

Increased climate seasonality during the Late Glacial in the Gebel Akhdar, Libya

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Abstract

Oxygen isotope analysis ($\delta^{18}\text{O}$) of caprine and bovine tooth enamel carbonates from the Haua Fteah cave (Gebel Akhdar massif, northeast Libya) reveals significant differences in palaeoseasonality during the last c. 70 ka. Data indicate different phases of human occupation of the region occurred under notably different climatic conditions. During the last glacial period, prior to the Last Glacial Maximum, a gradual increase in climate aridity occurred. This was followed in the late glacial (c. 16.6 – 14.7 ka) by considerably more arid conditions and much greater climate seasonality, which was likely produced by changing winter precipitation amounts and a strengthening of arid summer air masses. The high seasonality in the late glacial coincides with a period when human activity at the Haua Fteah greatly intensified. Significant changes in subsistence strategies and the seasonal exploitation of food resources also occurred at this time. The results presented here suggest that changes in the seasonal climate may have affected the seasonal supply of floral and faunal resources available to local human populations at the time, which resulted in changing subsistence practices.

Key words: Quaternary; palaeoclimate; seasonality; North Africa; Haua Fteah; stable isotopes; tooth enamel

1. Introduction

Seasonality plays an important role in abrupt climate change events, in influencing the distribution of floral and faunal species within a region, and in shaping human subsistence activities and landscape use (Denton et al., 2005; Snyder and Tartowski, 2006; Speth, 1987). Today, the Mediterranean climate is highly seasonal, being influenced by North Atlantic storm tracks and local cyclogenesis in winter, and in summer by tropical and sub-tropical anticyclone activity (Lionello et al., 2006; Sultan and Janicot, 2000). Late Pleistocene and Holocene palaeoseasonality records from the Mediterranean basin reveal spatially variable patterns of seasonal temperature and aridity changes (Cheddadi and Khater, 2016; Ferguson et al., 2011; Hallin et al., 2012; Nimmergut et al., 1999; Orland et al., 2012; Peyron et al., 2011). However, there is a lack of terrestrial palaeoseasonality data available for the North African Mediterranean coast, and it is not clear how the pattern of seasonal climate change compared with more northerly and easterly regions.

Here we present palaeoseasonality data from the Gebel Akhdar ('Green Mountain') massif, northeast Libya (Fig. 1). Data from the Gebel Akhdar not only provide an opportunity to consider Mediterranean palaeoseasonality from a North African context, but also provide a valuable opportunity to explore relationships between seasonal climate, environment and human subsistence choices. The Gebel Akhdar has an archaeological record that extends back to at least oxygen isotope stage (OIS) 5 (Douka et al., 2014; Jacobs et al., 2017) and was a likely coastal *refugium* during periods when surrounding Saharan areas were depopulated due to increased aridity (Barker et al., 2010; Cremaschi et al., 1998). Palaeoenvironmental data from the Gebel Akhdar show relatively low-magnitude long-term variations in temperature and aridity during the late Pleistocene and Holocene (Inglis, 2012; Prendergast et al., 2016b; Reade et al., 2016a;

2016b), which contrast with an archaeological record that displays significant changes in resource exploitation and landscape use across this time period (Hunt et al., 2011; Jones et al., 2016; Klein and Scott, 1986; Prendergast et al., 2016a). In particular, major changes in the seasonal pattern of resource exploitation have been identified (Prendergast et al., 2016a). Thus, palaeoseasonality data are required to evaluate the possible relationship between these changes and climatic/environmental change.

Seasonal climate variability in the Gebel Akhdar is explored here through oxygen isotope analysis of caprine and bovine tooth enamel carbonate ($\delta^{18}\text{O}_{\text{en}}$). We consider if changes in seasonality can contribute to our understanding of the subsistence changes identified in the archaeological record. Samples come from archaeological deposits excavated from two caves in the Gebel Akhdar, the Haua Fteah and Hagfet ed Dabba. The species analysed were the main prey species of human populations in the region, so the data are temporally tied to periods when humans were present within the local landscape (Klein and Scott, 1986; McBurney, 1967; McBurney and Hey, 1955). Samples date to seven distinct time slices between ~72 and 5 ka relating to the cultural phases originally defined in the Haua Fteah sequence by McBurney (1967) - Levallois-Mousterian, Dabban, Oranian, Capsian and Neolithic - and since dated with greater precision as part of a programme of renewed investigations at the site (Douka et al., 2014).

2. Background

2.1 Mediterranean palaeoseasonality

The Mediterranean climate is today typified by mild wet winters and hot dry summers. Records of palaeoprecipitation indicate that this mid-latitude winter-rainfall regime was dominant throughout the last glacial and interglacial (Abouelmagd et al., 2012; Kwiecien et al., 2009; Sultan et al., 1997). However, palaeoseasonality records show significant spatial diversity. Limpet shell data from Gibraltar indicate that seasonal

variations in sea surface temperature (SST) during the last glacial were $\sim 2^{\circ}\text{C}$ greater than it is today (Ferguson et al., 2011). Increased seasonality in temperature and precipitation during the last glacial is also inferred from vegetation and lake level studies from across southern Europe (Peyron et al., 1998). This is in contrast to the reduced seasonality reported from terrestrial and marine archives from the central Mediterranean during OIS 2 (c. 24 – 21 ka) (Hayes et al., 2005; Nimmergut et al., 1999). In the eastern Mediterranean reduced seasonal variation in precipitation is reported from the Levantine coast during OIS 4-3 (c. 70 – 53 ka), Heinrich Event 1 (c. 16 ka), and Younger Dryas (c. 12 ka) (Cheddadi and Khater, 2016; Hallin et al., 2012; Orland et al., 2012). During the Younger Dryas reduced seasonal temperature variation may also have occurred in this region (Hartman et al., 2016). Early Holocene (before c. 7.8 ka) terrestrial records from the central Mediterranean indicate that precipitation seasonality was stronger than it is today, while records from Turkey for the same time period show reduced seasonality, which increased in the mid-Holocene (after c. 6.5 ka) (Dean et al., 2018; Lewis et al., 2017; Peyron et al., 2011). Local to the Gebel Akhdar, dental cementum luminance analysis has suggested that the seasonal range in air temperatures was higher in the Neolithic (during the Holocene) than in the Palaeolithic (during the Pleistocene), but the qualitative method and lack of chronological resolution restrict comparison to other climatic records (Wall-Scheffler, 2007).

2.2 Study area: the Gebel Akhdar

The Gebel Akhdar is an upland area (maximum elevation $\sim 780\text{m}$) situated on the Mediterranean coast of northeast Libya (Fig. 1). In winter, Mediterranean cyclone activity and North Atlantic storm tracks bring precipitation to the region and in summer the northward movement of the Inter-Tropical Convergence Zone (ITCZ) brings hot, dry air from the central Sahara (Lionello et al., 2006; Sultan and Janicot, 2000). The difference

between the coldest and hottest mean monthly temperatures ranges from ~10-18°C, varying across the region with altitude (Ageena et al., 2014). The wettest months occur between December and February, when monthly total precipitation can exceed 100 mm (Şen and Eljadid, 1999; 2000). Rainfall events between May and September are extremely rare. Typically, mean annual temperatures are between 16 and 21°C, and mean annual precipitation is between 200 and 600 mm (Ageena et al., 2014; Elfadli, 2009; El Kenawy et al., 2009). Present day vegetation is dominated by maquis shrubland and steppic species (Hegazy et al., 2011).

