



# Up the mountain and back again: sequential stable isotope analysis reveals altitudinal migration in wild sheep (*Ovis cf. orientalis*) from the PPNA site of Nachcharini Cave, Lebanon

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## ABSTRACT

The Pre-Pottery Neolithic A (PPNA) marks an early phase in the transition from foraging to farming in Southwest Asia. Although this stage of *neolithization* shows evidence of early plant cultivation, subsistence strategies remained primarily dependent on hunting. While faunal data from the northern and southern Levant reflect regional differences in prey choice and hunting strategies, patterns in the central Levant are less well defined. In this study, we use stable carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope values measured sequentially in the tooth enamel of wild sheep (*Ovis cf. orientalis*) from the PPNA site of Nachcharini Cave in northeastern Lebanon to reconstruct seasonal mobility and ecology in this prey species. The isotopic sequences show negative covariation between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values, consistent with seasonal altitudinal migration between alpine  $\text{C}_3$ -dominant summer ranges and lower-elevation wintering grounds with mixed  $\text{C}_3/\text{C}_4$  vegetation. This mobility pattern suggests that sheep occupied the alpine zone only seasonally, requiring PPNA hunters to possess detailed ecological knowledge to target them during their highland presence. The broadly consistent placement of  $\delta^{18}\text{O}$  maxima suggests births clustered within a specific season, likely timed to align with forage availability and the physiological demands of migration, as seen in modern montane wild sheep. Low inter-individual  $\delta^{18}\text{O}$  variation supports relatively short-term faunal accumulation, while higher  $\delta^{13}\text{C}$  variation reflects dietary and environmental heterogeneity. These results reinforce the interpretation of Nachcharini Cave as a seasonal alpine hunting camp and highlight the role of logistical mobility and ecological knowledge in structuring PPNA subsistence practices in the central Levant.

## 1. Introduction

The forager–farmer transition in Southwest Asia involved a complex, regionally asynchronous set of changes that began in the late Epipaleolithic and extended into the early Neolithic (Bar-Oz et al., 2004; Zeder, 2012; Bar-Yosef, 2017; Munro et al., 2018). Within this transition, the Pre-Pottery Neolithic A (PPNA) represents an important period characterized by increasing sedentism and social cohesion (Bar-Yosef, 1989; Belfer-Cohen and Goring-Morris, 2010; Mithen et al., 2011). Although this early phase of ‘*neolithization*’ shows evidence of plant cultivation (Wright, 1994; Weiss et al., 2006), the predominance of hunting shows little change from the preceding Natufian period (Munro and Grosman, 2018; Munro et al., 2018). Indeed, Belfer-Cohen and Goring-Morris (2010, 2020) have stressed the need to understand the

PPNA as the end of a longer series of Epipaleolithic cultures and practices.

In both the northern and southern Levant, the PPNA is characterized by the appearance of larger settlements, substantial architectural investment, and the emergence of communal buildings. Notable examples include Jericho and Wadi Faynan 16 in the south (Goring-Morris and Belfer-Cohen, 2022), and Jerf el Ahmar and Göbekli Tepe in the north (Watkins, 2016). These structures are often interpreted as communal spaces and focal points for social activity, reflecting newly emerging social dynamics. The elaboration of such buildings has been described as a tipping point in the development of Neolithic cultures (Goring-Morris and Belfer-Cohen, 2022). While the PPNA is increasingly well represented in both the northern and southern Levant, the archaeological record in the central region remains sparse. This makes Nachcharini

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Cave, located in northeastern Lebanon, particularly significant as one of the few known PPNA sites in this environmentally and geographically distinctive region.

Zooarchaeological evidence from the PPNA reveals considerable regional variation in hunting strategies across the Levant. In the south, faunal assemblages are typically dominated by mountain gazelle (*Gazella gazella*), alongside deer species (*Capreolus*, *Dama dama*, *Cervus elaphus*), with smaller contributions from aurochs (*Bos primigenius*), wild pigs (*Sus scrofa*), and caprines (*Capra aegagrus*, *C. ibex*, *Ovis* spp.) (Horwitz et al., 1999). A few southern sites, including el Khiam and Wadi Faynan 16, are unusual in showing a greater emphasis on wild goat (Ducos 1997; Carruthers and Dennis 2007). Sites in the northern Levant tend to be dominated by remains of Persian gazelle (*Gazella subgutturosa*), along with cervids, aurochs, wild pigs, and caprines. Notably, equids (*Equus hemionus*) form a substantial, though secondary, part of many northern assemblages (Legge and Rowley-Conwy 2000; Helmer and Gourichon 2008; Conolly et al. 2011). In contrast, faunal evidence from the central Levant is extremely limited. A mixed PPNA/Natufian deposit from Kaus Kozah Cave in western Syria is dominated by caprines but otherwise resembles northern assemblages (Napierala, 2011). In this context, the faunal assemblage from Nachcharini Cave provides a rare opportunity to examine PPNA hunting strategies in an underrepresented part of the Levant.

