratios to evidence feeding strategies) or other evidence, such as patterns of dental microwear to evidence browsing or grazing in herbivores (Rivals et al., 2008).

4.2 Elucidating diet and drinking behaviours in animals

Diet and drinking behaviour are central aspects of an animal's ecological niche and evolution, and, in domesticated species, can also give an indication of how animals are managed by humans. Wild and domesticated herbivores, for example, may display plasticity of behaviour in response to environmental influences, such as varying the extent to which they browse or graze, or other aspects of dietary ecology. Such behaviours and differences in ecological niche can then be expressed in 'bulk' oxygen as well as carbon or nitrogen isotopic values. For example, in a study of late Pleistocene fauna from Valdegoba cave in northern Spain, Feranec et al. (2010) suggested differences in water use between different carnivore species as well as a higher drought tolerance of *Capra pyrenaica* compared to other herbivores. Similarly, García García and colleagues (2009) used 'bulk' oxygen isotopic analyses to explore niche partitioning among Middle Pleistocene herbivores in northern Spain, with δ^{18}O and δ^{13}C indicating that *Dama dama* foraged in more forested environments than other herbivores. At the same time, oxygen isotope data from sequentially sampled tissues can – through providing a point of reference in time – be particularly useful as a seasonal anchor for concurrent dietary isotope signals from carbon or nitrogen isotope analyses. A combination of oxygen and carbon isotope data derived from incremental dental enamel samples has been used, for instance, to illuminate the seasonal dietary ecology of bison in early and mid-Holocene North America (Gadbury et al., 2000; Widga et al., 2010) and Miocene bovids in Afghanistan (Zazzo et al., 2002).

In domestic fauna, feeding behaviours often reflect the resources made available to livestock by humans and the ways in which animals are integrated into human subsistence strategies, economies and everyday life. Combined isotope approaches, particularly oxygen and carbon data from tooth enamel, can be used to identify a broader spectrum of resources available to domestic fauna. For instance, using oxygen, carbon and nitrogen isotope analyses of 'bulk' bone collagen, a changed isotopic niche due to herding and foddering strategies has been suggested for Pre-Pottery Neolithic goats in Jordan (Makarewicz and Tuross, 2012). Bulk δ^{18}O values of bioapatite in conjunction with carbon and nitrogen isotope analyses have also been interpreted as evidence for the consumption of high δ^{18}O water from human-managed water reservoirs in Camelids in pre-contact Peru (Tomczyk et al., 2018). In addition to 'bulk' sampling approaches, time-series data from serial samples can be especially useful for investigating the seasonality of certain animal husbandry practices in the past. Many herders and livestock keepers, for example, seasonally provision animals with previously collected and stored fodder to bolster animal diet during challenging times, such as over the winter months. Foddering varies in timing and intensity, often related to herd structure; fodder availability; broader subsistence, economic and social goals; as well as the physical condition, age and sex of the animals. In highly seasonal environments and/or intensive husbandry systems in particular, foddering is essential to sustain animals and to reduce risk to herds (and therefore the subsistence base) and helps to achieve long-term production goals.

Using oxygen and carbon isotope time-series data, Balasse and co-workers have conducted several studies in order to explore the incidence of seaweed foddering in sheep in prehistoric Orkney, Scotland – an unusual and rare animal husbandry practice found today in the Orkney Islands, as well as in areas of France and Iceland. The higher δ^{13}C values present in seaweed compared to terrestrial plants, combined with δ^{18}O data, allowed the researchers to determine that seaweed foddering has been seasonally practised in Orkney since the Neolithic period (Balasse et al., 2009, 2006). In another Neolithic study, this time of cattle teeth from the site of Bercy, France, uncharacteristically low δ^{13}C values correlated with low (winter) δ^{18}O values, which has been interpreted as evidence of leaf foddering from closed canopy forests (Balasse et al., 2012a). In other environments, where both C3 and C4 plants are found, the seasonal growth of isotopically distinct, high δ^{13}C C4 grasses can be exploited to detect provisioning with fodder collected during the summer (see an example of this in Figure 5; see also Makarewicz, 2014 and Makarewicz and Tuross, 2006). Similar patterns have been shown at a Late Chalcolithic Tell site in Romania (Gillis et al., 2013), in several pre-pottery Neolithic-B (PPNB) sites in southern Jordan (Makarewicz, 2017), as well as amongst Indus cattle from Gujarat, India (Chase et al., 2014).

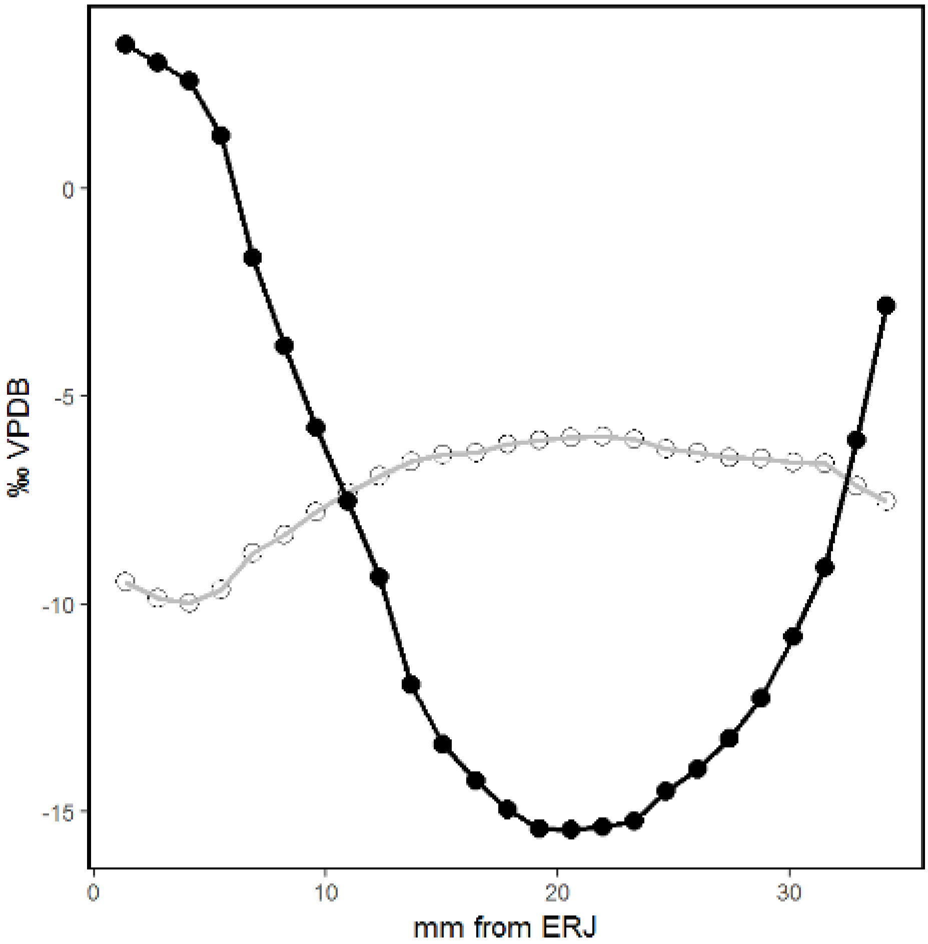

Figure 5:In environments with both C3 and C4 plants, foddered livestock may show high δ^{13}C values during winter (indicated by low δ^{18}O) if they are provisioned with C4 rich, high δ^{13}C fodder collected by herders during the summer, when C4 plants are naturally more abundant (data from Makarewicz and Pederzani, 2017).

In many of the case studies explored above, δ^{18}O is used to seasonally contextualise a dietary signal contained in δ^{13}C; however, it should be noted that feeding habits can also profoundly impact herbivore δ^{18}O values themselves. In herbivores, this is largely due to the impact of leaf water consumption, although it should be noted that a similar 'decoupling' of tissue δ^{18}O and $\delta^{18}O_{ew}$ is also common for non-obligate drinking predators, as has been observed in North American felids (Pietsch et al., 2011; Pietsch and Tütken, 2015). Therefore, amongst herbivores at least, dietary δ^{13}C information is often critical to contextualise and interpret δ^{18}O values (but see Blumenthal et al., 2018 for discussion of limitations). Leaf water is generally ^{18}O-enriched above environmental source water (see section 2.3), and browsing species that consume large quantities of leaves, relying on them as their primary source of water, often display elevated $\delta^{18}O_{bioapatite}$ values compared to their grazing (and often obligate-drinking) counterparts (Kohn et al., 1996; Robinson et al., 2016; Sponheimer and Lee-Thorp, 1999; Stowe and Sealy, 2016). However, in some cases, where both grazing and browsing taxa meet almost all water requirements through leaf water, a reverse scenario with higher δ^{18}O values in grazers (relative to browsers) can occur (Bocherens et al., 1996; Makarewicz and Pederzani, 2017). This is brought about by the higher degree of leaf water enrichment in grasses, particularly C4 grasses, compared to dicotyledonous plants (see section 2.3) (Makarewicz and Pederzani, 2017). At the same time, dietary changes in herbivorous taxa through time can alter how dependent animals of a certain species are on drinking water and therefore how susceptible they are to leaf water enrichment signals (Faith, 2017). Studies, especially those including non-obligate drinking herbivorous taxa, therefore greatly benefit from the dietary information contained in δ^{13}C in order to clarify potential dietary impacts on δ^{18}O, while the combination of the two isotopic systems has the power to highlight seasonality of diet as part of animal husbandry systems or wild animal ecological niches.