Alluvial, tufa, and speleothem deposits indicate that the amount of moisture in the Gebel Akhdar landscape varied with time. However, there is no evidence that hyper-arid conditions, which are apparent in Late Quaternary records from elsewhere in North Africa, occurred in the Gebel Akhdar during the last 100,000 years (Prendergast et al., 2016b; Reade et al., 2016a). Low-magnitude variations are nonetheless evident, with periods of increased aridity identified during OIS 2 and 3 (Prendergast et al., 2016b; Reade et al., 2016a). These appear to correspond to increased landscape instability (Inglis, 2012; Reade et al., 2016a). Coinciding with these changes, species compositions of mammalian and molluscan assemblages vary (Klein and Scott, 1986; McBurney, 1967). However, faunal evidence comes solely from archaeological deposits, such that it is not possible to infer whether these changes reflect changing environments and habitats, or changing cultural preferences and subsistence strategies. Carbon isotope studies indicate no significant (isotopic) change in vegetation throughout the last glacial-interglacial cycle until the mid-Holocene, when a notable C₄ vegetation component is identified (Reade et al., 2016b). It has been postulated that this change is indicative of human influence on the environment, rather than a response to climatic changes (Reade et al., 2016b).

The history of human activity in the Gebel Akhdar has been investigated through large-scale excavations at the Haua Fteah cave (32.90°N, 22.05°E, ~50m asl), extensive landscape surveys, and a number of smaller excavations, including in the Hagfet ed Dabba cave (32.68°N, 21.56°E, ~360m asl) (Fig. 1). Excavations at the Haua Fteah have revealed a stratified, discontinuous sequence of human occupation that spans the late Pleistocene and Holocene. 'Middle Palaeolithic' (Pre-Aurignacian and Levalloiso-Mousterian), 'Upper Palaeolithic' (Dabban) 'Epipalaeolithic' (Oranian and Capsian), and 'Neolithic' occupation phases, determined largely on variations in the lithic technologies present in each unit, have been identified (McBurney, 1967). The upper-most Pre-Aurignacian level at the site has been dated to 71.9 ± 7.6 ka (Douka et al., 2014). The samples included in this study come from the overlying deposits, which span the Levalloiso-Mousterian to Neolithic cultural deposits, providing material from time periods within OIS 4 to 1 (Table 1). This study also analyses material from Hagfet ed Dabba, thought to date to OIS 3 based on correlation with the lithic assemblage at Haua Fteah (McBurney, 1967; McBurney and Hey, 1955).

Throughout these cultural phases, the Haua Fteah cave and surrounding environs appear to have been utilised by human populations year-round, although the specific focus of these activities varied seasonally (Prendergast et al., 2016a; Wall-Scheffler, 2007). Subsistence predominately focused on large mammal exploitation, and particularly on the hunting of Barbary sheep (*Ammotragus lervia*), mainly during summer and autumn (Klein and Scott, 1986; McBurney, 1967; Wall-Scheffler, 2007). Marine shellfish were utilised year-round in the late glacial Oranian and primarily during the cooler seasons in the later Capsian and Neolithic cultural phases (Hunt et al., 2011; Prendergast et al., 2016a). Terrestrial molluscs and wild plants were also used as food resources, although the seasonal pattern of exploitation of these resources is not known

(Barker et al., 2010; 2012; Hunt et al., 2011). Of particular note is the considerable intensification of human activity at Haua Fteah during the late glacial, and its coincidence with a notably different pattern of seasonal resource exploitation (Prendergast et al., 2016a). This study considers whether changing patterns of climate seasonality may have influenced the seasonal pattern of resource availability at this time.

3. Material and methods

3.1 Rationale

Intra-tooth $\delta^{18}\text{O}_{\text{en}}$ analysis was performed on *A. lervia*, *Bos* sp. and domestic caprid teeth from the Gebel Akhdar to infer climate seasonality. During mineralisation tooth enamel acquires a $\delta^{18}\text{O}$ signature directly related to that of the animal's body water, which reflects the isotopic composition of ingested water, and in turn is influenced by external factors, such as temperature, precipitation amount and humidity (Bryant et al., 1996; d'Angela and Longinelli, 1990; Huertas et al., 1995; Longinelli, 1984; Luz and Kolodny, 1985; Podlesak et al., 2008). The enamel nearest the tooth's occlusal surface becomes fully mineralised earlier than the enamel nearest the enamel-root junction (ERJ), such that changes in ingested water $\delta^{18}\text{O}$ during the period of mineralisation are recorded as down-tooth variations in $\delta^{18}\text{O}_{\text{en}}$ (Balasse, 2002; Fricke et al., 1998; Zazzo et al., 2010). This signal is dampened in comparison to the original input, as a result of the duration and progression of mineralisation and the animal's body water turnover rate (Passey and Cerling, 2002; Passey et al., 2005; Zazzo et al., 2005). As caprid and bovid teeth form over several months to years, down-tooth changes in $\delta^{18}\text{O}_{\text{en}}$ record seasonal variations in ingested water $\delta^{18}\text{O}$ (Fricke et al., 1998; Higgins and MacFadden, 2004; Sharp and Cerling, 1998).

Ingested water is predominately derived from drinking water and from water contained in the diet. The contribution of the two pools to an animal's body water is

dependent on species' ecology and behaviour. *A. lervia* meet their water requirements solely through dietary sources (Cassinello, 1998; Hampy, 1978), thus their $\delta^{18}\text{O}_{\text{en}}$ typically reflects that of plant water, which is mediated by water availability, temperature and relative humidity (Barbour, 2007; Gat et al., 2007; Marshall et al., 2008). *Bos* sp. and domestic caprids require access to drinking water; sources can include meteoric, surface and ground waters. The $\delta^{18}\text{O}$ of these pools are affected by climatic parameters such as temperature, rainfall amount, humidity, evaporative modification, and air mass trajectory (Dansgaard, 1964; Darling et al., 2005; Rozanski et al., 1992). The seasonal fluctuation of $\delta^{18}\text{O}$ in surface and plant waters is highly variable, but ultimately depends on the $\delta^{18}\text{O}$ of water entering the system combined with the process of evapotranspiration (Alstad et al., 1999; Ehleringer et al., 1992; Gat et al., 2007). In the context of the Gebel Akhdar environment, seasonal minima in plant and surface water $\delta^{18}\text{O}$ occur in winter, when they most closely reflect the $\delta^{18}\text{O}$ of precipitation ($\delta^{18}\text{O}_{\text{precip}}$). The strongest climate variable influencing $\delta^{18}\text{O}_{\text{precip}}$ is precipitation amount; $\delta^{18}\text{O}$ maxima occur in summer, when water input to these sources is at its minimum and evapotranspiration at its maximum (Dawson et al., 2002; Ehleringer and Dawson, 1992; Prendergast et al., 2015).