Located at an altitude of ~2100 masl in the Anti-Lebanon Mountains of Lebanon, Mugharat an-Nachcharini (Fig. 1) is the highest known early Neolithic site in the Levant. New radiocarbon dates place its primary occupation between approximately 11,000 and 11,600 cal BP, within the early PPNA (Rhodes, 2025). Evidence for the use of composite hunting tools comes from the lithic assemblage, which includes both

Khiam points and Hagdud truncations (Hutchings, 1991, 2011; Rhodes et al., 2020). Wild sheep (*Ovis* cf. *orientalis*) and goat (*Capra aegagrus* or *Capra ibex*) comprise the majority (~80 %) of the faunal assemblage, with a notably higher incidence of sheep among the caprines (~85 %). The mortality profile suggests a focus on prime-age adults, though several sub-adult individuals are also present. Taken together, the lithic and faunal evidence support the interpretation of Nachcharini as a short-term, task-specific hunting camp focused on wild sheep exploitation, that was used intermittently over several centuries (Rhodes, 2025). In this study, we use stable carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope values measured sequentially in the tooth enamel of wild sheep from Nachcharini to reconstruct patterns of seasonal altitudinal migration. Examining how this prey species moved across the landscape clarifies behavioral patterns and reveals how seasonal mobility shaped hunting strategies during the PPNA.

Stable isotope signatures are incorporated into the hard tissues of herbivorous mammals through the plants they consume and the water they drink, allowing researchers to reconstruct aspects of ancient ecology, including mobility patterns. Because tooth enamel forms incrementally and does not remodel after formation, it preserves the isotopic composition present at the time of mineralization (Fricke and O'Neil, 1996; Fricke et al., 1998; Kohn et al., 1998). Sequential sampling of enamel enables analysis at an intra-annual (e.g., seasonal) scale, providing insight into environmental conditions and animal behavior over time (Bryant et al., 1996; Fricke and O'Neil, 1996). Each enamel sample reflects a time-averaged signal of the isotopic variations during tooth mineralization, with a degree of signal attenuation (Balasse, 2002, 2003; Passey and Cerling, 2002; Zazzo et al., 2012; Green et al., 2025). This approach is particularly effective in hypsodont taxa, where tall tooth crowns offer extended developmental sequences for sampling. Previous studies have shown that sequential stable isotope analysis can successfully track altitudinal mobility in both modern and archaeological caprines (Balasse and Ambrose, 2005; Fisher and Valentine, 2013; Tornero et al., 2016a, 2018; Makarewicz, 2017; Makarewicz et al., 2017; Janzen et al., 2020; Hirose et al., 2021; Messana et al., 2023).

Here we use sequential stable isotope analysis of wild sheep teeth from Nachcharini Cave to reconstruct seasonal patterns of movement and environmental interaction in this prey species. Our study specifically addresses three questions:

- Do the serial isotope sequences provide evidence for seasonal altitudinal migration?
- What do patterns of  $\delta^{18}\text{O}$  variation reveal about the timing and duration of birth seasons?
- Does inter-individual variation in  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values support a brief timespan of faunal accumulation at Nachcharini?

By reconstructing seasonal patterns of movement and life history in wild sheep, this study offers new insight into the ecological knowledge, logistical mobility, and subsistence strategies of PPNA groups in the central Levant, particularly their use of high-altitude zones peripheral to major settlement sites.

## 2. Methodological background

### 2.1. Stable carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotopes

Stable carbon isotope values measured in the tissues of mammalian herbivores reflect the isotopic composition of the plants consumed and are thus useful for investigating dietary changes associated with seasonal variability in the local plant community, seasonal movement between different plant communities, and human augmentation of animal diet (Balasse et al., 2003, 2012, 2024; Makarewicz and Tuross, 2006; Britton et al., 2009; Tornero et al., 2016a,b, 2018; Makarewicz, 2017; Makarewicz et al., 2017). Plant  $\delta^{13}\text{C}$  values are predominantly controlled by photosynthetic pathway, temperature, and aridity



Fig. 1. Map of region showing location of Nachcharini Cave and other early Neolithic sites.

(Farquhar et al., 1989; O'Leary et al., 1992). C<sub>3</sub> plants (i.e., most trees, shrubs, herbs, and cool season grasses) and C<sub>4</sub> plants (i.e., tropical grasses) have different carbon-fixation pathways leading to different  $\delta^{13}\text{C}$  values. The average  $\delta^{13}\text{C}$  value of C<sub>3</sub> plants is approximately  $-26.5\text{‰}$ , while C<sub>4</sub> plants have an average of  $-12.5\text{‰}$  (Vogel, 1978; Kohn, 2010). The  $\delta^{13}\text{C}$  values of modern plants are approximately  $1.5\text{‰}$  lower than during pre-industrial times due to the broad scale burning of fossil fuels following the Industrial Revolution (Friedli et al., 1986). Additionally, the  $\delta^{13}\text{C}$  values of sheep enamel is enriched in  $^{13}\text{C}$  by a diet-tissue isotopic spacing of approximately  $14.1\text{‰}$  (Cerling and Harris, 1999). Typically, an enamel  $\delta^{13}\text{C}$  value of less than  $-8\text{‰}$  is taken to indicate a pure C<sub>3</sub> diet, while a  $\delta^{13}\text{C}$  value greater than  $-2\text{‰}$  demonstrates a pure C<sub>4</sub> diet (Cerling et al., 1997). Notably, however, in water-stressed environments, a conservative enamel  $\delta^{13}\text{C}$  value cut-off for a pure C<sub>3</sub> diet is argued to be closer to  $-7\text{‰}$  or even  $-6.5\text{‰}$  (Cerling et al., 1997; Wang et al., 2008). Using the non-overlapping cut-off points for pure C<sub>3</sub> and C<sub>4</sub> diets, it is possible to investigate the proportion of each plant type consumed by herbivores (Phillips, 2012).