4.3 Seasonality and season of birth

Due to the limited lactation period in dairy livestock following parturition, the timing of animal births in these ungulates strongly determines the season and length of milk availability. Herders may therefore choose to stagger the births of new animals by controlling mating times in order to extend the period of milk yield into the autumn and winter season. If environmental (and animal physiological) constraints allow, this can even extend as far as creating multiple birthing seasons, usually in spring and autumn, or continuous births year-round, in some species. Analysis of animal birth season and seasonality therefore provides key insights into the structure of dairy economy and the strategies employed by livestock herders in the past.

In order to estimate the season of birth in ungulates, such as cattle and sheep, intra-tooth 'seasonal' shifts in δ^{18}O (linked to seasonal shifts in $\delta^{18}O_{ew}$) are used in conjunction with tooth eruption times. By measuring the position of seasonal δ^{18}O peaks and troughs along the tooth crown in relation to the enamel root junction (ERJ; which forms at a known time in the life of many common domestic ungulates), it is possible to estimate in which season the tooth was formed. Differences between individuals can indicate whether animals were born in the same season or not (e.g. Balasse et al., 2012b, 2012a, 2003; Frémondeau et al., 2012). Archaeological data are then compared to data from modern animals of known birth seasonality, and thus season of birth can be inferred. Using this approach, Balasse et al. (2003) demonstrated the presence of two separate birthing seasons in Late Stone Age sheep in South Africa. This study, as well as most earlier studies, relied mainly on qualitative visual assessment of data according to location of seasonal maxima on the tooth crown, in conjunction with those modern reference sets of animals with known birth timing (e.g. Balasse et al., 2003; Balasse and Tresset, 2007; Blaise and Balasse, 2011; Henton et al., 2010; Towers et al., 2011), revealing inter-individual variability and grouping animals into 'seasons' (see Figure 6 for an example of two birthing seasons). This is still the case for studies that are mostly interested in uncovering the number of birthing seasons, often termed 'birth seasonality' (e.g. Buchan et al., 2016; Gron et al., 2015; Henton, 2012). Using these techniques, herding systems with multiple birthing seasons have been identified for early Neolithic funnel beaker cattle husbandry in Scandinavia and in Early Bronze Age Britain (Gron et al., 2015; Towers et al., 2011). Investigations of sheep in late Roman and medieval Flanders revealed an absence of manipulation of birth season, in accordance with a proposed economic focus on wool production instead of dairy (Buchan et al., 2016). It should be noted, however, that birth seasonality is more complex to manipulate in sheep (being strongly dependent on photoperiod) than in cattle and goats, which are less seasonal breeders (Balasse et al., 2003) and that a pronounced economic and subsistence importance of dairy production can also be achieved without manipulation of birth season, which is a fairly high risk strategy.

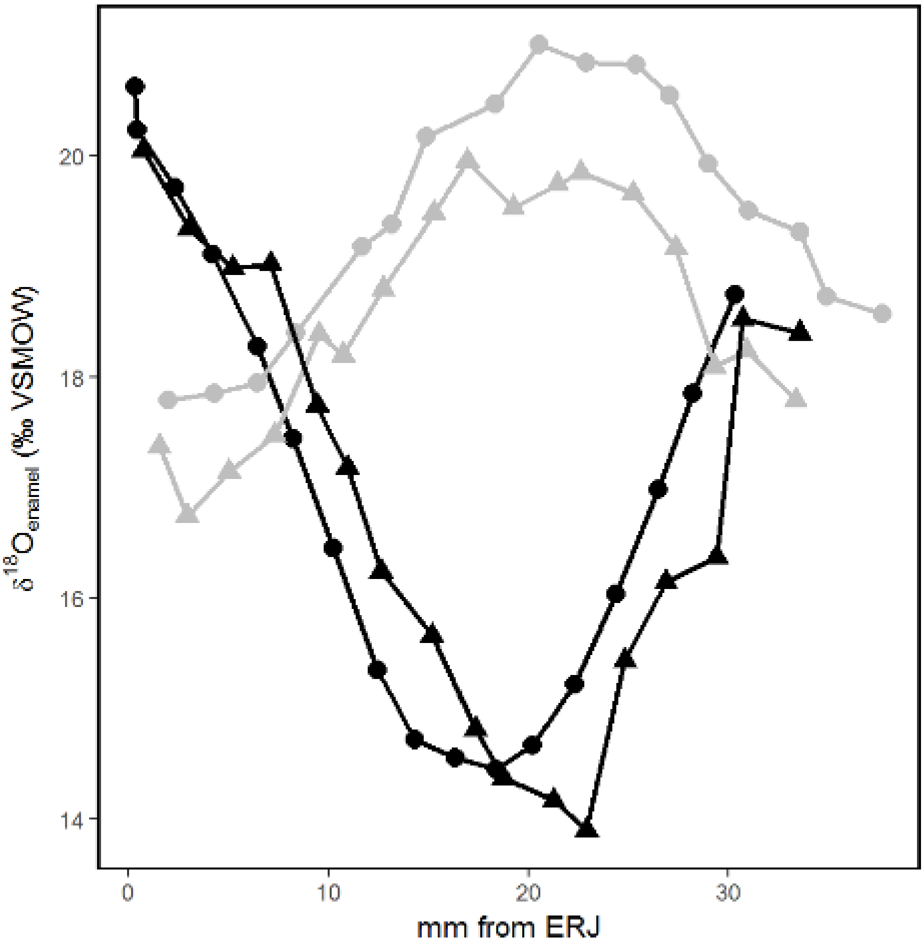

Figure 6: Two distinct birthing seasons (black points versus grey points) manifest in the different positions of δ^{18}O seasonal peaks and troughs on the tooth axis. This fictitious example (data generated using random numbers and sine functions) resembles a herd with a spring (black) and autumn (grey) birthing season, assuming a ~6 month offset between tooth growth and full enamel mineralisation.

Recently, studies have extended this approach to yield data that can lead to the more precise assignment of season of birth and quantify the spread of the birthing season. In order to help achieve this, and again using modern reference samples, the Balasse group introduced a method for removing influences of crown height variability (not due to wear). Differences in crown height had previously led to great uncertainties in estimating season of birth, as large inter-individual differences in the crown height of unworn teeth (as well as overall tooth size) tend to obscure the impact of subtle differences in season on variability of the distance of δ^{18}O seasonal extrema from the ERJ (e.g. Balasse et al., 2012b; Blaise and Balasse, 2011). Removal of the influence of crown height is achieved by using information from a δ^{18}O time-series model using non-linear regression based on a cosine curve.

From this model, the distance on the tooth representing one year is extracted and the distances of δ^{18}O minima that are used for determining birth season are normalised by dividing by this measure, removing the influence of crown height while simultaneously translating ERJ distances into a time measurement (Balasse et al., 2012b). Analysis of a modern reference group of sheep from the Orkney Islands confirmed that this method could accurately identify season of birth using the δ^{18}O series of the second mandibular molar with an uncertainty of less than 6 weeks. This 6-week residual uncertainty is mostly related to inter-individual differences in tooth formation timing relative to birth and normal differences in the timing of birth within a cohort (Balasse et al., 2012b). Similar models for predicting birth seasonality have also been devised for cattle teeth, albeit using different approaches based around the combining of δ^{13}C and time-series data, exploiting the slight differences in δ^{13}C between ruminants and non-ruminants due to their different digestive systems (Towers et al., 2014). The full development of the rumen digestive system in cattle takes place shortly after birth and can be detected as a small shift to higher δ^{13}C values in tooth enamel (Cerling and Harris, 1999; Hedges, 2003; McDonald et al., 2010; Metges et al., 1990; Passey et al., 2005b; Towers et al., 2014). In the model proposed by Towers and colleagues, this change can then be cross-related to the seasonal information (δ^{18}O), specifically the position of the first δ^{18}O peak, in order to determine the seasonal timing of birth. The strong linear correlation of the estimated birth timing from this method with the results generated by Balasse's model suggests that this is also a valid approach for ruminants (Towers et al., 2016, 2014). However, no extensive testing on a modern reference population of known birth season was conducted and slight uncertainties concerning tooth crown height and tooth development timing remain. Nonetheless, both of the above modelling approaches have served to greatly improve the quality of season of birth information that can be extracted from δ^{18}O time-series data from cattle and sheep, and even pigs (e.g. Frémondeau et al., 2012), while allowing better insight into the resolution that is achievable using such methods.

Subsequently, these modern reference data sets and models have permitted very valuable insights into past herd management for dairy production. For example, for cattle at the Neolithic site of Bercy, France, (Balasse et al., 2012a) and in Eneolithic sheep from Cheia, Romania (Tornero et al., 2013), moderate extensions of birthing season compared with that of a modern population were found. However, due to the fairly small differences observed in both studies, it remains unclear if this variability was affected by prehistoric herders or was instead rooted in the natural variation of birth seasonality due to environmental differences which are not apparent in modern managed herds. In another example, the management of cattle for year-round production of fresh dairy could be identified through strong staggering and multiple seasons of birth in Iron Age and Scandinavian Interface Period sites on the Orkney Islands, where climatic conditions usually preclude extended birthing seasons (Towers et al., 2016). Given the evidence for animal foddering in prehistoric Orkney (e.g. Balasse et al., 2009), it seems likely that such practices were necessary to underpin a husbandry system with well-managed, staggered birthing seasons, underlining the great importance of – and the investments made for – dairy production (Towers et al., 2016).

4.4 Mobility and provenancing

One of the most common applications of oxygen isotopic analysis in archaeological research is the exploration of human and animal mobility and provenance. Usually in combination with strontium isotopes or other ‘mobility’ indicators (e.g. lead isotopes), this approach exploits the geospatial patterns in $\delta^{18}O$ of environmental water and the preservation of such signals in biological tissues of different remodelling and formation periodicities. Mobility can be investigated in different ways using the isotopic composition of animal or human bones and teeth, yielding information on different temporal and spatial scales. Some approaches focus on characterising residential mobility or migration over the lifetime of an individual, or overall range or territory size in fauna, while methods employing sequential sampling can highlight higher resolution timescales and seasonal mobility. As well as the examination of individual lifetime histories, using the same technique of comparing place of burial (or deposition) with place of origin (as inferred by the isotopic composition of tooth or bone tissue), the provenance of animal remains can also be interpreted in the context of animal trade or exchange, either as meat or as artefacts manufactured from tooth or bone. In this way, the origin of faunal funerary offerings can also be explored and social networks surrounding the burial rite can be elucidated.