3.2 Sample selection

Tooth enamel from 28 *A. lervia*, 6 *Bos* sp. and 5 domestic caprids from the Haua Fteah, 9 *A. lervia* from the Hagfet ed Dabba, and 2 modern domestic caprid from the Gebel Akhdar are analysed for their oxygen isotope composition in this study. Caprid teeth were upper and lower third molars (M3s). Bovid samples were upper and lower M2s and M3s. Further sample information is provided in Supplementary Table 1. The stratigraphic provenance, cultural attribution and chronological association of the archaeological samples are detailed in Table 1. These samples do not show direct evidence of human

manipulation (e.g. cut marks, burning, fracturing), but examples of such modifications have been identified on other skeletal elements from the same species found within the same contexts at the sites (Klein and Scott, 1986). The modern caprid teeth were collected from discarded mandibles found during landscape surveying fieldwork and are analysed to provide comparative data from the modern Gebel Akhdar environment. Samples from the Haua Fteah are curated in the Museum of Archaeology and Anthropology, University of Cambridge. Samples from the Hagfet ed Dabba are curated in the Natural History Museum, London.

3.3 Enamel sampling and isotopic analysis

Enamel samples were collected down the length of the tooth at approximately 3mm intervals, using a 1 mm-diameter cylindrical drill bit held perpendicular to the tooth growth axis. Between 7 and 16 samples were collected per tooth, as determined by crown height, and enamel was sampled through the enamel depth, ending as close to the enamel-dentine junction as was possible. In total, 306 individual enamel samples were collected. Powdered enamel was chemically pre-treated following the method described by Balasse et al. (2002) to remove organic and secondary carbonate material. The treated powder was isotopically analysed at the Godwin Laboratory, Department of Earth Sciences, University of Cambridge. Samples were analysed on an automated Gasbench interfaced with a Thermo Finnigan MAT 253 isotope ratio mass spectrometer, being reacted with 100% orthophosphoric acid for 2 hours at 70°C in individual vessels. All analyses were performed on the carbonate phase of the enamel and results are reported with reference to the international standard VPDB calibrated through the NBS19 standard (Coplen, 1995). The long-term analytical precision for $^{18}\text{O}/^{16}\text{O}$ is better than $\pm 0.11\%$. Statistical analysis was performed using SPSS v. 19 (Statistical Package for Social Sciences) and statistical significance was accepted at $p < 0.05$.

4. Results

$\delta^{18}\text{O}_{\text{en}}$ intra-tooth profiles are displayed in Figures 2, 3 and 4 and results are summarised in Table 2 and 3. The full dataset is available in Supplementary Table 1. The data presented in Figures 2 and 4 have been wiggled-matched to remove noise introduced by differences in birth season and rate of tooth development. Profiles were aligned on the x-axis using the intra-tooth $\delta^{18}\text{O}_{\text{en}}$ minima/maxima. There are three exceptions: HR108 and HR223 do not display clear minima/maxima and the presented sequences are plotted in relation to measurements from the enamel-root junction. HR17 possesses 2 potential maxima, separated by a potential outlying data point; in this instance the profile was shifted according to the maximum that produced a sequence most similar to the other profiles within that grouping. Supplementary Figure 1 and 2 display the unaligned $\delta^{18}\text{O}_{\text{en}}$ profiles and further details of the alignments made are listed in Supplementary Table 1.

4.1 *Modern caprids*

The two modern domestic caprids produced very similar results (Fig. 2a, Table 2). The mean $\delta^{18}\text{O}_{\text{en}}$ for each animal is $-4.0 \pm 1.1\text{‰}$ and $-4.1 \pm 0.8\text{‰}$, respectively, and the intra-tooth amplitude of variation is 3.7‰ and 3.1‰ . That this similarity occurs despite the samples being found at two different locations within the Gebel Akhdar, approximately 50km apart, is notable. No information regarding how these animals were reared is available, but the similarity in results suggests they had access to isotopically similar water sources, which was seasonally variable.

4.2 *Haua Fteah*

Mean $\delta^{18}\text{O}_{\text{en}}$ values for *A. lervia* vary by stratigraphic layer from $-1.4 \pm 0.6\text{‰}$ in the Neolithic (Layer VIII, Fig. 2d) to $1.1 \pm 0.7\text{‰}$ in the Dabban (Layer XX, Fig. 2h). Of much greater significance is the variation in the amplitude of intra-tooth $\delta^{18}\text{O}_{\text{en}}$ by stratigraphic

layer (Kruskal-Wallis, $H(6)=18.696$, $p<0.05$). The largest intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation, and by inference severity of seasonality, is recorded in the Layer XIV-XV samples, which are associated with the late glacial Oranian occupation at the Haua Fteah (Fig. 2f). Mean intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation for this layer is $6.1\pm 0.8\text{‰}$ (Table 2). In comparison, across all other layers, *A. lervia* mean intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation ranges from $2.4\pm 0.7\text{‰}$ in the Neolithic (Layer VI, Fig. 2c) to $4.5\pm 0.6\text{‰}$ in Dabban (Layer XVII, Fig. 2g) (Table 2). For absolute $\delta^{18}\text{O}_{\text{en}}$ values, while both intra-tooth $\delta^{18}\text{O}_{\text{en}}$ maxima and minima vary significantly between temporal periods ($H(7)=25.469$ and $H(7)=20.698$, respectively, $p<0.05$), over time the variability of the seasonal maximum isotope values (3.8‰) is notably greater than the variability of the seasonal minimum isotope values (2.5‰). This indicates that temporal change affected the seasonal maximum greater than the seasonal minimum.

For the Neolithic, both wild *A. lervia* and domestic caprid samples were analysed. Results indicate no difference between these two groups either in the amplitude of intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation (Mann-Whitney, $U=26.000$, $z=0.123$, $p>0.05$) or in the absolute $\delta^{18}\text{O}_{\text{en}}$ maximum and minimum values ($U=30.500$, $z=0.678$ and $U=32.000$, $z=0.858$, respectively, $p>0.05$), suggesting the animals had access to isotopically identical waters. The amplitude of intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation in the Neolithic samples (Fig. 2b-d) is low in comparison to the late glacial Oranian samples (Fig. 2f), and the *A. lervia* samples display the lowest absolute $\delta^{18}\text{O}_{\text{en}}$ values in the entire data set. The Neolithic domestic caprids have a similar average amplitude of intra-tooth variation to the modern domestic caprid samples ($3.1\pm 1.5\text{‰}$ compared to $3.4\pm 0.3\text{‰}$), and absolute $\delta^{18}\text{O}_{\text{en}}$ values that are $\sim 2\text{-}4\text{‰}$ higher than the modern specimens (Table 2).

Bos sp. samples were available for analysis from the Oranian and Capsian layers at Haua Fteah. Results show no difference in the mean amplitude of intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation between the Oranian ($2.3\pm 0.8\text{‰}$, Fig. 3b) and Capsian ($2.0\pm 0.8\text{‰}$, Fig. 3a)

($U=5.500$, $z=0.443$, $p>0.05$). A sinusoidal pattern of variation is only weakly expressed in all teeth and is small compared to the contemporaneous *A. lervia* samples (Table 2). Mean $\delta^{18}\text{O}_{\text{en}}$ for *Bos* sp. are approximately 3‰ lower than for *A. lervia* in the Oranian phase, and approximately 1‰ lower than for *A. lervia* in the Capsian phase.