In warm and arid environments, such as those in northeastern Lebanon, plant communities contain both C<sub>3</sub> and C<sub>4</sub> plants. The  $\delta^{13}\text{C}$  values of plants in these environments fluctuate seasonally based on differences in moisture availability, humidity, and nighttime temperature (Ehleringer and Dawson, 1992). The higher soil temperature requirements of C<sub>4</sub> plants means that they come into fluorescence later than C<sub>3</sub> plants, typically during the late spring and early summer, and stop growing earlier during the mid to late autumn (Liang et al., 2002; Yamori et al., 2014). Plants adapted to dry environments generally show greater water use efficiency (hence more enriched  $\delta^{13}\text{C}$  values) than those growing in wet areas, and a strong negative correlation has been shown between plant  $\delta^{13}\text{C}$  and precipitation at both a regional (Ferrio et al., 2005) and global scale (Kohn, 2010). The  $\delta^{13}\text{C}$  values of C<sub>3</sub> plants have been shown to fluctuate seasonally, with more enriched values ( $2\text{--}3\text{‰}$ ) occurring during the warmer and drier season in response to the reduction of stomatal conductance to restrict water losses (Farquhar et al., 1989; Ehleringer and Monson, 1993; Zazzo et al., 2008). Northeastern Lebanon is situated in a transitional area between the Mediterranean and Irano-Turanian phytogeographic zones, and both of these biomes are relatively depleted in  $^{13}\text{C}$  during the late winter, spring, and early summer due to reduced C<sub>4</sub> biomass and high-water availability promoting C<sub>3</sub> growth (Hartman and Danin, 2010; Yamori et al., 2014). Studies of modern plants in southern Levant report a range of  $\delta^{13}\text{C}$  values between  $-29.5\text{‰}$  and  $-22.5\text{‰}$  for C<sub>3</sub> plants and  $-14.5\text{‰}$  and  $-11.9\text{‰}$  for C<sub>4</sub> plants (Winter, 1981; Hartman and Danin, 2010). There is typically an altitudinal transition in the dominant photosynthetic pathway in regions where both C<sub>3</sub> and C<sub>4</sub> plants are present, wherein C<sub>4</sub> plants are found at lower elevations and C<sub>3</sub> plants dominate at higher elevations, due to differences in temperature and humidity (Tieszen et al., 1979; Wooller et al., 2001). An altitudinal gradient in the  $\delta^{13}\text{C}$  of C<sub>3</sub> plants has also been suggested with values becoming more enriched with increasing altitude (Körner et al., 1991). Several studies have reported an increase in the  $\delta^{13}\text{C}$  values of C<sub>3</sub> plants with increasing elevation. This pattern has been explained by the high carboxylation rates relative to stomatal conductance at higher elevations (Morecroft and Woodward 1990; Körner et al., 1991; Li et al. 2009). However, several more recent studies have documented a negative association between  $\delta^{13}\text{C}$  values of C<sub>3</sub> plants and elevation (Makarewicz and Tuross 2006; Liu et al. 2016; Tornero et al. 2018). Notably, a significant negative correlation was also shown between the  $\delta^{13}\text{C}$  values of ungulates (tissues/faeces) and grazing altitude (Lazzerini et al., 2021; Eastham and Feranec, 2024). The specific factors influencing this relationship are thought to be site specific, with several authors proposing that local climatic factors influence water availability and thereby complicate the relationship between plant  $\delta^{13}\text{C}$  and elevation (Morecroft and Woodward 1990; Liu et al. 2007).

The oxygen stable isotope values of mammalian bioapatite are primarily derived from ingested water and plants consumed (Longinelli,

1984; Luz et al., 1984). At middle and high latitudes, the  $\delta^{18}\text{O}$  values of meteoric waters are primarily controlled by water vapor source and transport patterns, as well as seasonal variation in ambient temperature, which leads to  $^{18}\text{O}$ -enriched rains during the summer and  $^{18}\text{O}$ -depleted rains in winter (Dansgaard, 1964; Gat, 1996; Rozanski et al., 1993). The  $\delta^{18}\text{O}$  values of meteoric water are indirectly reflected in the  $\delta^{18}\text{O}$  values of plant tissues, however, plant water typically has higher (i.e., more enriched)  $\delta^{18}\text{O}$  values than meteoric water due to the influence of transpiration (Yakir, 1992). Further, the degree of difference between the  $\delta^{18}\text{O}$  values of meteoric and leaf water is also affected by plant physiology, rooting depth, and relative humidity (Cernusak et al., 2016; Dodd et al., 1998). Because sheep are semi-obligate drinkers their  $\delta^{18}\text{O}$  values are affected by both the water they drink, and the plant water ingested through their diet (Makarewicz, 2017). In mountainous regions, the altitude effect causes a decrease in  $\delta^{18}\text{O}$  values with increasing altitude, due to a gradual removal of moisture from uplifted air masses with a preferential removal of  $^{18}\text{O}$  during condensation (Rozanski et al., 1993). Additionally, high elevation water sources (e.g. streams and rivers) may also be seasonally supplied with snowmelt or ice-melt, generating a release in the spring/early summer of water accumulated through cold-condition precipitation with lower  $\delta^{18}\text{O}$  (Bhatia et al., 2011). The  $\delta^{18}\text{O}$  values of precipitation in the Anti-Lebanon Mountains varies seasonally between  $-13.0\text{‰}$  and  $-3.5\text{‰}$ , whereas the values of spring water are more constant ranging annually between  $-9.07\text{‰}$  and  $-8.35\text{‰}$ , with minor seasonal fluctuations reflecting the contribution of runoff from the snowmelt. An altitude effect of  $0.14\text{‰}/100\text{ m}$  has been reported for the Anti-Lebanon Mountains based on precipitation samples collected over one year (Koeniger et al. 2016).