4.4.1 Seasonal patterns of mobility in fauna

Reconstructions of seasonal-scale movements of past herbivore populations inform central aspects of palaeoecology, faunal resource exploitation and animal husbandry. Knowledge of the movement behaviours of prehistoric prey species enables us to explore how past human groups exploited the faunal resources around them, what hunting strategies they employed and the interactions between subsistence behaviours and the broader environmental and ecological setting. Reconstructing the palaeoecological behaviours of prey species can also help us better understand the relationships between subsistence activities, hominin mobility patterns, seasonality of site occupation and social and resource networks. In livestock-keeping societies, seasonal movement can also be a central component of a variety of animal husbandry strategies, particularly amongst mobile pastoralist communities (Aguilar et al., 1994; Bacon, 1954; Chang, 2006; Fernandez-Gimenez and Le Febre, 2006; Fratkin, 1994; Kerven et al., 2004; Oba and Lusigi, 1987). In seasonal or marginal environments in particular, herders may choose to move animals on a seasonal basis to provide better access to pasture and in order to ‘escape’ seasonal extremes. In mobile pastoralist communities, movement of animals and people also often follows social, political and cultural practices, intertwined with subsistence and husbandry decisions. Through the reconstruction of how, when and where animals were moved, we can better understand prehistoric herder decision-making and the complex interplay of subsistence strategies within broader economic, social and political contexts.

One of the first studies to utilise the sequential sampling of herbivore teeth in order to glean information on seasonal mobility patterns focused on prehistoric herders in South Africa (Balasse et al., 2002). In the study, sequential enamel oxygen isotope data were used to provide a cyclical seasonal context for the geospatial information obtained from strontium isotope analysis (Balasse et al., 2002). Dual isotope approaches are still commonly used (e.g. Britton et al., 2009; Chase et al., 2014; Evans et al., 2007; Valenzuela-Lamas et al., 2016; Widga et al., 2010). While a time lag of unknown magnitude between δ^{18}O and strontium isotopic compositions (due to the long residence time of strontium in the body) may introduce some uncertainties in the inference of season of movement using oxygen isotopes (Montgomery et al., 2010), overall good correlation between the two isotopes have been observed in modern animals of known origin and migration route (Britton, 2009; Britton et al., 2009). These isotopic systems can therefore be useful together, through analysis of their general co-variation (or lack thereof), in assessing the extent and directionality of mobility strategies.

Changes in δ^{18}O alone may also be useful to infer mobility patterns; however, this is the subject of ongoing methodological research and academic discussion. For example, a number of researchers have argued that oxygen isotope data may be able to evidence ‘mobility against the season’ in certain circumstances. In this model, employed mostly to reconstruct the movements of domesticates/managed animals, mobile herders drive their animals in a seasonal pattern that aims to reduce climatic and environmental extremes, particularly in marginal environments such as steppes, deserts or mountainous regions. This could also be true of wild long-distance thermostressed migratory taxa, such as caribou. In these circumstances, animals would be expected to move to 'cooler' regions during the summer months and 'warmer' regions in the winter. In summer, this can be achieved by moving to a higher latitude or a higher altitude, both of which entails relocation to areas characterised by comparatively low δ^{18}O values in environmental water (Bowen and Wilkinson, 2002; Dansgaard, 1964; Rozanski et al., 1993). The intra-tooth profiles of such animals, whether domestic or wild, should deviate from the seasonal sinusoid δ^{18}O curve of a stationary animal and exhibit substantially reduced intra-tooth δ^{18}O variability, as has been demonstrated in modern comparative work (Britton et al., 2009) and, on this basis, argued for in archaeological case studies (Henton, 2012; Henton et al., 2014, 2010; Pellegrini et al., 2008; Pilaar Birch et al., 2016). On the basis of this, mobility against the season has been proposed for some sheep from the pre-ceramic layers of Çatalhöyük (Henton, 2012; Henton et al., 2010), Late Upper Palaeolithic red deer in the northeaster Adriatic region (Pilaar Birch et al., 2016), as well as to some degree for red deer in the Epigravettian of northern Italy (Pellegrini et al., 2008). In an alternative approach, a higher level of inter-animal variability in $\delta^{18}O_{bioapatite}$ has been put forward as an indicator of transhumant activities, due to animals having access to water outside of the 'local' range (Mashkour, 2003). However, others have argued that reduced intra-group variation is consistent with non-migratory behaviour, for example in late Pleistocene European Bison (Julien et al., 2012).

Although some differences in data interpretation are to be expected due to differences in the spatial patterns of $\delta^{18}O_{ew}$ at different sites (based on local hydrology and topography), the case studies above highlight the difficulties inherent in the use of intra-tooth oxygen isotope data to identify past seasonal movement patterns without reference to other isotope data, such as strontium. Indeed, a multitude of other factors can impact the seasonal amplitude of δ^{18}O in herbivore tooth enamel and intra-group variability in addition to movement. Confounding factors that may produce similar isotopic patterns in non-mobile animals and mobile animals are, for instance: the ingestion of water sources with buffering effects, such as lakes, rivers or groundwater (as suggested by Dufour et al., 2014; Henton et al., 2014); intra-group variability in drinking water source (Knockaert et al., 2017); or differences in feeding behaviour in animals ingesting large proportions of leaf water in arid or semi-arid environments (Blumenthal et al., 2017; Levin et al., 2006; Makarewicz and Pederzani, 2017). At the same time, considerable challenges are associated with defining the range of 'local' variation to be expected in a stationary animal, a problem also encountered in provenancing studies and research investigating human residential mobility (see sections 4.4.2 and 4.4.3).

For all of these reasons, some researchers have chosen to focus on the shape of δ^{18}O seasonal curves (as opposed to their amplitude) when investigating seasonal mobility, incorporating simple theoretical models (e.g. Henton et al., 2017; Hermes et al., 2017). By far the most popular methodological approach, however, is the incorporation of other isotope systems into archaeological studies of faunal intra-annual movements, most commonly strontium (e.g. Britton et al., 2009; Evans et al., 2007; Gigleux et al., 2017; Valenzuela-Lamas et al., 2016). In such studies, the relationship between seasonal climatic shifts and seasonal changes in underlying lithology can be co-related. Some studies have also made use of concurrent δ^{13}C time-series data, exploiting the small seasonal changes in plant δ^{13}C caused by varying degrees of water stress throughout the year (O'Leary, 1995) to identify relocation to cooler high altitude environments during the summer (Tornero et al., 2017). This approach is particularly relevant for targeting vertical movement patterns and has been used to identify vertical movements of mouflon during the Late Glacial Maximum in the Caucasus region (Tornero et al., 2016) and for caprine herds from the Chalcolithic period in central Anatolia (Makarewicz et al., 2017). It should be noted that over-winter foddering may obscure this relationship through the creation of a negative association between δ^{13}C and δ^{18}O (Chase et al., 2014; Dufour et al., 2014; Makarewicz and Pederzani, 2017), although the co-analysis of wild fauna may go some way to discerning foddering and vertical transhumance in domesticates in certain regions (Makarewicz, 2017). However, dual/multi-isotope methods combining δ^{18}O with $^{87/86}$Sr or, to a lesser extent, δ^{13}C remain the most powerful means of elucidating seasonal movements of both wild and domestic animals in archaeological case studies. The combination of different isotope systems helps to overcome the limitations of single systems and strengthen interpretations, offering valuable insights that are impossible to gain from any other archaeological science methods. Model-based approaches are also proving fruitful and are likely to increase into the future, likely incorporating the methodological approaches of modern spatial ecology, including GIS tools and computational models incorporating Bayesian inferences (Britton, 2017). As with other areas of isotope bioarchaeology, however, modern data sets from individuals of known behaviours have proven (and will remain) paramount in the reconstruction of seasonal mobility patterns.

4.4.2 Animal origin and animal products: exchange, transport, trade

Live animals and their products are valuable commodities that have been transported, exchanged, gifted and traded throughout prehistory and the historic period. Herders frequently exchange or trade live animals as part of social, economic and political networks, and animal-derived products such as meat, bone tools, jewellery or ivory can undergo wide circulation. Through tracing animals and their products, and comparing point of origin to point of deposition, we can glimpse the shape and character of the networks of exchange, transport, gifting and trade that operated in past societies. By exploiting the predictable geospatial patterns in $\delta^{18}O_{ew}$ and therefore in $\delta^{18}O_{bioapatite}$, we can glean information about the geographical origin of an animal or an animal-derived product. Assignments are usually based on comparisons with modern local $\delta^{18}O_{precip}$ values obtained from proximal GNIP stations or through isoscape-style interpolation, or in comparison with local modern or archaeological animals. Formalised statistical approaches for this are become increasingly common to establish provenance (e.g. Bowen et al., 2014; Wunder, 2010). However, although $\delta^{18}O_{ew}$ does vary spatially (and predictably), because large regions are characterised by similar

$\delta^{18}O_{ew}$ values, bulk $\delta^{18}O_{bioapatite}$ values themselves are usually insufficient to infer specific provenance in most areas (e.g. Hamilton et al., 2018; Pietsch et al., 2011).