4.3 Hagfet ed Dabba

A. lervia from Hagfet ed Dabba show mean intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation of $4.5\pm 0.9\text{‰}$ for Layer II, $4.7\pm 0.5\text{‰}$ for Layer VI, and $3.9\pm 1.0\text{‰}$ for Layer VI (Table 3). There is no significant difference in the amplitude of variation between these layers ($H(2)=1.867$, $p>0.05$), nor in the absolute maximum and minimum $\delta^{18}\text{O}_{\text{en}}$ values ($H(2)=1.770$ and $H(2)=0.291$, respectively, $p>0.05$). The Hagfet ed Dabba intra-tooth profiles (Fig. 4b-d) display a clear pattern of sinusoidal variation and are most similar in absolute value and magnitude to the Dabban intra-tooth profiles from the Haua Fteah, which is consistent with the relative chronology determined for the site based on lithic technologies (McBurney, 1967).

5. Discussion

5.1 The timing of the seasonal signal

Each *A. lervia* and domestic caprid tooth analysed records a broadly sinusoidal pattern of isotopic variation. For the modern domestic caprids, the phase of the intra-tooth signal (i.e. the position at which maximum/minimum value occurs along the tooth) is similar. Maximum $\delta^{18}\text{O}_{\text{en}}$ values occur between 16-24mm from the enamel-root junction, which indicates a spring birth (Blaise and Balasse, 2011). The phase of the intra-tooth signal in the archaeological data varies considerably between animals both within and between layers (Supplementary Figure 1). This difference is likely the result of variability in the rate of tooth development between different animals and in the season of birth. The onset of M3 formation in *A. lervia* can vary between individuals by up to 6

months (Ogren, 1962). A similar variability in the M3 isotopic signal has been demonstrated in domestic caprids, when season of birth was known to have occurred over a relatively short time period (Blaise and Balasse, 2011). Variation may also be produced by different seasons of birth. In modern *A. lervia* populations 30-50% of births can occur outside of the main April-May birth season (Cassinello and Gomendio, 1996; Gray and Simpson, 1983). This means that changes in the *timing* of seasonal extremes cannot be reliably inferred from our caprid samples. The bovid samples also do not prove informative for assessing the timing of seasonal extremes, displaying only weak, inconsistent sinusoidal patterns of variation.

5.2 Tooth enamel isotopes as a proxy for climate seasonality

The bovid samples analysed in this study (n=6) display relatively small intra-tooth ranges, which is in contrast to the high magnitude and clearly resolved *A. lervia* intra-tooth signatures. We interpret this difference as an indication that the Gebel Akhdar *Bos* sp. population had access to a relatively homogenous, seasonally invariable water source, which the *A. lervia* population was not utilising. In other environments bovid $\delta^{18}\text{O}_{\text{en}}$ has been shown to display considerably higher intra-tooth variation, interpreted as representing seasonal change in the $\delta^{18}\text{O}$ of drinking water (Fricke et al., 1998; Zazzo et al., 2002). The exception to this is a population where the main drinking water source was derived from groundwater (Fricke et al., 1998). Unlike surface water, groundwater $\delta^{18}\text{O}$ does not typically vary seasonally, and its $\delta^{18}\text{O}$ reflects a long-term annual mean $\delta^{18}\text{O}_{\text{precip}}$ (Darling, 2004). This lends support to the suggestion made previously by Reade et al. (2016a) that *Bos* sp. in the Gebel Akhdar environment could have been sourcing a considerable proportion of their drinking water from springs fed by local groundwater. If the precipitation in the Gebel Akhdar in the past was highly seasonal as it is today, groundwater sources may have provided the only year-round supply of drinking water

in the region. We therefore do not consider the *Bos* sp. samples analysed here, in the context of the Gebel Akhdar environment, to be a good proxy for palaeoseasonality. Instead, the data may provide a better proxy for annual average precipitation $\delta^{18}\text{O}$, which in the context of the Gebel Akhdar environment relates to winter rainfall.

In contrast to the bovid samples, the *A. lervia* and domestic caprid samples display clear sinusoidal patterns of intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation, and significant variations in the magnitudes of these signals are observed with time. As *A. lervia* acquires its water almost exclusively through dietary sources, the majority of this change represents variations in leaf water $\delta^{18}\text{O}$, which is strongly influenced by relative humidity (Dawson et al., 2002; Marshall et al., 2008). Under winter rainfall conditions, relative humidity is high and leaf water may therefore be closely aligned with $\delta^{18}\text{O}_{\text{precip}}$ values. In summer, under low relative humidity, leaf water $\delta^{18}\text{O}$ will be enriched by transpiration (Ehleringer and Dawson, 1992). Thus, intra-tooth $\delta^{18}\text{O}_{\text{en}}$ minimum values represent a winter ‘humid’ signal, and intra-tooth $\delta^{18}\text{O}_{\text{en}}$ maximum values represent a summer ‘arid’ signal. Changes in the magnitude of difference between these two values reflect the magnitude of the seasonal wet-dry cycle.

Unlike *A. lervia*, domestic caprids require regular access to drinking water and studies in similar Mediterranean semi-arid environments have interpreted intra-tooth $\delta^{18}\text{O}_{\text{en}}$ as representative of seasonal variations in drinking water $\delta^{18}\text{O}$ linked to seasonal temperature change (Hallin et al., 2012). However, in the context of the Gebel Akhdar, where year-round rainfall does not occur, we argue this interpretation is not applicable. Heavy reliance on drinking water in such an environment would require groundwater resources to be utilised during the summer dry period, which would produce $\delta^{18}\text{O}_{\text{en}}$ variation more similar to that observed for the bovids. This is not the pattern we observe in the Gebel Akhdar data, and the similarities between the Neolithic *A. lervia* and domestic

caprids strongly suggest that a significant proportion of the domestic caprids water requirements were being met by water contained in the diet.

Seasonal mobility, either over large lateral distances or altitudinal gradients also influences intra-tooth $\delta^{18}\text{O}$ (Balasse, et al., 2002; Britton et al., 2009). However, none of the species analysed in this study are known to undertake long-distance seasonal migrations, and while modern *A. lervia* populations display different seasonal habitat preferences within a defined home range, this does not equate to seasonal variations in the plant species composition of their diet (Hampy, 1978; Ogren, 1962). Altitudinal mobility within the Gebel Akhdar may contribute to the intra-tooth $\delta^{18}\text{O}_{\text{en}}$ signatures, although we argue its influence is limited. Altitudinal $\delta^{18}\text{O}_{\text{precip}}$ gradients in the Eastern Mediterranean are $\sim 0.2\text{‰ } 100\text{m}^{-1}$ (El-Asrag et al., 2003) indicating that with a maximum elevation of 870m, the influence of such movement in the Gebel Akhdar would be less than 2‰. Furthermore, as seasonal migration is a behaviour typically used to limit exposure to seasonal climatic or environmental extremes, it is commonly represented by a reduction in the amplitude of intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation (Britton et al., 2009). In the context of the Gebel Akhdar, utilising coastal areas in winter and upland areas in summer would provide the most stable year-round environmental conditions, but this would dampen the intra-tooth $\delta^{18}\text{O}$, meaning that the true magnitude of climate seasonality within the Gebel Akhdar would be greater than what is represented in the $\delta^{18}\text{O}$ signatures. Therefore, we argue that $\delta^{18}\text{O}$ intra-tooth profiles from the Gebel Akhdar can be used to infer seasonal climate variation.

5.3 Late Quaternary palaeoseasonality in the Gebel Akhdar

From the Haua Fteah and Hagfet ed Dabba sequences, we observe an increase in the magnitude of intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation, and therefore the magnitude of climate seasonality, from the Levallois-Mousterian (c. 73.3 – 64.0 ka) to the Dabban phase (c.