Stable isotope studies of wild and domestic caprines engaging in seasonal vertical mobility have identified a common pattern in sequentially collected  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values characterized by negative covariation (i.e., an inverse relationship between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values) (Tornero et al., 2016a, 2018; Makarewicz, 2017; Isaakidou et al. 2019; Varkuleviciute et al., 2021; Messana et al., 2023). In regions where both C<sub>3</sub> and C<sub>4</sub> plants are present, animals that graze at higher altitudes during summer months are associated with sequences wherein the lowest  $\delta^{13}\text{C}$  values correspond with the highest  $\delta^{18}\text{O}$  values. During the winter months, individuals grazing at lower altitudes have enamel isotope sequences wherein the highest  $\delta^{13}\text{C}$  values occur in correlation with the lowest  $\delta^{18}\text{O}$  values. It is important to note that animals seasonally inhabiting higher elevation areas (i.e., summering in alpine C<sub>3</sub> grasslands/shrublands) can show a reduced amplitude of intra-tooth variation in  $\delta^{18}\text{O}$  values due to the ingestion  $^{18}\text{O}$ -depleted water from water sources supplied by snowmelt.

## 2.2. Ecology and life history of *Ovis orientalis*

Today, the distribution of Asiatic wild sheep is restricted to Armenia, southern Azerbaijan, Cyprus, northern Iraq, southern and western Iran, and central Turkey. In contrast, during the Late Pleistocene wild sheep ranged across the geographic area referred to as the "Fertile Crescent" (Yeomans et al., 2017). The full extent of their ancient distribution is contested as it overlaps with the range of bezoar (*Capra aegagrus*) and Nubian ibex (*Capra ibex nubiana*) making the identification of archaeological bones and teeth difficult. The presence of wild sheep at PPNA sites in Lebanon and Jordan demonstrate that they still inhabited local environments after the Younger Dryas and thus coped with this climatic event. Because wild sheep are extinct in modern Lebanon, we use Anatolian wild sheep (*Ovis gmelinii anatolica*) as an analogue to better understand the ecological and life history variables that could influence patterns of variation in stable isotope values. Modern Anatolian wild sheep preferentially live in open spaces, inhabiting medium to high altitude ( $\sim 1000$  to  $2000\text{ masl}$ ) mountain shrublands and steppes, with altitudinal movement occurring in some populations following seasonal cycles: winter is spent in the midlands to lowlands, while in the summer the majority individuals move to high elevation shrublands and steppes



(Turan, 1990; Arihan, 2000; Özü, 2009). Males weigh 45 to 74 kg, while females weigh 35 to 50 kg. Body length from nose to tail varies from 105 – 140 cm. The breeding season occurs in November and December each year and the gestation period is approximately five months (148 days) with lambing occurring predominantly in May and June, but can extend into September. Observational studies have reported that lambs can feed on vegetation as soon as 10 – 15 days after birth (Arihan, 2000). It is unknown whether the wild sheep from Nachcharini were hunted during the spring as they moved to higher elevations on the plateau, or during the autumn as they began their descent to lower elevations to graze throughout the winter. The autumn migration would have provided the PPNA hunters with fatter animals with higher quality skin.

### 3. Materials

#### 3.1. Nachcharini Cave

Nachcharini Cave is located in the central ‘Ard al-Kichek plateau of the Anti-Lebanon Mountains (al-Jebel ash-Sharqi) in eastern Lebanon (Fig. 1). The modern climate of northeastern Lebanon is strongly seasonal with hot, dry summers (May to September) and cool, wet winters (November to March) with precipitation falling as either rain or snow between mid-October and mid-May. Mean annual temperature on the plateau (~2100 masl) is approximately 4.5 °C and around 17 °C at lower altitudes (~800 masl). Most of the precipitation occurs during the winter period when the plateau receives significant snowfall (~1600–1800 mm). Snow melt typically occurs between March and April. The landscape surrounding Nachcharini Cave is characterized by rolling land broken by karstic sinkholes that create small, steep-walled canyons and valleys. Much of the Anti-Lebanon Mountains support open shrubland vegetation including Aleppo oak (*Quercus infectoria*) on the lower western slopes (up to 1,300–1,400 masl) and Greek juniper (*Juniperus excelsa*) at higher elevations (Pabot 1959, Zohary 1973).

Nachcharini was first discovered by Jacques Besançon from Lumière University around 1970 and subsequently excavated by Bruce Schroeder from the University of Toronto between 1972 and 1974. AMS dates indicate an age of approximately 10,900 to 11,600 cal BP and fall well within the range of PPNA sites in the region (e.g. Netiv Hagdud in the Jordan Valley). The faunal remains recovered from Nachcharini Cave are likely the result of a series of hunting events that occurred over the span of several centuries (Rhodes, 2025). The lithic assemblage is dominated by Khiam points and Hagdud truncations thought to have been components of composite hunting tools (review in Rhodes et al., 2020). Impact fractures on the distal end of many of the Khiam points suggest massive failure consistent with high-velocity impact indicating that these are armatures for light projectiles. Wild caprines dominate the faunal assemblage (~80 %), with a limited additional presence of mountain gazelle (*Gazella gazella*, ~14 %), and red deer (*Cervus elaphus*, ~2%). Taken together, lithic and faunal data support the interpretation of Nachcharini as a task-specific site focused on the hunting of sheep (Rhodes et al., 2020; Rhodes, 2025).