Therefore, as with the reconstruction of seasonal mobility patterns in animals, studies of faunal provenance commonly employ dual or multi-isotope approaches, often combining $\delta^{18}O$ with strontium, sulphur and/or carbon and nitrogen isotope analyses to narrow down the region of origin. For example, using $\delta^{18}O$ and $^{86/87}Sr$ of bulk enamel samples, Laffoon and co-workers reconstructed exchange networks of tooth pendants in the pre-colonial Caribbean and identified long distance movement of the pendants (or their constituent raw materials) between the Caribbean islands and (most likely) mainland South America (Laffoon et al., 2014). Similarly, a larger multi-isotope study of Formation period worked bone artefacts in central Peru suggested a marine origin for the raw materials at a site at more than 3000 m above sea level (Sayre et al., 2016). This finding was supported by other archaeological evidence for intensive trade networks between the site and regions of the Pacific coast (Sayre et al., 2016). Similar approaches were used to identify the geographical origins of a pre-colonial deposition of faunal remains on Dos Mosquises Island, where no mammalian fauna was natively present, linking the island with the Lake Valencia Basin and suggesting the deposition of faunal remains might be linked to seasonal subsistence activities on the island by mainland communities (Laffoon et al., 2016). Long distance trade at the Maya site of Ceibal, Guatemala, specifically of non-local dogs, was also established using a similar multi-isotope framework (Sharpe et al., 2018).

Isotope provenancing, including $\delta^{18}O$ analysis, has also been used to characterise past and present ivory trade. Using elephant remains of known origin, Coutu et al. (2016) successfully constructed a reference data set of oxygen, carbon, nitrogen and strontium stable isotope data to provenance elephant ivory imported to Europe between the 19th and mid-20th centuries. The results showed a variety of regions of origin, but with a focus on interior East Africa. These data not only provide valuable evidence for European colonial trade and historic poaching regions, but they are also highly applicable to investigations of the modern illegal ivory trade.

Despite their great archaeological potential, oxygen isotope provenancing studies are somewhat limited in their capabilities by some methodological challenges common to other applications of oxygen stable isotope analysis. As studies often rely on the conversion of $\delta^{18}O_{bioapatite}$ values to $\delta^{18}O_{ew}$ values, they face the challenges and uncertainties associated with such formulae that are also an issue in palaeoclimate research (see section 4.1). Variability in animal behaviour in terms of mobility, drinking source and diet also present possibilities to disrupt the relationship between $\delta^{18}O_{bioapatite}$ and $\delta^{18}O_{ew}$ that underpins the use of these methods in assigning geographical origin. Due to these issues, and the relatively low geographic specificity of any single isotopic system, many of the above studies highlight the benefits of using oxygen isotope analysis alongside other isotope systems, particularly when the region of possible origin cannot be constricted *a priori*. Advances are currently being made to accomplish such integration by using Bayesian geostatistical models. Bayesian geostatistical approaches to assigning provenance are already relatively widely used in bioarchaeology and are incorporated into software such as IsoMAP and the IsoriX R package (Bowen et al., 2014; Courtiol et al., 2016). These are often based on a single isotope system, but incorporation of several isotope tracers into Bayesian or multivariate geostatistical models to further constrain spatial origin has great potential in archaeological studies. Such approaches overlay several probability surfaces and are already proving useful in food authentication studies (e.g. Chiocchini et al., 2016; Goitom Asfaha et al., 2011; Kelly et al., 2011; Van der Veer, 2013) and in migration ecology (e.g. Hobson et al., 2012; Hobson and Kardynal, 2016). Applications to bioarchaeology are still rare, but Bayesian inferences have been used in some studies, for example in a recent investigation of late precolonial/early colonial human mobility in the Circum-Caribbean region (Laffoon et al., 2017) (see section 4.4.3 for more information on human mobility).

However, even when using sophisticated statistical methods, it is often impossible to pinpoint exact locations of origin from many possible provenance regions, and isotopic provenancing studies greatly benefit from research questions that are framed in a way to accommodate the limits of the technique (e.g. ‘either/or’ premises, or using study areas that are constrained, such as islands, or have otherwise relatively simple environment and lithological parameters). In such circumstances, it is often much easier to *exclude* potential regions of origin or decide between several previously specified possible regions than to identify new potential areas of origin unconstrained by prior information. Where studies are appropriately designed, isotopic provenancing of archaeological faunal remains can prove fruitful in questions of exchange, transport and trade, especially when informed by (and interpreted within the framework of) other types of archaeological evidence.

4.4.3 Human residential mobility and life histories

Human mobility and place of childhood residence is intimately tied to key concepts of demography, settlement and mobility patterns, marriage traditions, cultural exchange, identity and ethnicity, as well as individual life history. Humans move for a multitude of reasons related to subsistence, social and marriage networks, exchange or trade, amongst many others, and through reconstructing their movements we are afforded a glimpse at the nature and structure of past communities and the individuals that formed them. Residential mobility of human individuals in the past can be assessed in different ways depending on the nature of the research question.

When using isotopic approaches to identify non-locals within a larger community and to characterise the degree of mobility within a group, an initial step normally involves defining a range of values typical of a local, stationary population in the study area. This may involve single or multi-isotope systems. Any individuals who deviate from this range of values may be considered non-local and to have a different place of origin. Oxygen isotope approaches to human mobility are underpinned by the same theoretical approaches as animal mobility and provenance studies: that $\delta^{18}O_{bioapatite}$ values can ultimately be related to values in $\delta^{18}O_{ew}$ across an oxygen isoscape. However, what exactly constitutes a 'local range' and the most appropriate method to define it are at the centre of much ongoing debate in human mobility studies (Lightfoot and O'Connell, 2016). As with palaeoclimate, animal mobility and animal provenancing studies, how faithfully $\delta^{18}O_{ew}$ and $\delta^{18}O_{precip}$ are mirrored in biological tissues is a key factor in determining how well any of these approaches operate; identifying and quantifying sources of 'isotopic noise' is essential. In human tissues, this becomes arguably even more challenging due to high behavioural complexity and the impact of unknown cultural practices and more complicated physio-biological histories on $\delta^{18}O_{bioapatite}$. With human tooth enamel – the most commonly used analyte in mobility studies – complex formation and mineralisation processes can add further complications (see section 4.1), especially considering non-fixed birth seasonality and variability in the age of weaning in humans. So far, there is very little consensus on the timing and duration over which human tooth enamel mineralises and therefore 'collects' isotopic input (Boyde et al., 1989; Smith and Tafforeau, 2008). This has led to some uncertainties regarding what period of time is recorded in 'bulk' enamel samples and whether or not they may contain seasonal biases. Given that humans can be born at any time during the year, this potential seasonal bias would be expressed differently in individuals born in different months.

By attempting to characterise a 'local range' of $\delta^{18}O$ values in a stationary community, bioarchaeologists seek to quantify the sources of 'noise' introduced by differences in environment, cultural practice and physiology explored above. This is most commonly attempted by characterising the variation in local $\delta^{18}O_{ew}$ that is thought to be equivalent with drinking water consumed (Chenery et al., 2010; Dupras and Schwarcz, 2001; Schuh and Makarewicz, 2016; Ugan et al., 2012), or by combining local modern day $\delta^{18}O_{precip}$ values with $\delta^{18}O_{bioapatite}$ values from a group that is presumed or known to be local (Evans et al., 2006b, 2006a; Knipper et al., 2017; Oelze et al., 2012a; Price et al., 2007; Prowse et al., 2007;

Schwarcz et al., 1991). Comparisons with $\delta^{18}O_{ew}$ or $\delta^{18}O_{precip}$ (which are often used interchangeably) involve the use of drinking water conversion formulae. This introduces a potentially large amount of statistical uncertainty depending on the strength of the linear correlation involved in the regression procedure (Daux et al., 2008; Pollard et al., 2011). Furthermore, different conversion formulae published for humans can yield widely different results (Chenery et al., 2012; Daux et al., 2008; Longinelli, 1984; Pollard et al., 2011). Additionally, the spread of $\delta^{18}O$ values observed in a human population drinking from the same water source is thought to be at least ~2 ‰, and meta-analysis of a large number of published data sets recently showed that the actual spread of values in a stationary population is likely greater than 3 ‰ in most archaeological groups due to behavioural and physiological variability (Lightfoot and O'Connell, 2016). Many researchers therefore advocate defining a 'local range' based on comparison with distributions of $\delta^{18}O_{precip}$ in a known stationary population, for example as determined by Sr isotope analysis (Chenery et al., 2010; Evans et al., 2006b, 2006a). Alternatively, non-local individuals can be identified by analysing the distribution of human $\delta^{18}O$ for statistical outliers that appear to deviate from the overall distribution of $\delta^{18}O$ values (e.g. Eckardt et al., 2009; Kendall et al., 2013; Quinn et al., 2008; White et al., 1998). The widespread difficulty of (and disagreement on) defining a 'local range' is also illustrated by the debate surrounding the origin of the crew members of the Mary Rose (Bell et al., 2010, 2009; Millard and Schroeder, 2010).

Statistical identification of individual migrants using oxygen isotopic data (either alone or alongside other approaches) is often very challenging in archaeological case studies, where sample sizes are generally small and the distribution of analysed values likely presents an unknown mixture of local and non-local individuals. The robustness of these methods therefore largely depends on sample size, the particular value distribution and statistical method used (see Lightfoot and O'Connell, 2016 for extensive discussion). In practice, many studies combine estimations of local variation based on $\delta^{18}O_{ew}$ and $\delta^{18}O_{bioapatite}$ in presumably local populations, along with statistical assessment of outliers in the $\delta^{18}O_{bioapatite}$ distribution to identify non-local individuals. Dual/multi-isotope studies (particularly in combination with strontium isotope analysis) are common.