32.8 – 22.0 ka), and from the Dabban to the Oranian phase (c. 16.6 – 14.7 ka). After the peak in seasonality during the late glacial (the Oranian phase), a decline is then observed in the Capsian phase (c. 12.6 – 7.9 ka) and Neolithic phase (c. 7.4 – 6.2 ka). The lowest magnitude of seasonal variation is observed within Neolithic Layer VI (c. 6.3 ka). However, the possible influence of dietary changes on the Gebel Akhdar caprid isotope $\delta^{18}\text{O}_{\text{en}}$ signal in the Neolithic, namely the considerable increase of C_4 plants to the diet, should also be considered (Reade et al., 2016b).

In conjunction with changes in the magnitude of variation, temporal changes to absolute $\delta^{18}\text{O}_{\text{en}}$ values also occur in the Gebel Akhdar data. A steady decrease in *A. lervia* intra-tooth $\delta^{18}\text{O}_{\text{en}}$ minima of $\sim 2.5\text{‰}$ occurs across the time periods considered (Fig. 2, Table 2). Taking into account the influence of the glacial-interglacial change in global ice volume on ocean $\delta^{18}\text{O}$ and $\delta^{18}\text{O}_{\text{precip}}$ (Adkins et al., 2002; Schrag et al., 1996), and considering a change in precipitation source as unlikely (Abouelmagd et al., 2012; Sultan et al., 1997), the majority of the variation in intra-tooth $\delta^{18}\text{O}_{\text{en}}$ minimum values ($\sim 1.5\text{‰}$) most likely represents a climatic influence on $\delta^{18}\text{O}_{\text{precip}}$ values. Within the Gebel Akhdar, $\delta^{18}\text{O}_{\text{precip}}$ is most strongly influenced by the amount of precipitation (Prendergast et al., 2015). This is similar to observations at the Soreq cave site (Israel, 31.45°N, 35.03°E), where weighted annual average $\delta^{18}\text{O}_{\text{precip}}$ increased by $1.02 \pm 0.11\text{‰}$ for every 100mm decrease in annual precipitation amount (Bar-Matthews et al., 2003). If a similar relationship occurs between $\delta^{18}\text{O}_{\text{precip}}$ and precipitation amount in the Gebel Akhdar, a 1.5‰ decrease in minimum $\delta^{18}\text{O}_{\text{en}}$ values would equate to an increase in winter rainfall of an order of $\sim 100\text{-}200\text{mm}$. While a change of this magnitude would influence local plant and animal communities, it is no greater than the year-to-year rainfall variability that occurs today in the Gebel Akhdar (Şen and Eljadid, 1999; 2000), and it is unlikely to have resulted in a major shift in the dominant ecosystem type in the region. Therefore,

our data suggest a relatively consistent winter rainfall amount occurred in the Gebel Akhdar through OIS 4 – 1. It is important to note that $\delta^{18}\text{O}_{\text{en}}$ is dampened relative to the original input signature. However, this dampening is related to animal physiology, such that the temporal change observed here reflects the external environment.

A. lervia intra-tooth $\delta^{18}\text{O}_{\text{en}}$ maxima display greater temporal variation than minimum values, indicating that changes to summer conditions were of a greater magnitude than winter conditions over the time period considered. Once glacial-interglacial ice volume $\delta^{18}\text{O}$ changes have been accounted for, we observe a temporal variation of $\sim 2.8\text{‰}$ in intra-tooth $\delta^{18}\text{O}_{\text{en}}$ maxima. The highest intra-tooth maxima occur in samples dating to the late glacial (c. 16.6 – 14.7 ka), indicating that seasonal aridity was more severe at this time. This could be driven by higher temperature, lower rainfall amount, and/or changes in wind speed/direction. The increased aridity is unlikely to relate to higher temperatures, as other palaeoclimate archives from within the Gebel Akhdar and surrounding Mediterranean indicate colder temperatures during this time period (e.g. Cheddadi and Khater, 2016; Hayes et al., 2005; Nimmergut et al., 1999; Prendergast et al., 2016b). A modest decrease in precipitation amount in the Gebel Akhdar has been shown during the late glacial, while across North Africa a contemporaneous reduction in the northward limit of monsoon-derived precipitation and an increase in the Saharan dust flux to the Mediterranean environment suggest greater aridity in the Sahara and a strengthening of arid air mass movements northwards (Bout-Roumazeilles et al., 2007; Prendergast et al., 2016b; Yan and Petit-Maire, 1994). It therefore seems most likely that the pattern observed in our data was driven by the interplay of a relatively small reduction in (winter) rainfall, combined with an enhancement in the strength and aridity of the summer air masses, both in terms of intensity and duration of each season.

The general pattern of increasing seasonality from OIS 4 to 2 that is observed for the Gebel Akhdar is also reflected in vegetation, lake level, and marine mollusc archives from western and northern Mediterranean regions, which show increased temperature and precipitation seasonality (Ferguson et al., 2011; Peyron et al., 1998). These are in contrast to the reduced seasonality reported from the eastern Mediterranean Levantine coast (Cheddadi and Khater, 2016; Hartman et al., 2016; Orland et al., 2012). From the late glacial to the Holocene the magnitude of seasonal variation decreases in the Gebel Akhdar. An early Holocene reduction in seasonality is also reported from Turkey (Dean et al., 2018; Lewis et al., 2017), while increased seasonality is recorded in the eastern Mediterranean (Orland et al., 2012; Stevens et al., 2001). These records highlight the high degree of variability across the basin and between archive type.

By directly comparing enamel isotope-based seasonality data, some of this between-archive noise can be removed. In this instance, comparable enamel-based seasonal data are available for the Levantine coast for OIS 4-3 (c. 70-53 ka) (Hallin et al., 2012) and for the late glacial (c. 16 – 11.5 ka) (Hartman et al., 2016). Comparing the data from Haua Fteah Layers XXXII, XXXIII, XXXIV (c. 73 – 64 ka) with that of Hallin et al.'s (2012), we observe a similar magnitude of $\delta^{18}\text{O}_{\text{en}}$ variation between the Gebel Akhdar's *A. lervia* ($3.5 \pm 0.7\text{‰}$) and the Levantine gazelle ($2.8 \pm 0.6\text{‰}$) and goat ($3.7 \pm 1.5\text{‰}$). Data from both regions support the interpretation of a relatively weak seasonal amplitude during this time period, although we do not find evidence for year-round rainfall in the Gebel Akhdar, as is proposed for the Levant (Hallin et al., 2012). Absolute $\delta^{18}\text{O}_{\text{en}}$ values from the Gebel Akhdar are higher than those from the Levant, suggesting that the southwest part of the Eastern Mediterranean basin may have been more arid than the eastern coast at this time.