#### 3.2. Sample selection

The teeth of ten individual wild sheep from Nachcharini Cave were selected for oxygen and carbon isotope analyses. Maxillary teeth were chosen for analysis over mandibular teeth because they were considerably more abundant in the faunal assemblage. This included nine M3s and four M2s. For three individuals it was possible to sample M2 and M3 teeth still embedded in the maxilla thus providing a longer archive of stable isotope variation during dental development. Several of the M3 teeth were loose (i.e., not embedded in the maxilla). Distinguishing between loose M1s from M2s on morphological grounds can be challenging, and because these teeth have different developmental timelines (Weinreb and Sharav, 1964; Millhaud and Nezeit, 1991)

misidentification can be problematic. To avoid this, we prioritized M3s, which are morphologically distinctive even when isolated. Tooth wear and gross morphological differences were used to ensure that sampled teeth came from distinct individuals (Table 1). To estimate age-at-death, we assessed tooth wear using the system developed by Grant (1982), as modified by Greenfield and Arnold (2008). Grant’s method assigns categorical wear stages to individual molars (Tooth Wear Stage, TWS) and generates a cumulative Mandibular Wear Score (MWS) based on the summed wear of the lower first, second, and third molars (M1–M3). Greenfield and Arnold calibrated these MWS values against a modern reference sample of known-age sheep and goats to assign approximate age ranges. Although the original system was developed using mandibular teeth, we applied these criteria to maxillary specimens by inferring age-at-death from comparable wear patterns. Age estimates for upper molars should therefore be considered relative and are reported primarily to contextualize the sampled population in broad developmental terms (e.g., juvenile, young adult, older adult). Because tooth enamel does not remodel once formed, its isotopic composition reflects conditions during a specific period of the animal’s life (Bryant et al., 1996; Fricke & O’Neil, 1996; Zazzo et al., 2010; Balasse et al., 2012). The crown of the second molar (M2) forms during the first year of life over approximately 10–12 months, while the third molar (M3) begins developing at around 10 months and completes by the end of the second year (Weinreb and Sharav, 1964; Millhaud and Nezeit, 1991). Enamel mineralization in sheep is delayed by five to six months relative to crown formation (Zazzo et al., 2010; Balasse et al., 2012).

#### 3.3. Sequential sampling and chemical pretreatment

Prior to sampling tooth enamel surfaces were cleaned with a hand-held Dremel. A series (9–16) of sequential enamel samples were then collected perpendicular to the tooth growth axis and spanning crown height from the apex to the enamel-root junction (ERJ). Samples were collected with a 1 mm diameter diamond burr on a handheld dental drill and were spaced by ~ 2 mm along the growth axis. Enamel powder was pre-treated with 0.1 M of acetic acid [CH<sub>3</sub>COOH] (0.1 ml/mg sample) for 4 h, rinsed five times with distilled water, and then freeze-dried. This protocol is recommended for archaeological samples to eliminate contamination from exogenous carbonates. Although enamel carbonate is relatively resistant to diagenesis due to its high crystallinity and low porosity, δ<sup>13</sup>C and δ<sup>18</sup>O values may still be affected by post-depositional

**Table 1**

Summary of specimen data. Tooth type and side are given along with wear-stage data following Grant (1982), as modified by Greenfield and Arnold (2008). Grant TWS refers to the categorical wear stage of individual molars, while Grant MWS is a cumulative score based on the summed wear of mandibular molars (M1–M3). Wear stages and associated age estimates are based on mandibular scoring systems but have been applied to maxillary teeth and should be considered approximate. Where both M2 and M3 were present for a specimen, they are listed together and assigned a single MWS and age estimate.

Specimen	Side	Tooth	Grant TWS	Grant MWS	Greenfield & Arnold Age
NA-F179	L	M3	8	31–33	2–3 yr
NA-FF5131	R	M2	11	36–39	4–5 yr
NA-F44	R	M3	12	36–44	4–8 yr
NA-F42	L	M2/ M3	–	27	1–2 yr
NA-F7001	L	M2/ M3	–	29	2–3 yr
NA-F6007	L	M3	10	34–38	3–4 yr
NA-F5567	L	M3	11	36–39	4–5 yr
NA-F46	L	M3	11	36–39	4–5 yr
NA-F196	R	M2/ M3	–	30	2–3 yr
NA-F5518	R	M3	Not readable	–	–