Oxygen isotope analysis, normally in combination with strontium or other isotope analyses, has been applied to diverse topics in archaeological mobility studies. In Britain, this has included the degree of mobility during the Bronze Age and Iron Age (Evans et al., 2006a; Jay et al., 2013); the Roman period (Chenery et al., 2011, 2010; Eckardt et al., 2009; Evans et al., 2006b; Leach et al., 2009); and the medieval period (Groves et al., 2013; Kendall et al., 2013; Müldner et al., 2009; Roberts et al., 2013). The movement of individuals, social networks and marriage patterns in Bronze Age Europe (Knipper et al., 2017; Oelze et al., 2012b) and the Bell Beaker phenomenon (Parker Pearson et al., 2016) has also been the focus of much study. Pellegrini and colleagues (2016) recently applied a combination of isoscape-style geospatial modelling with outlier analysis to a large data set of previously published human $\delta^{18}O_{bioapatite}$ from this period in Britain. By statistically identifying outliers through comparison with a predictively modelled $\delta^{18}O_{bioapatite}$ isoscape, the researchers identified a comparatively high degree of mobility in communities surrounding archaeologically important centres, such as Stonehenge.

Human mobility and life histories – and their relationship with status, social structure and burial customs – have also been a focus of research in a variety of prehistoric South and Central American contexts such as the Maya period (Price et al., 2010; Somerville et al., 2016), the Late Intermediate Period in Peru (Marsteller et al., 2017) and among pre-Columbian horticulturalists in Brazil and Argentina (Loponte et al., 2017). Moreover, the extent of human mobility and migration represents a key aspect of research on past nomadic pastoralism in the Eurasian steppe (e.g. Gerling, 2015; Gerling et al., 2012; Ventresca Miller et al., 2018), although isotopic studies of human remains are still relatively sparse. Beyond period studies, much thematic research has also been conducted, such as on the origin of sacrificial victims (Knudson et al., 2009; Price et al., 2007; Toyne et al., 2014; Turner et al., 2013; White et al., 2007, 2002, 1998) and the nature of marital residency patterns during and following the transition to agriculture (Bentley et al., 2007, 2005; Burns et al., 2012).

Another approach to the reconstruction of individual lifetime mobility involves the comparison of a $\delta^{18}O$ value related to childhood with one representing adult location. Childhood $\delta^{18}O$ signals can be extracted from enamel or dentine samples, while adulthood $\delta^{18}O$ values can be obtained from the analysis of bone or be inferred from $\delta^{18}O_{ew}/\delta^{18}O_{precip}$ at the burial site. However, while all human tooth enamel is formed during childhood and adolescence, just as in other animals, different teeth are formed at different times of life and over different amounts of time. This is an important consideration in choosing samples – especially when comparing data from multiple individuals – and researchers should be as consistent as possible to minimise the introduction of individual variability that is not related to geographic origin (see also comments above and in section 4.1). To reconstruct residence relocation from comparison of tooth and bone values, it is generally assumed that an individual grew up and died in the same locale if childhood and adult isotopic values match. Similarly, a mismatch would indicate movement to a different region sometime during a person's lifetime. This is arguably a relatively robust way of identifying residential mobility, as it does not necessarily rely on conversions to drinking water values. However, defining what constitutes as a 'mismatch' between childhood and adult values is essentially analogous to establishing a 'local range' on a population or group level and comes with the same challenges.

In addition to identifying non-local individuals or characterising the degree of mobility in a given individual, community or region, many researchers also seek to isotopically identify the specific region of origin of non-local individuals by employing a provenancing approach that is analogous to the provenancing of animal remains/products (see section 4.4.2). This is often attempted with archaeologically 'anomalous' burials with unusual grave goods or with particularly prominent human remains, such as Richard III (Lamb et al., 2014); Ötzi the Tyrolean glacier mummy (Hoogewerff et al., 2001; Müller et al., 2003); the Amesbury archer

(Evans et al., 2012); and the Gristhorpe Man (Melton et al., 2010). However, as with studies of animals, provenance based solely on δ^{18}O is relatively uninformative, not least given the high isotopic variability that stationary local populations can exhibit (Lightfoot and O'Connell, 2016). Combinations of several isotope systems, or *a priori* restriction of possible regions of origin, are therefore advisable and few provenancing studies rely solely on δ^{18}O.

In addition to climatic or geographic influences, and the influences of physiology and growth explored above, the relatively high variability in δ^{18}O values observed within human groups may also be rooted in behavioural differences between individuals and communities. The enormous diversity of human behaviour, and cultural and social practices, adds another layer of complexity to interpreting the oxygen isotopic composition of human tissues. Culinary practices involved in food preparation and beverage production, as well as ingestion of lactate before weaning is completed, can been seen as altering human tissue isotope values in a way that is strongly determined by cultural and social factors. This has long been recognised as a source of 'noise' when analysing palaeoclimate or provenance from human remains (e.g. Bryant et al., 1996a), but has only recently received increasing attention, with some studies attempting to shift cultural modification from problem to proxy in order to explore elusive culinary and weaning practices.

4.5 Breastfeeding and weaning practices

Infant feeding practices have long been of interest to archaeologists and anthropologists, and studies of past breastfeeding and weaning behaviours can illuminate infant and maternal health, birth spacing and demography, community structures and contemporary societal norms. As with other aspects of life in the past pertaining to women and children, without direct means of determining these practices from the archaeological record, these behaviours can be elusory, even in relatively recent (historical) periods where accounts of past practices can be both scarce and conflicting (but see review in Fildes, 1986).

Isotopic approaches offer one such direct method of accessing this information and, in archaeological case studies, nitrogen isotope analyses of tooth and bone collagen are now commonly used to reconstruct breastfeeding and weaning practices (Reynard and Tuross, 2015; Tsutaya and Yoneda, 2015). Nitrogen isotope approaches are based on the established trophic level effect on δ^{15}N and subsequent drop in δ^{15}N during/following weaning (see Fogel et al., 1989) and have been used to explore past infant feeding practices in a range of contexts and case studies: from Later Stone Age South Africa (Clayton et al., 2006) to post-Medieval Scotland (Britton et al., 2018). By comparison, a far smaller number of studies have employed oxygen isotope analysis to investigate breastfeeding practices and determine weaning age in past societies. These studies have utilised the oxygen-bearing mineral components of tooth enamel (Wright and Schwarcz, 1999, 1998)) and bone (Britton et al., 2015a; White et al., 2004) and have great potential for more widespread usage, particularly in cases where the collagen required for δ^{15}N analysis is not preserved (Britton et al., 2015a). Furthermore, given that nitrogen isotopes can be potentially complicated by both the dietary intake of the mother and influenced by metabolic or other physiological stresses (Reitsema, 2013), oxygen studies may offer a valuable corroborating or alternative line of evidence.

The application of oxygen isotope analyses to studies of past breastfeeding and weaning practices are based on the premise that – due to isotopic fractionation – the breast milk of a lactating woman will have higher δ^{18}O values compared to the water she ingests, inducing elevated δ^{18}O values in her infant's tissues. This is because body water is ^{18}O-enriched relative to drinking water, mostly due to the discrimination against ^{18}O during expiration of water vapour (Bryant and Froelich, 1995; Kohn et al., 1996). Breast milk is formed from this body water and therefore exhibits higher δ^{18}O values than 'local' drinking water, as confirmed by recent studies on modern dairy cows (Lin et al., 2003). Mineralised tissues – whether contemporary-forming bone or tooth enamel – record this enrichment until weaning commences, with later forming tissues reflecting values more similar to the (local) maternal range when weaning is complete (Figure 7).

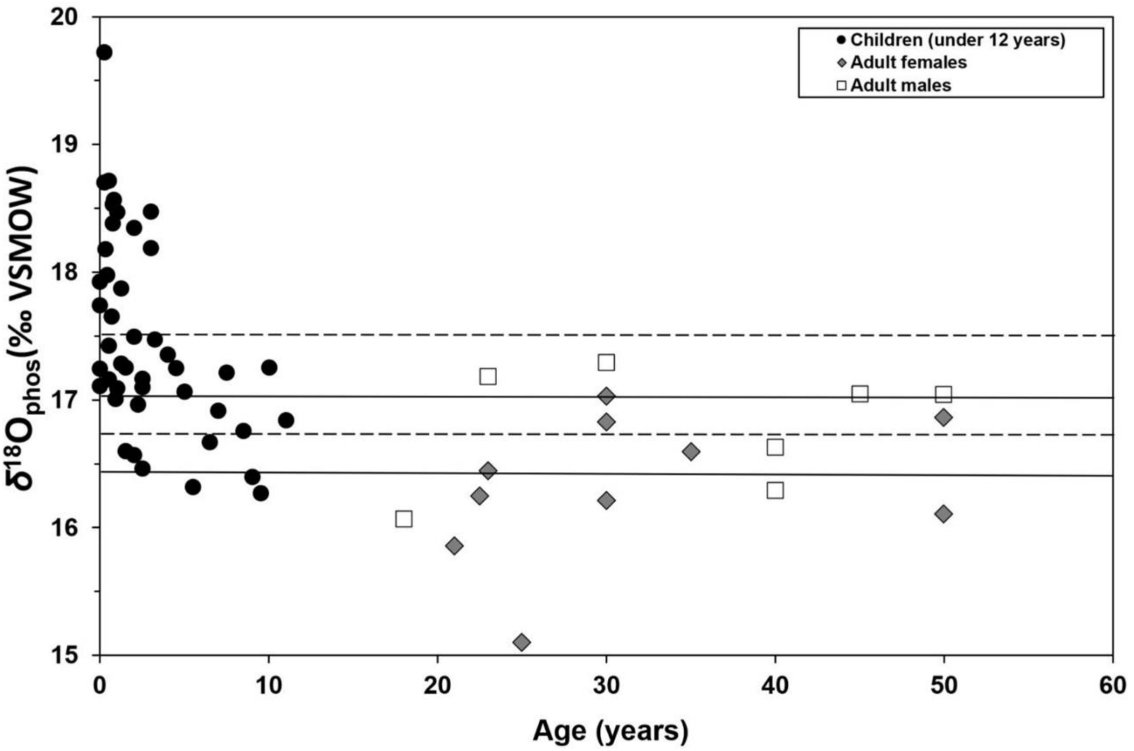

Figure 7: Oxygen isotope composition of bone phosphate of adults and non-adults from the medieval site of Wharram Percy, England, plotted against age (years). High oxygen isotope values in infants (< 3 years of age) reflects ^{18}O-enrichment in lactate relative to local drinking water. Local water range (converted to estimated bioapatite values) is depicted between the solid lines, and the range of 'local' measured human tooth enamel values from a proximal is shown between dashed lines (image adapted from Britton et al. 2015a: 234, Figure 4).