The most significant period of seasonal aridity in the Gebel Akhdar (c. 16.6 – 14.7 ka) and the following reduction in the Younger Dryas/Early Holocene (c. 12.6 – 7.9 ka) coincide chronologically with the gazelle enamel-based seasonal data from the Levantine coast, which correspond to the Early (c. 16 -14 ka) and Late Natufian (c. 12.9 - 11.5 ka) archaeological phases (Hartman et al., 2016). In the Levant, $\delta^{18}\text{O}_{\text{en}}$ changes have been interpreted as indicating a decline in temperature between the Early and Late Natufian, but not an increase in aridity (Hartman et al., 2016). Most interesting for the comparison with the Gebel Akhdar record is that, while a decrease in the amplitude of intra-tooth $\delta^{18}\text{O}_{\text{en}}$ variation is identified for both regions between the earlier and later archaeological phases, Hartman et. al (2016) observe greater change in the wet season signature, whereas the Gebel Akhdar data clearly show greater variation in the dry season signature. While part of this difference may lie in the temporal span of the two periods (the Late Natufian phase is restricted to the Younger Dryas, while the Capsian phase may stretch into the Holocene), this nonetheless again highlights the spatial diversity of climate seasonality in the Mediterranean environment, and the need for local records from which to make comparisons with archaeological archives. In the context of this comparison, the shift in the magnitude of seasonality in the Gebel Akhdar appears to have been far greater than that evident in the Levant.

5.4 Impacts on resource availability in the Gebel Akhdar

Large seasonal variations in environmental aridity, mediated by the combined effect of dry season intensity and amount of winter rainfall, would have resulted in considerable seasonal variations in the plant and animal resources available in the local landscape. Under increased seasonal aridity, drought-sensitive species in particular would find it increasingly difficult to maintain a year-round presence in the region. The increased seasonality that occurred in the late glacial coincides with a time when human

activity at the Haua Fteah intensified (Barker et al., 2010). A concurrent and significant increase in marine and terrestrial mollusc exploitation is also noted and has been suggested to indicate a high level of resource pressure (Prendergast et al., 2016a). In particular, the year-round exploitation of marine shellfish as a food resource may have acted as an important dietary supplement (Prendergast et al., 2016a). This pattern of mollusc exploitation could indicate a reduction in terrestrial resource availability caused by increased seasonal environmental aridity. However, the potential role of cultural preference in food selection should not be overlooked. It is also possible that the increasingly arid conditions in adjacent regions of North Africa increased the population within the Gebel Akhdar, which would have increased pressure on local food sources, independent of local climate change. Marine and terrestrial mollusc exploitation is also evident in the Capsian and Neolithic phases (Hunt et al., 2011). In these periods, marine shellfish collection appears to have been an activity largely restricted to the winter months (Prendergast et al., 2016a), suggesting that terrestrial food sources during the summer dry season were likely available in greater abundance than in the Oranian phase.

Large mammal exploitation at the Haua Fteah and Hagfet ed Dabba predominately focused on the Barbary sheep (*A. lervia*), although large bovids were also targeted (Klein and Scott, 1986; McBurney, 1967). The persistence of *A. lervia* as the dominant prey species is not particularly informative from an environmental perspective. This species, while adapted to xeric environments, has a wide environmental tolerance and thus its presence throughout the faunal assemblage at the Haua Fteah does not necessarily indicate a persistently arid environment. Hunting of *A. lervia* appears to have occurred year-round during all cultural phases, with a slight emphasis on the summer and autumn months particularly in the Capsian (Wall-Scheffler, 2007). This coincides with the winter exploitation of marine shellfish (Prendergast et al., 2016a) and could indicate seasonal

variations in resource availability. Sample size has restricted the analysis of the season of hunting for *Bos* sp. at the Haua Fteah (Klein and Scott, 1986). However, larger abundances in the faunal assemblage during the Levallois-Mousterian and Capsian do correspond to the periods of relatively low seasonal variation, indicating that the species may have occurred in greater numbers in environments with less year-round variability.

The increase in humidity and decline in seasonality that occurred from the Oranian to the Neolithic phases is likely to have produced an increasingly stable environment. This coincides with evidence for an increase in resource management by human populations. Wild plant exploitation, and potentially the delayed use of these resources, is evident in the Capsian and Neolithic phases (Barker et al., 2010; Lucarini et al., 2016) and domestic caprids are present in the faunal record during the Neolithic (Klein and Scott, 1986; McBurney, 1967). The role of climate in these changes is not clear, but a less seasonally variable climate would have resulted in more consistent year-round access to certain resources, which could have increased opportunities for planned, rather than opportunistic, resource utilisation.

6. Conclusion

This study presents the largest terrestrial palaeoseasonality study available for North Africa to date. We interpret our results as indicative of changes in seasonal aridity in the Gebel Akhdar, produced by the interaction between the amount of winter precipitation and the strength of the summer dry season. This was produced by the complex interplay of moist mid-latitude and dry low-latitude air masses. While previous palaeoenvironmental archives have indicated relatively stable climate conditions throughout the late Pleistocene and Holocene in the Gebel Akhdar, they have only been able to assess such changes at supra-annual scales. This study demonstrates that

significant changes in the magnitude of climate seasonality occurred across the last glacial and present interglacial cycle.

Variations in the seasonal climate cycle would have had a considerable impact on the floral and faunal resources available to local human populations. The greatest magnitude of climate seasonality is identified in the late glacial (c. 16.6 to 14.7 ka), which coincides with a period of intensified human activity in the Haua Fteah cave and changes in seasonal food resource exploitation. The increased seasonal aridity could have been produced by a modest decrease in winter precipitation and an intensification of arid air masses reaching the Gebel Akhdar from the Sahara during the summer. Significant increases in seasonal aridity likely reduced the availability of drought-sensitive flora and fauna in the region, thus altering the range of subsistence options available to human populations at the time.

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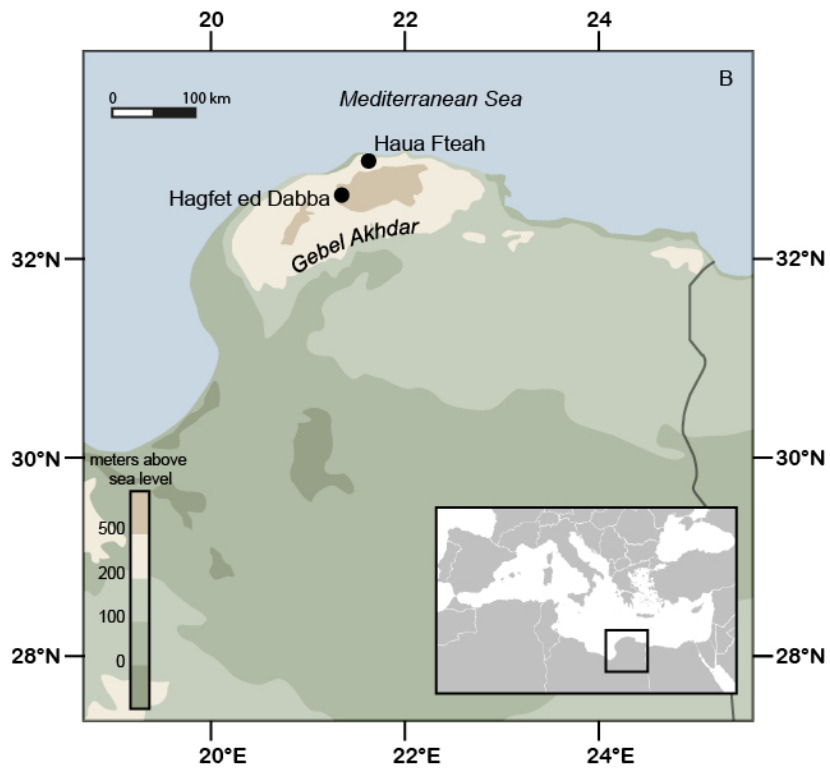


Figure 1: Location of the Gebel Akhdar, Haul Fteah and Hagfet ed Dabba on the North African coastline.