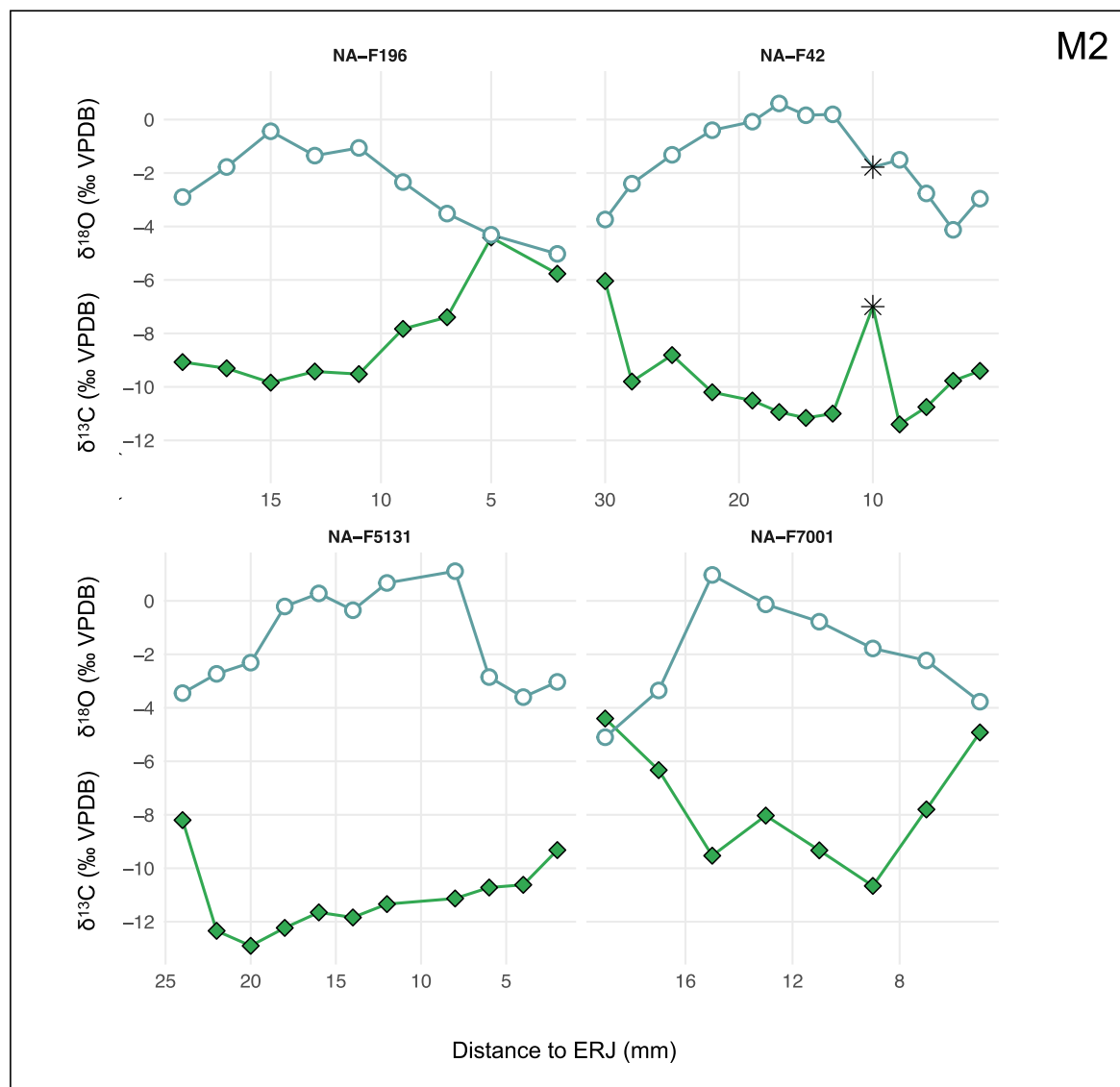
alteration. Even with established pretreatment protocols, exogenous carbonates or chemical changes can influence results and should be considered when interpreting stable isotope data.

Samples weighing approximately 500  $\mu\text{g}$  were reacted with 100 % phosphoric acid in individual vessels using an automated cryogenic distillation system (Kiel IV device), interfaced with a Delta-V Plus isotope ratio mass spectrometer (IRMS) at the Ján Veizer Stable Isotope Laboratory, University of Ottawa, Canada. Analytical precision was  $\pm 0.05$  ‰ for  $\delta^{13}\text{C}$  and  $\pm 0.07$  ‰ for  $\delta^{18}\text{O}$  (1 $\sigma$ ), based on repeated measurements of standards and internal quality control duplicates. A total of 134 archaeological samples were analyzed, and 9 internal quality control duplicates were distributed throughout the analytical run. Replicate values typically differed by  $< 1$  ‰, confirming reproducibility and instrumental stability over time. All values were calibrated using the international carbonate standard NBS-19 ( $\delta^{13}\text{C} = +1.95$  ‰;  $\delta^{18}\text{O} = -2.20$  ‰) and cross-checked against additional international standards (NBS-18, LSVEC) and in-house blind standards (e.g., “Lalime” and “dol-2”) to ensure accuracy and monitor analytical drift. Results are reported as  $\delta$ -values in parts per thousand (‰) relative to the international standard Vienna Pee Dee Belemnite (V-PDB).