Initial studies made use of tooth enamel, with early forming teeth demonstrating enrichment of between 0.5 ‰ and 1.2 ‰ in the oxygen-bearing carbonate and phosphate components (Wright and Schwarcz, 1999, 1998). Until recently, only limited studies had focused on bone (e.g. White et al., 2004), perhaps not least due to the susceptibility of the carbonate fraction to diagenesis (e.g. Kohn et al., 1999; Nelson et al., 1986) and the relative complexity of isolating and analysing the phosphate-bearing fraction (see section 3). In a recent, more extensive study on a large British medieval skeletal assemblage, the efficacy and potential of bone phosphate, alongside tooth enamel phosphate, for the reconstruction of weaning practices has been more clearly demonstrated (Figure 7) (Britton et al., 2015a). Focusing on the deserted medieval village site of Wharram Percy, Yorkshire, the study compared collagen δ^{15}N values to phosphate δ^{18}O in bones of individuals of different ages, including neonates, infants, children, sub-adults and adults. The adult range largely reflected local predicted drinking water values. However, the results from the young children demonstrated that (as with δ^{15}N) δ^{18}O was elevated in infancy, with δ^{18}O phosphate values lowering by more than 1 ‰ and becoming close to the adult mean value after the age of ~3 years. The results of this study were significant in confirming that the investigation of past weaning practices using archaeological bone need not be restricted to samples with protein preservation (as with δ^{15}N analysis) and that δ^{18}O analysis of bone phosphate can be applied at older sites or sites in warmer regions where collagen is often poorly preserved. The study also highlighted slight, but perhaps crucial, differences in the length of the weaning process as evidenced in the protein and mineral phase, emphasising that the investigation of protein source (δ^{15}N) and water source (δ^{18}O) should perhaps be employed in tandem in archaeological studies (Britton et al., 2015a). In light of the incremental nature of enamel formation, future studies may also wish to focus on more detailed sequential sampling of dental enamel to gain more highly resolved insights into the timing and process of weaning in specific individuals.

Despite the clear potential of this approach, there are some challenges. For example, as with nitrogen isotopes, some physiological changes have been associated with changes in δ^{18}O tissue values. For example, in a recent controlled feeding study, a minor ^{18}O-enrichment (~0.7‰) was determined in the bone apatite phosphate of a growth-depressed pig compared to the control group (Warinner and Tuross, 2010: 487). This could indicate that certain physiological or metabolic conditions could also influence skeletal δ^{18}O values. As with nitrogen isotopes, this raises the issue of the osteoarchaeological paradox in studies of infant feeding practices based on bone chemistry in archaeology: that *survivors* are not sampled and that those who are sampled may have (fatally) suffered from conditions that influenced their isotope chemistry (Beaumont et al., 2015). At the same time, sampling of individuals who died at a young age may skew patterns of breastfeeding observed in the population, as such individuals might have differed in the nutrition they received. Other broader osteological issues, such as the natural variability in infant growth that leads to uncertainties in ageing infant remains (sometimes by as much as half a year or more), could influence the level of precision possible in any stable isotope study of non-adults. Choice of skeletal element sampled, from slower growing components to bones with more rapid turnover rates, could also influence such studies.

With bone mineral $\delta^{18}O$ studies, difficulties in interpreting a ‘weaning signal’ may also arise due to variation in water source amongst the adult population. While this is well known to also be the case with nitrogen isotopes (and related to protein source in diet), studies of bulk bone apatite oxygen isotope values in adult populations have not been as extensive as dietary isotope studies and variability (or even the potential for variability) has yet to be fully characterised. Differences could arise, for example, due to the selection or use of different available water sources (such as stream water or well water) or due to varied culinary practices that could serve to differentially influence the oxygen isotope ratios of fluids consumed (deviating them from the ‘local’ value). The influence of culinary practices, such as cooking, brewing or boiling, on oxygen isotope ratios of both beverages and food has only recently began to be explored in experimental studies (Brettell et al., 2012; Royer et al., 2017) (see section 4.6). Furthermore, there may be specialist complementary foods exclusively provided to infants during the weaning process, such as paps or pulps (panadas), which may be heated, or animal milks which may not necessarily feature in the contemporary adult diet. Furthermore, in addition to adult and, potentially, infant diets being varied in terms of inputs, weaning practices themselves (in terms of the timing and process) could also potentially vary between individuals within any one population. These factors, as with variations in adult protein source and nitrogen isotope studies, could also be expected to produce at least subtle inhomogeneity in bone phosphate oxygen values amongst individuals within the same age classes. Finally, as with other applications of bone oxygen isotope studies, sample diagenesis (particularly with regards to the carbonate moiety, but also phosphate; see section 3.2) and pretreatment, especially the removal of organics ahead of phosphate analysis, remain potential complications currently inhibiting more widespread application.

While the sequential sampling and oxygen isotope analysis of tooth enamel does have great potential for illuminating *individual* infant feeding practices, there are also further complicating factors that must be considered. As well as potential changes in adult body water values arising from food and drink consumed (see above), the δ^{18}O value of local environmental water can be expected to shift seasonally at mid- and high-latitudes (see section 2.1). This could lead to a natural, seasonal variability in maternal body water, and thus breast milk, and, potentially, to seasonal variations in local herbivore milk or other weaning foods provided to infants. In bone data, where tissue turnover is rapid, this could lead to a 'season of death' effect, with higher values recorded in those dying following warmer periods than in those dying following cooler ones. In incremental dental enamel oxygen isotope studies, such variations, combined with changes due to the weaning process itself, and the effects of specific culinary practices on certain foods could lead to a messy palimpsest of sequential isotope data that would be difficult to interpret. In other species, such as herbivores, restricted birth seasonality could at least provide an anchor point for such interpretations, although this is not the case with humans and other year-round reproducing species.

In light of these issues, there is a need for further fundamental studies, including studies on adult oxygen isotope variability in archaeological case studies, and modern experimental studies to explore the influence of water source/culinary practices, seasonality and individual physiology/health status on adult body water. The exploration of inter-individual differences, as well as intra-tooth differences in the same individual, will provide useful additional data and help to define the parameters/constraints for sampling human tooth enamel to reconstruct past weaning practices. In bone studies, archaeological applications should be conducted alongside nitrogen isotope studies, not only to provide corroborating evidence of age at weaning but also to explore the different aspects of the weaning process (predominant water versus predominant protein source).

4.6 Culturally mediated practices, culinary processes and the alteration of oxygen isotope ratios of ingested fluids

Culinary traditions, individual and group dietary choices, and food preparation techniques often play a central role in individual and group identity, shaping and being shaped by day-to-day activities and beliefs. Consumption of certain foods is often tied to age, social status, specific occasions and identities and is therefore intimately intertwined with key concepts being studied in archaeology and bioarchaeology. Culinary processes, such as cooking, that could lead to isotopic-enrichment (or depletion) in ingested fluids, or the consumption of liquids that may otherwise significantly deviate from ‘local’ environmental values due to other cultural practices (such as dairying), have increasingly gained attention in the recent archaeological literature. As a challenge to palaeoclimate and mobility studies using human remains, cultural practices have been recognised for some time as a modulating influence on tissue oxygen isotopic composition (e.g. Bryant et al., 1996a), but more in-depth research on this topic has only emerged within the last few years.

Recent publications have sought to empirically demonstrate the influence of such processes on fluids and foodstuffs, normally using experimental approaches, and have then speculated as to their potential impact on the application of oxygen isotope analysis to archaeological human remains (e.g. Brettell et al., 2012; Royer et al., 2017; Tuross et al., 2017). A smaller number of publications have attempted to identify possible culinary sources of isotope enrichment in archaeological skeletal materials (e.g. later life wine consumption in Richard III; Lamb et al., 2014). These publications highlight both the challenges and the potential posed by this distinctively human problem for oxygen isotope analysis in archaeological studies.

A number of different culturally mediated processes can serve to modify the oxygen isotope composition of fluids intended for consumption, including stewing, boiling, fermentation and distillation, as well as biological processes that induce fractionation at the source (e.g. lactation in ruminants; Lin et al., 2003) (Figure 8). As with other aspects of isotope bioarchaeology, experimental studies are proving vital to quantifying the isotopic influence of cultural modifications on food and drink, and for estimating the potential influence that consuming these products could have on human tissue oxygen isotope values. For example, changes of more than 10 ‰ have been measured in the $\delta^{18}O$ values of liquid in experimentally slow-cooked stews and of up to ~25 ‰ in plain water allowed to 'stew' for 3 hours (Brettell et al., 2012). Smaller changes of up to ~1 ‰ have been observed during the different stages of brewing and in boiled plain water (Brettell et al., 2012). As well as culinary preparation techniques (such as stewing, boiling, fermentation and distillation), other culturally mediated processes can serve to modify the oxygen isotope ratio of fluids for consumption, for example because they involve biological processes that induce fractionation at the source. Cow's milk, like other mammalian lactate, has been demonstrated as being enriched in the heavier isotope, not only relative to body water but also to local environmental waters (Lin et al., 2003). Given that dairying has been a common feature of many agricultural economies since the Neolithic, if raw milk was being consumed then this could be another 'cultural' source of liquids with high $\delta^{18}O$.