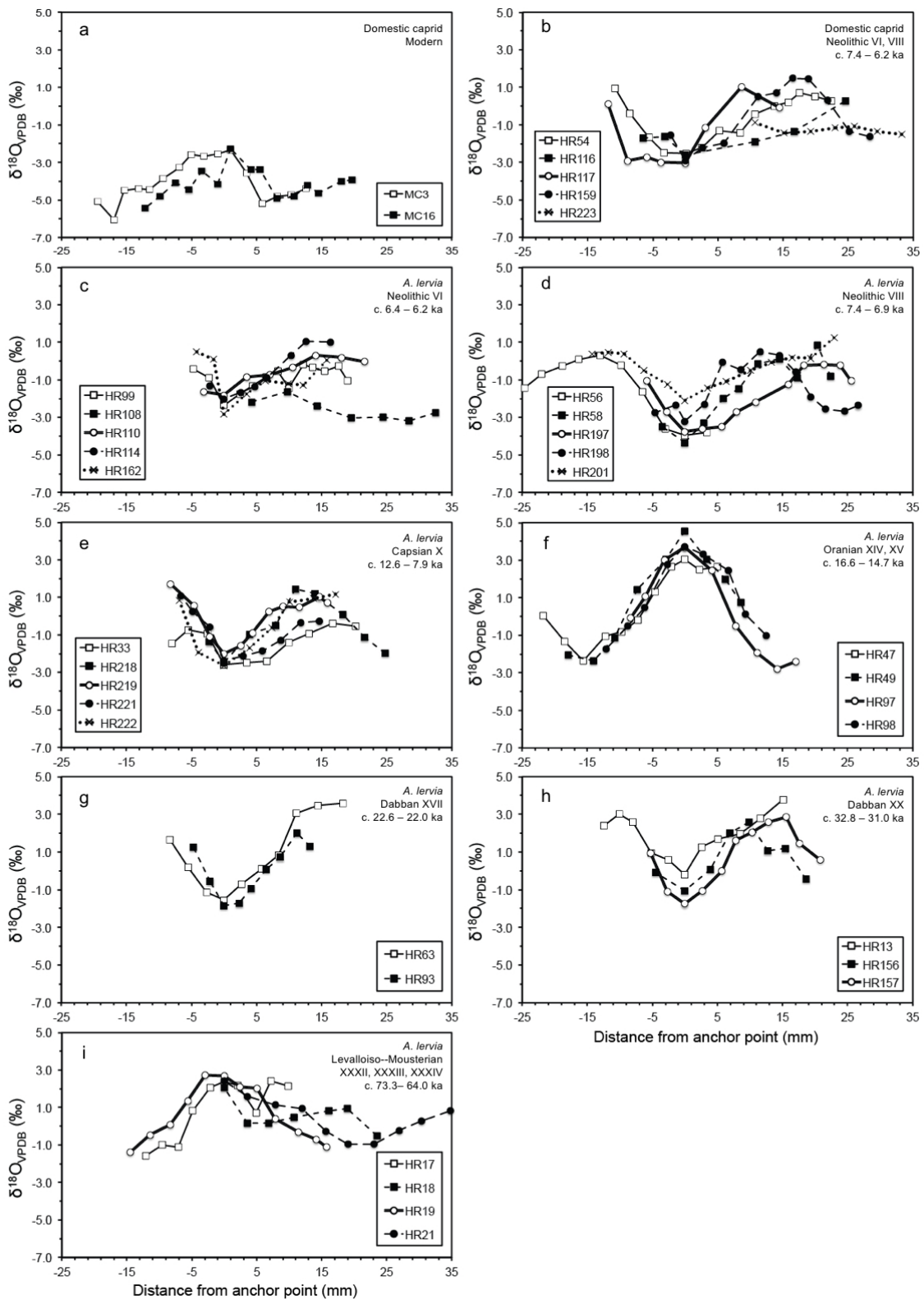


Figure 2: Modern domestic caprid from the Gebel Akhdar and archaeological *A. lervia* and domestic caprid wiggle-matched $\delta^{18}\text{O}$ intra-tooth profiles from Haua Fteah. Each line represents a sampled tooth. Archaeological samples are grouped by stratigraphic provenance.

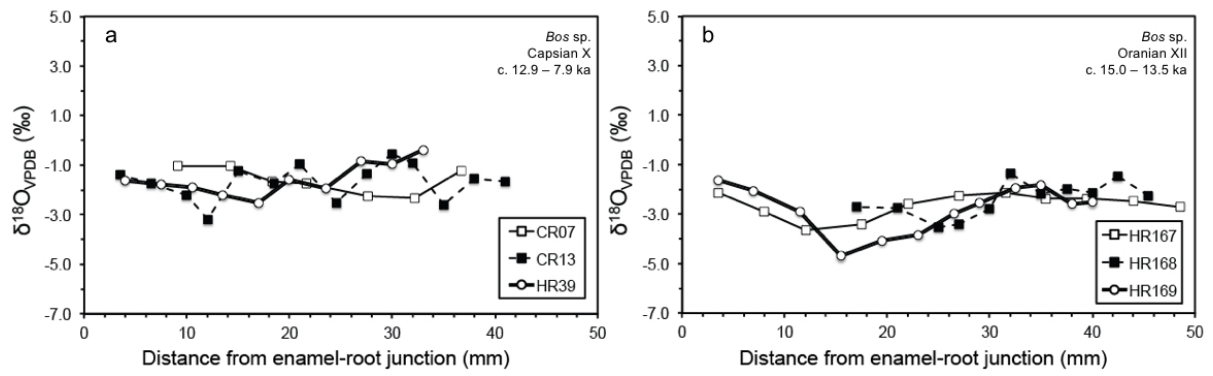


Figure 3. *Bos sp.* $\delta^{18}\text{O}$ intra-tooth profiles, grouped by stratigraphy, with each line representing a sampled tooth. Profiles are plotted in relation to measurements from the enamel-root junction.