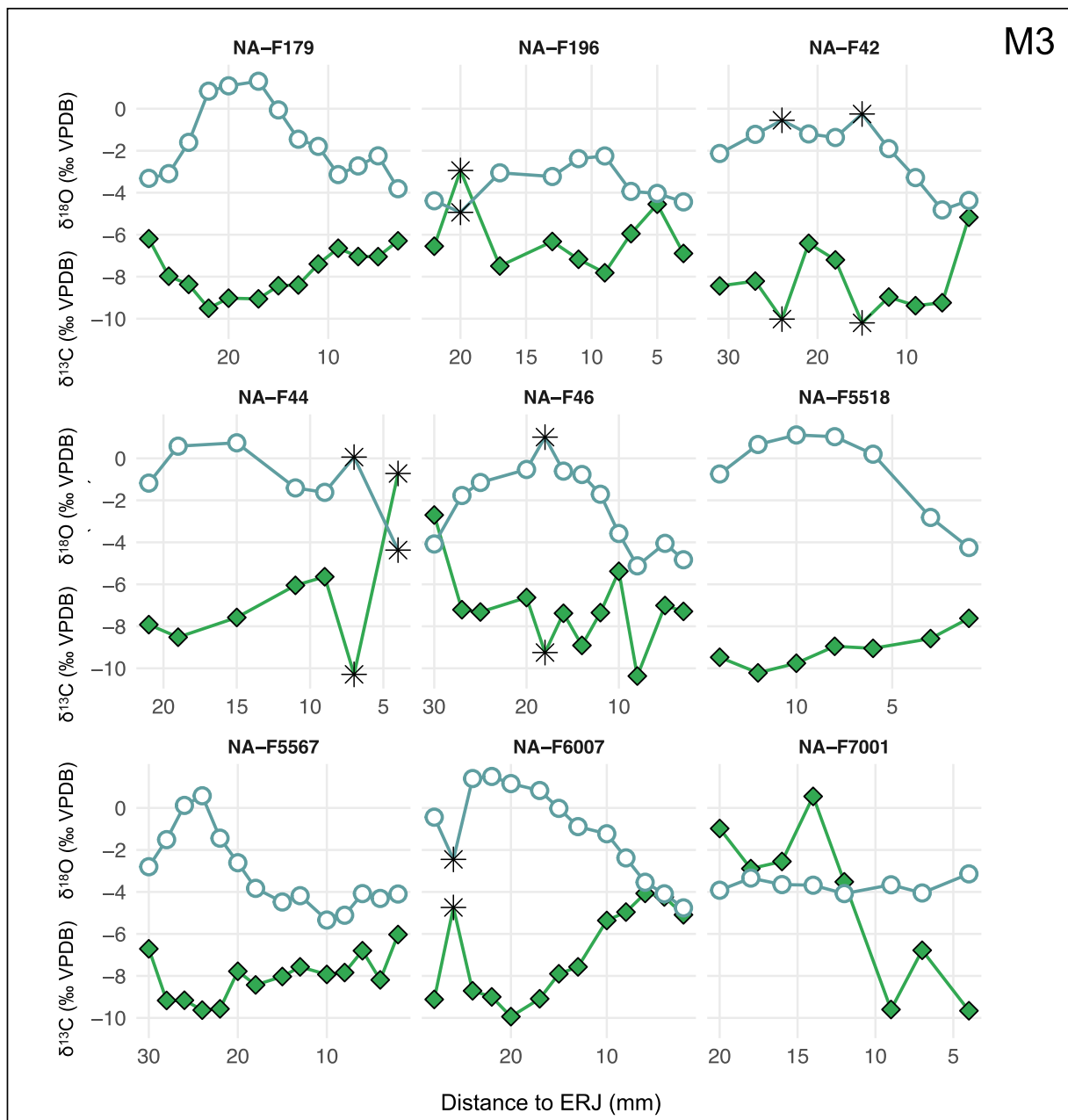
### 3.4. Data analysis

To assess the nature of the relationship between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values, we visually inspected each specimen's isotopic sequences using the plotted data (Figs. 2 and 3). An inverse relationship between  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values, where  $\delta^{13}\text{C}$  decreases as  $\delta^{18}\text{O}$  increases, and vice versa, is consistent with seasonal altitudinal migration, as animals move between isotopically distinct lowland and upland environments (Tornero et al., 2016a; Makarewicz et al., 2017; Isaakidou et al., 2019; Janzen et al., 2020).

To investigate season of birth, we used the method developed by Balasse et al. (2012), which involves normalizing the isotopic data using a cosine model to account for tooth size variability. This model includes the following parameters: X (period of the cycle in mm, corresponding to the length of the crown formed over a year); A ((max-min)/2, amplitude of the stable isotope signal measured in enamel, in ‰); M (mean, in ‰); and  $x_0$  (delay, i.e., the position in the tooth crown where  $\delta^{18}\text{O}$  is highest). Specimens were eligible for modelling only if the tooth preserved enough length to capture at least half an annual cycle of  $\delta^{18}\text{O}$  variation and exhibited a clear seasonal pattern, defined by the presence of both a



**Fig. 2.** Individual stable carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope sequences for M2 teeth of Nachcharini sheep. The y-axis shows  $\delta^{13}\text{C}$  values as indicated by green diamonds and  $\delta^{18}\text{O}$  values as indicated by blue outlined circles. The x-axis shows sample position relative to the enamel-root junction (ERJ). Star markers indicate values potentially altered by diagenesis.



**Fig. 3.** Individual stable carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope sequences for M3 teeth of Nachcharini sheep. The y-axis shows  $\delta^{13}\text{C}$  values as indicated by green diamonds and  $\delta^{18}\text{O}$  values as indicated by blue outlined circles. The x-axis shows sample position relative to the enamel-root junction (ERJ). Star markers indicate values potentially altered by diagenesis.  $\delta^{13}\text{C}$ .

maximum and a minimum  $\delta^{18}\text{O}$  value. Teeth that did not meet these criteria were excluded from modelling. Cosine modelled (i.e.,  $x_0/X$ ) values from Nachcharini specimens were then compared with modern sheep reference datasets for which the season of birth was known (Balasse et al., 2020, 2023; Balasse and Ambrose, 2005; Fabre et al., 2023). We recognize that a difference between the  $x_0/X$  values of upper and lower molars has been shown in a relatively small ( $n = 8$ ) sample of modern domestic sheep (Balasse et al., 2020). Balasse et al. (2020) demonstrated a shift ( $-0.073$ , equivalent to approximately 26 days) in the isotopic record of upper and lower M3s, which the authors suggest could be linked to a later onset of tooth growth in the upper dentition. Because the degree to which  $x_0/X$  values differ between upper and lower molars is unknown for wild sheep, we did not apply a correction factor.