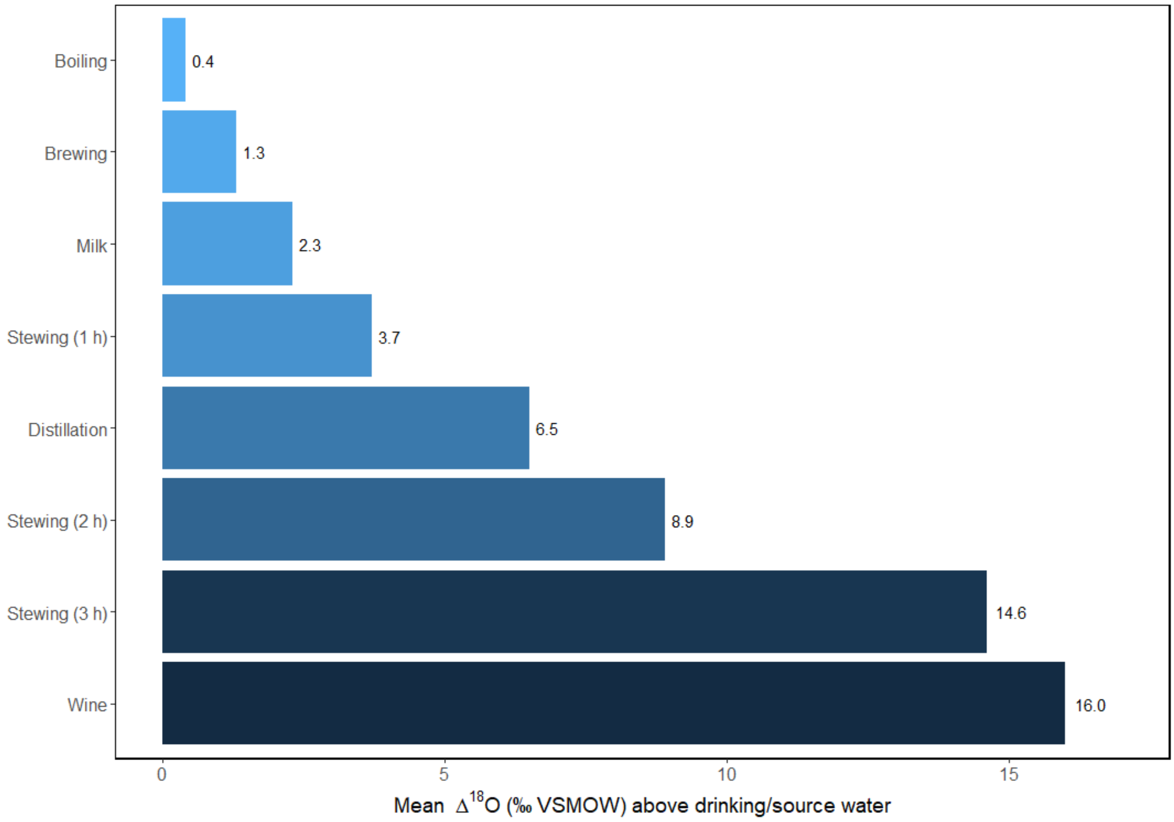

Figure 8: A variety of products consumed by humans can be isotopically altered by culinary or biological practices. Isotopic alterations of several processes are here expressed as the mean enrichment either above local drinking water (milk), precipitation (wine) or above source water used to produce each end product (boiling, brewing, stewing, distillation). Data were collected from Brettell et al., 2012(boiling, brewing, stewing; using the 'mean all pans' values for the stewing experiment); Chesson et al., 2010 and Lin et al., 2003(milk); Meier-Augenstein et al., 2012(distillation of whisky; using production water and bulk whisky $\delta^{18}O$ of Scottish whiskies); West et al., 2007(wine; using wine water and mean annual precipitation $\delta^{18}O$ of wines from the western US; note that ^{18}O enrichment in wine over source water is strongly driven by climatic factors).

Additionally, the heating of foods has been shown experimentally to also alter the $\delta^{18}O$ of the macronutrient solid fraction of both meat and sweet potatoes (Tuross et al., 2017), and differences ($\Delta^{18}O$ values) of between –2.8 to 5.1 ‰ have recently been observed in meat and fish cooked in a variety of ways (Royer et al., 2017). However, the contribution of water from solid food to the diet may be far smaller than the contribution of liquids to body water. At the same time, only certain kinds of food preparation techniques that 'significantly reduce the water content of food significantly would have a sizeable effect' (Daux et al., 2008: 1146), further reducing their contribution to body water. Nonetheless, these results do highlight yet another area in which cultural modifications in human foodways could influence the oxygen isotope values of human tissues.

A variety of cultural processes surrounding subsistence regimes and food procurement and preparation therefore have the potential to alter the oxygen isotope composition of dietary fluids, which could deviate strongly from local environmental waters. In the past, the consumption of these culturally modified foods or fluids (as opposed to unmodified ‘plain’ water) as a percentage of overall fluid ingested is likely to have been a product of a complex interplay between general availability, cultural preferences, personal taste/choice and economic and social status. For example, the consumption of water as ‘small beer’ (ale), wort drinks (herbal teas) and pottage (extended stewing/cooking) would have been common throughout the medieval period (see Brettell et al., 2012, and references therein). Modern nomadic communities in Central Asia illustrate how pastoralist communities may rely almost exclusively on dairy products and boiled soups and teas as water sources (Enkhtungalag et al., 2015; Ohno et al., 2005). Culturally mediated behaviours such as these could therefore lead to oxygen isotope values in bones and teeth from local human skeletons that deviate slightly or more significantly from any anticipated local value. This could influence whole groups, populations or specific individuals within groups. Certain age classes, for example, could be expected to be more greatly influenced than others, such as infants and children on weaning or post-weaning diets that may include higher quantities of ruminant milk. This poses a significant challenge for provenancing and mobility studies: not only could culinary ‘outliers’ be mistaken for non-local individuals, but such intra-group variability would also make it more difficult to define a ‘local’ range of values. The former issue could be addressed by incorporating a dual or triple isotope approach in mobility studies, including strontium isotope analysis (e.g. Leach et al., 2009), or strontium and lead isotope analysis in combination (e.g. Shaw et al., 2016), alongside oxygen. The latter could be aided by ensuring a ‘local’ baseline is statistically defined with sufficient conservatism and large margins of error (Lightfoot and O’Connell, 2016). An additional line of evidence could also be gleaned through the analysis of the bones or teeth of local domestic animals (and obligate drinkers), such as sheep or cows, to provide an estimate of local environmental waters; however, this practice is not common.

As well as posing challenges, the impact of cultural choices on the δ^{18}O of ingested fluids (and by inference on co-forming mineralised tissues) also has potential as a great source of information to explore individual and group dietary practices in the past. Multi-tissue analyses of the same individual could also illuminate changes in imbibing habits during life through the comparison of earlier forming teeth with later forming bones (e.g. Lamb et al., 2014). However, before such approaches can become mainstream in isotope bioarchaeology, a greater number of experimental and proof-of-concept studies are required. This should be achieved through research that seeks to characterise the influence of various culinary processes on food and drink themselves, but also through research that targets potentially ‘affected’ groups to test hypotheses that are grounded in other historical or archaeological evidence. For example, the comparison of higher to lower status groups within the same populations (which could be linked, for example, to the availability and consumption of imported commodities such as wine). Even with further work, however, it is unlikely that δ^{18}O of human tissues could ever be relied upon as a sole indicator of culinary practice and dietary choice. To resolve this issue of equifinality, an emphasis in future research should also be on determining sources of corroborating evidence, whether that be from contemporary material culture and other archaeological evidence or, indeed, the development of complementary biomolecular or other archaeological science approaches to identify the direct consumption of heated or otherwise modified liquids. As with many other areas of isotope bioarchaeology, cautious method development and limited initial case studies should take precedence over the desire for immediate ‘impact’ (Pollard, 2011).

5 Conclusions and outlook

Growing out of tentative beginnings in palaeoclimatology and isotopic provenancing, oxygen isotope bioarchaeology has flourished into a multifaceted field covering applications of astonishing breadth. This variety of application is rooted in the multitude of influences governing the complex systems that define δ^{18}O values in biological tissues, which is in itself a mixed blessing. Many, if not all, of these applications face very similar challenges of equifinality, where the other factors that may impact δ^{18}O tissue values need to be filtered out, or otherwise excluded, in order to isolate the desired signal of temperature, aridity, location or water source. An in-depth knowledge of local isotopic systems in which humans and animals operate, and careful study designs incorporating as much *a priori* information as possible, are therefore the essential basis of nuanced and meaningful applications of oxygen isotopic analyses to bioarchaeology.

The intricacy of oxygen isotope systematics in archaeological settings is exacerbated by the anthropogenic nature of the skeletal assemblages that form the basis of oxygen isotope analysis in bioarchaeology, be they faunal or human remains. Where we already grapple with behavioural plasticity and individual or population differences in unmanaged wild animals, human decision-making and culturally mediated actions add a further layer of complexity to the isotopic system of managed animals and humans themselves. Anthropogenically derived assemblages therefore present us with isotopic evidence that is inherently shaped by human activity and affords us a view into the past only through the lens of culturally mediated behaviour. This has led to a seemingly ever-growing list of challenges to isolating a ‘faithful’ isotopic signal of movement or temperature, for example. However, we argue that not all of these challenges are insurmountable, and that the anthropogenic nature of archaeological materials presents one of their most important advantages. Ultimately, bioarchaeology aims to illuminate human culture and activity, and by analysing skeletal remains directly from archaeological sites we are offered a unique spatial and chronological link to that human activity. Combination with archaeological information to produce a more rounded picture of the past is much more easily achieved using bioarchaeological materials than for isotopic archives of natural origin, which are often far removed from archaeological sites.