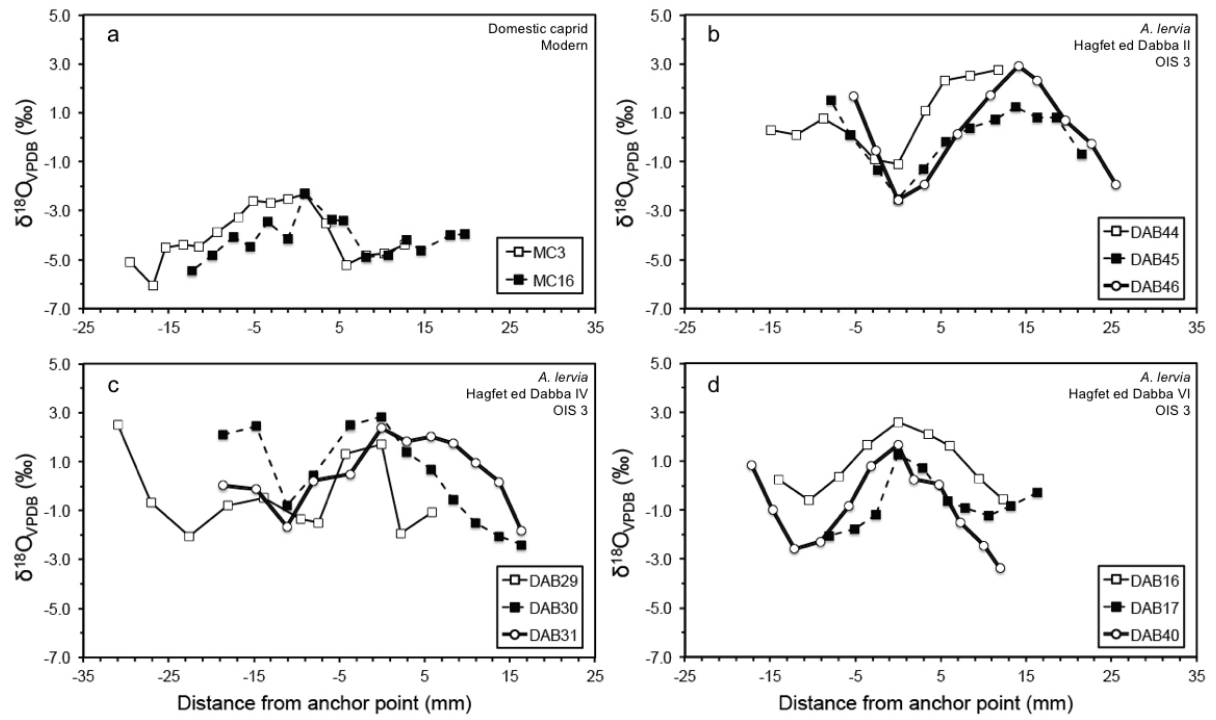


Figure 4: Modern domestic caprid from the Gebel Akhdar and archaeological *A. lervia wiggled-matched* $\delta^{18}\text{O}$ intra-tooth profiles from Hagfet ed Dabba. Each line represents a sampled tooth. Archaeological samples are grouped by stratigraphic provenance.

Table 1: The chronology of the Haua Fteah archaeological sequence according to McBurney (1967) and the Bayesian statistical model from Douka et al. (2014) at 68.2% and 95.4% confidence. Age estimations from specific layers/layer groupings from which samples analysed in this study come from are also provided. The listed age estimates presented are made using dates published in Douka et al. (2014) with correlations in site stratigraphy made between the McBurney excavations and the recent TRANS-NAP excavations. Dates with a * are based on a single sample, dates in italics are from Bayesian model estimates, all others are determinations from multiple radiocarbon samples.

Phase	Layers (McBurney, 1967)	Proposed Age (ka) for cultural phases			Age estimations for specific layers/layer groupings from which samples in this study came	
		McBurney (1967)	Douka et al. (2014)		Layer	Proposed Age (ka)
			68.2%	95.4%		
Levalloiso- Mousterian	XXXIV-XXV	65 - 40	68.1 -48.7	73.3 – 43.5	XXXII,XXXIII,XXXIV	73.3 – 64.0
					XX	32.8 – 31.0
Dabban	XXV-XVI	40 - 15	40.0 -18.1	43.5 – 17.1	XVII	22.6 – 22.0*
					XIV, XV	16.6 – 14.7
Oranian	XV-XI	15 - 10	16.1 -13.1	17.2 – 12.5	XII	15.0 – 13.5
Capsian	X-IX	10 - 7	12.3 -9.3	12.7 – 7.9	X	12.6 – 7.9
					VIII	7.4 – 6.9
Neolithic	VIII-IV	7 - 4.7	7.7 -6.2	9.3 – 5.4	VI	6.4 - 6.2*

Table 2. Summary of results for each tooth analysed from the Haua Fteah and modern samples. For each stratigraphic grouping mean and standard deviation (SD), (or mid-point if n=2) statistics are provided Cultural attributions follow McBurney (1967).

Layer	Proposed Age (ka)	Cultural attribution	Species	Number of teeth sampled (total number of analyses)	Mean intra-tooth mean $\delta^{18}\text{O}$ (VPDB, ‰)	Mean intra-tooth maximum $\delta^{18}\text{O}$ (VPDB, ‰)	Mean intra-tooth minimum $\delta^{18}\text{O}$ (VPDB, ‰)	Mean intra-tooth range $\delta^{18}\text{O}$ (VPDB, ‰)
n/a	Modern	n/a	Domestic caprid	2 (31)	-4.1	-2.3	-5.7	3.4
VI, VIII	7.4 - 6.2	Neolithic	Domestic caprid	5 (46)	-1.1 ± 0.4	0.6 ± 0.9	-2.5 ± 0.6	3.1 ± 1.5
VI	6.4 - 6.2	Neolithic	<i>A. lervia</i>	5 (44)	-1.1 ± 0.8	0.0 ± 1.0	-2.4 ± 0.6	2.4 ± 0.7
VIII	7.4 - 6.9	Neolithic	<i>A. lervia</i>	5 (58)	-1.4 ± 0.6	0.6 ± 0.5	-3.5 ± 0.9	4.0 ± 0.7
X	12.6 - 7.9	Capsian	<i>A. lervia</i>	5 (47)	-0.7 ± 0.5	1.0 ± 0.8	-2.4 ± 0.3	3.4 ± 0.7
XIV, XV	16.6 - 14.7	Oranian	<i>A. lervia</i>	4 (38)	0.7 ± 0.4	3.8 ± 0.6	-2.3 ± 0.4	6.1 ± 0.8
XVII	22.6 - 22.0	Dabban	<i>A. lervia</i>	2 (19)	0.5	2.8	-1.7	4.5
XX	32.8 - 31.0	Dabban	<i>A. lervia</i>	3 (30)	1.1 ± 0.7	3.1 ± 0.6	-1.0 ± 0.8	4.1 ± 0.5
XXXII, XXXIII, XXXIV	73.3 - 64.0	Levalloiso-Mousterian	<i>A. lervia</i>	4 (39)	0.6 ± 0.2	2.4 ± 0.3	-1.1 ± 0.6	3.5 ± 0.7
X	12.6 - 7.9	Capsian	<i>Bos</i> sp.	3 (31)	-1.6 ± 0.1	-0.7 ± 0.4	-2.7 ± 0.5	2.0 ± 0.8
XII	15.0 - 13.5	Oranian	<i>Bos</i> sp.	3 (34)	-2.6 ± 0.2	-1.7 ± 0.4	-4.0 ± 0.6	2.3 ± 0.8

Table 3. Summary of results for each tooth analysed from the Hagfet ed Dabba. Cultural attributions follow McBurney (1967).

Layer	Proposed Age	Cultural attribution	Species	Number of teeth sampled	Total number of analysis	Mean intra-tooth mean $\delta^{18}\text{O}$ (VPDB, ‰)	Mean intra-tooth maximum $\delta^{18}\text{O}$ (VPDB, ‰)	Mean intra-tooth minimum $\delta^{18}\text{O}$ (VPDB, ‰)	Mean intra-tooth range $\delta^{18}\text{O}$ (VPDB, ‰)
II	OIS 3	Dabban	<i>A. lervia</i>	3	33	0.3 ± 0.4	2.4 ± 0.8	-2.1 ± 0.8	4.5 ± 0.9
IV	OIS 3	Dabban	<i>A. lervia</i>	3	35	0.2 ± 0.5	2.6 ± 0.2	-2.1 ± 0.3	4.7 ± 0.5
VI	OIS 3	Dabban	<i>A. lervia</i>	3	31	-0.2 ± 1.0	1.9 ± 0.7	-2.0 ± 1.4	3.9 ± 1.0