To ameliorate the inherent challenges of working in an under-defined analytical system and to exploit this unique strength of anthropogenically derived archives, we envisage significant developments in data generation, analysis and interpretation in oxygen isotope bioarchaeology in the coming years. We believe that important progress can be achieved by continued and expanded modern experimental work to guide and improve future archaeological application. Modern case studies will help to achieve a deeper and more widely applicable understanding of oxygen isotope systematics in animal tissues, both in a mechanistic sense, but also through empirical observation of isotopic effects in different environments. For instance, we have recently seen modern experimental work that has elucidated important aspects of the mechanics of isotopic equilibration during tooth enamel formation (Green et al., 2017; Trayler and Kohn, 2016). Empirical studies of modern animals have contributed to the development of approaches to isolate vertical transhumance (e.g. Tornero et al., 2017). This work highlights the value of modern mechanistic and comparative studies and we hope to see such developments continue in the field. However, due to limitations in extrapolating information from modern comparative studies to taxa other than the study taxon, we believe that a focus on mechanistic understanding, as well as a combination with modelling approaches, is key.

As with other areas of isotope bioarchaeology, multi-isotope studies that combine the strengths of several isotope systems should remain the ideal approach in many cases, particularly in geospatial studies reconstructing mobility or place of origin. To similar ends, mobility and climate studies exploiting comparisons between different taxa to isolate the desired driver of δ^{18}O variability can help to filter out and discern dietary and physiological impacts. To better understand such factors, as well as to improve life history reconstructions, we also foresee great value in studies that incorporate analyses of different skeletal elements and broaden the range of tissues that can be analysed (e.g. combined carbonate, phosphate and collagen analyses on the same samples).

In addition to developments in data generation and study design, additional focus is needed on improving inferences that can be made from existing data sets through novel modes of data handling and analysis. Recent years have seen both the creation of large datasets and data sharing through repositories that enhance our understanding of isotope systematics through empirical observation. Such work is likely to grow in prominence in the coming years and some attempts at establishing data repositories for specific regions are currently underway (e.g. IsoArcH, Salesse et al., 2017), although isotope bioarchaeology (along with other fields of isotope science) has yet to benefit from a single standardised, user-populated repository akin to GenBank (Britton, 2017; Pauli et al., 2017, 2015). Alongside the more routine use of larger and larger data sets facilitated through better mechanisms of data archiving and sharing, we are also likely to see an increasing uptake and refinement of modelling approaches that enable interpretation and analysis of isotope values in more formalised frameworks that better incorporate the mechanistic and empirical insights into isotopic systems that are continuously developing. This can be seen as part of a heightened awareness of the need for more formal modelling in isotope bioarchaeological studies in general, which can contribute to more robust inferences on ecology, life history and material exchange but also lead to a more conscious approach to method uncertainty (e.g. Pollard et al., 2011; Pryor et al., 2014). We view these developments as very promising and already successful routes in pushing the limits of oxygen isotope bioarchaeology.

However, alongside future advances in data generation, handling, analysis and interpretation, we also emphasise the important contributions and improvements that can be made incrementally by framing case studies to accommodate the limits of the technique to yield more meaningful archaeological results. While important developments are continually being made in improving our understanding of oxygen isotopic systems, stable isotope bioarchaeology already represents a powerful tool, provided that it is wielded in a way that is appropriate to current capabilities of different approaches. This must include a strong theoretical foundation and awareness of the limitations and uncertainties inherent in projecting the empirical relationships underlying all oxygen isotopic applications onto past environments and cultural contexts where many variables are unknown. In spite of these ‘unknowns’, we underline the value of relative comparisons in systems that are consistent in sampling, analysis and taxon choice – particularly in palaeoclimate research. In this way, the impact of many limitations related to animal behaviour and tissue growth can be lessened substantially. We also highlight the advancements made by studies focusing on quantifying estimate uncertainty and providing new modern comparative data sets. The increased awareness and characterisation of method limitations that such work has brought is, in our opinion, critical to mindful study design and to generating meaningful and robust insights into the past. Finally, as a fundamentally archaeological discipline, we should not forget the wealth of knowledge contained in the material record that can aid us in constructing hypothesis-based studies that incorporate *a priori* information to their advantage. It is only through continued integration with other lines of evidence such as zooarchaeological information, historical documents and archaeological context that *testable* research questions can be formed – singularly the most vital part of constructing successful oxygen isotope studies.

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7 Appendix

Table 1: Selected references to species-specific studies of the correlation between local environmental water, ingested water and mammal body water or skeletal tissues (adapted from Britton 2009: 37, Table 2.3). (*Latin names given where specified in the literature).

Reference	Species*	Analyte
Longinelli and Peretti Padalino, 1980	Laboratory rat (*Rattus norvegicus*)	Blood
Longinelli, 1984	Domestic pig (*Sus scrofa*), Human (*Homo sapiens sapiens*)	Blood, bone phosphate
Luz et al., 1984	Human (*Homo sapiens sapiens*), dog (*Canis* familiaris), muskox (*Ovibosmoschatus*), laboratory rat (*Rattus norvegicus*)	Bone phosphate Blood
Luz and Kolodny, 1985	Laboratory rat	Breath CO_2, bone phosphate
Levinson et al., 1987	Human (*Homo sapiens sapiens*)	Tooth phosphate, urinary stone phosphate
Ayliffe and Chivas, 1990	Australian Macropoda (kangaroos and wallabies)	Bone phosphate
D’Angela and Longinelli, 1990	Woodmice (*Apodemus sylvaticus, A. flavicollis*), deer (*Cervus elephus*), cattle (*Bos taurus*), sheep (*Ovis aries*)	Bone phosphate
Luz et al., 1990	White-tailed deer (Odocoileus virginianus)	Bone phosphate
Yoshida and Miyazaki, 1991	Various cetacean taxa (whales, dolphins and porpoises)	Bone phosphate

Ayliffe et al., 1992	African elephant (*Loxodonta africana*), Asian elephant (*Elephas maximus*)	Bone and tooth phosphate
Sánchez Chillón et al., 1994	Fossil horses (*Equus stenonis*)	Bone and tooth phosphate
Bryant et al., 1994	Horse (*Equus caballus*), Plains zebra (*E. burchelli*), mountain zebra (*E. zebra*)	Enamel phosphate
Delgado Huertas et al., 1995	Goat (*Capra* sp*.*), Ibex (*Capra ibex*), mouflon (*Ovis ammon musimon*), roe-deer (*Capreolus capreolus*), horse (*Equus caballus*), rabbits (*Oryctolagussp.*), hares (*Lepus sp.*)	Bone phosphate
Stuart-Williams and Schwarcz, 1997	Canadian beaver (*Castor canadensis*)	Bone, enamel and dentine phosphate
Iacumin and Longinelli, 2002	Reindeer (*Rangifer tarandus*), fox (*Vulpes vulpes, Alopex lagopus, Vulpes zerda*), golden jackal (*Canis aureus*)	Bone and tooth phosphate
Longinelli et al., 2003	Reindeer (*Rangifer tarandus*), mice (*Pitymus* sp., *Microtus arvalis, Arvicola terrestris*)	Bone/tooth phosphate
Hoppe et al., 2004a	North American plains bison (*Bison bison*)	Enamel carbonate
Navarro et al., 2004	Arvicolinae (*Myodes* sp. and *Microtus* sp.)	Enamel phosphate
Hoppe, 2006	North American feral horse (*Equus caballus*)	Enamel carbonate
Daux et al., 2008	Human (*Homo sapiens sapiens*)	Enamel phosphate
Podlesak et al., 2008	Woodrats (*Neotoma cinera, N. stephensi*)	Blood, breath CO2, hair, enamel

		phosphate, enamel carbonate
Tuross and Warinner, 2008	Pigs (*Sus scrofa*)	Muscle, fat, blood, collagen, hair
Kirsanow and Tuross, 2011	Sprague-Dawley rat (*Rattus norvergicus*)	Enamel carbonate and phosphate, collagen, subcutaneous fat, hair
Gehler et al., 2012	Arvicolinae (*Arvicola terrestris*, *Myodes glareolus*, *Microtus agrestis*, *Microtus arvalis*) and Myroidea (*Apodemus sylvaticus*, *Mus musculus*, *Rattus norvegicus*)	Enamel carbonate
Royer et al., 2013	Myroidea (*Apodemus sylvaticus*, *Arvicola sapidus*, *A. terrestris*, *Chionomys nivalis*, *Ilberomys cabrerae*, *Microtus arvalis*, *M. agrestis*, *M. Terricola duodecimcostatus*, *M. T. subterraneus*, *Myodes glareolus*)	Enamel phosphate
Pietsch and Tütken, 2015	Bobcat (*Lynx rufus*) and Puma (*Puma concolor*)	Bone phosphate, hair
Ciner et al., 2016	Sperm whale (*Physeter macrocephalus*), Short-finned pilot whale (*Globicephala macrorhynchos*), Cuiver's beaked whale (*Ziphius cavirostris*), killer whale (*Orcinus orca*), pygmy sperm whale (*Kogia beviceps*)	Enamel phosphate, bone phosphate
Holobinko et al., 2011	Human (*Homo sapiens sapiens*)	Enamel carbonate
Kamenov and Curtis, 2017	Human (Homo sapiens sapiens)	Enamel carbonate