We also assessed birth season qualitatively by examining the position of  $\delta^{18}\text{O}$  maxima along the enamel sequence. This analysis included all

specimens with  $\delta^{18}\text{O}$  profiles that were at least 18 mm in length and had an amplitude greater than 1.5 ‰. Full  $\delta^{18}\text{O}$  sequences were plotted by tooth type (M2 and M3) to visually compare the relative position of peak values (Fig. 5). Because enamel forms progressively from the cusp toward the enamel-root junction (ERJ) and is not remodelled after mineralization, the isotopic profile captures a time-ordered record of climate, diet, and environment during tooth development (Fricke and O'Neil, 1996; Balasse et al., 2003). When multiple individuals exhibit peak values in similar crown positions, this pattern suggests a constrained and possibly synchronized birth season (Bryant et al., 1996; Balasse et al., 2003; Tornero et al., 2016a). Because this method is not normalized or directly calibrated to tooth size, peak positions can only be interpreted as broad groupings along the crown rather than precise calendar dates.

Considering that sheep hunting events are interpreted to have taken

place in the areas surrounding Nachcharini Cave over a relatively short duration of time (~ 600 years), we predict that the enamel isotope sequences of individual sheep will show a similar range of values and similar amplitudes of variation. To test this prediction, we compared inter-individual variation in  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  maxima, minima, and amplitude observed in the Nachcharini sheep to that reported for modern domestic sheep raised under known conditions over an overlapping time period (Balasse et al., 2009, 2012; Blaise and Balasse, 2011), and Late Pleistocene wild sheep thought to have lived contemporaneously or within a short time span of each other (Tornerio et al., 2016a). All statistical analyses were completed using R version 4.4.1 with a threshold of significance at  $p$ -value < 0.05. Data visualizations were prepared using the R packages ggplot2 and circlize.

#### 4. Results

Stable isotope results are presented in Tables 2–4 and Figs. 2–5 (also see Supplementary Materials). The range of enamel  $\delta^{13}\text{C}$  values observed in the Nachcharini sheep suggests that their diets included plants with  $\delta^{13}\text{C}$  values between approximately –27 ‰ and –15 ‰, consistent with foraging across a diversity of plant communities, from purely  $\text{C}_3$  to mixed  $\text{C}_3/\text{C}_4$ . Most  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  sequences display sinusoidal patterns indicative of seasonal rhythmicity (Figs. 2 and 3). In M2s,  $\delta^{18}\text{O}$  values range from –5.1 ‰ to 1.1 ‰, with intra-tooth amplitudes between 4.6 ‰ and 6.1 ‰ and midpoints from –2.7 ‰ to –1.24 ‰ (midpoint = (min + max)/2). In M3s,  $\delta^{18}\text{O}$  values range from –5.3 ‰ to 1.5 ‰, with amplitudes from 0.9 ‰ to 6.3 ‰ and midpoints from –3.61 ‰ to –1.24 ‰.  $\delta^{13}\text{C}$  values range from –12.9 ‰ to –4.4 ‰ in M2s (amplitudes: 4.7 ‰ to 6.3 ‰; midpoints: –10.6 ‰ to –7.1 ‰), and from –10.4 ‰ to 0.6 ‰ in M3s (amplitudes: 2.6 ‰ to 10.2 ‰; midpoints: –8.9 ‰ to –4.6 ‰).

In nearly all specimens,  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values display an inverse relationship, with increases in  $\delta^{18}\text{O}$  corresponding to decreases in  $\delta^{13}\text{C}$ , and vice versa (Figs. 2 and 3). This negative covariation is consistent with seasonal altitudinal migration, as sheep moved between isotopically distinct highland and lowland environments. Similar patterns have been reported in wild mountain sheep (*Ovis canadensis*) from western North America during the Ferment period (ca. CE 1100–1350; Fisher and Valentine, 2013), and in Late Upper Paleolithic wild sheep (*Ovis orientalis*) from Armenia (Tornerio et al., 2016a), where inverse  $\delta^{18}\text{O}$ – $\delta^{13}\text{C}$  covariation was likewise interpreted as evidence of seasonal vertical migration. A subset of values in several specimens deviates markedly from the expected intra-tooth pattern, particularly where  $\delta^{18}\text{O}$  or  $\delta^{13}\text{C}$  values exhibit abrupt spikes or isolated outliers that are inconsistent with the sinusoidal trend observed in adjacent samples. These data points, which may reflect diagenetic alteration or analytical error, are identified based on their anomalous magnitude and position within the sequence and are marked with star symbols in Figs. 2 and 3.

**Table 2**

Descriptive statistics for individual Nachcharini sheep stable isotope values. SD indicates standard deviation from the mean. Mid indicates the midpoint value ((min + max)/2). A indicates the amplitude of variation.

Specimen ID	Tooth	$\delta^{13}\text{C}$ values					$\delta^{18}\text{O}$ values						
		Min	Max	Mean	SD	Mid	A	Min	Max	Mean	SD	Mid	A
NA-F179	M3	–9.50	–6.19	–7.80	1.10	–7.85	3.31	–3.81	1.31	–1.54	1.78	–1.25	5.12
NA-F196	M2	–9.84	–4.41	–8.06	1.90	–7.13	5.43	–5.03	–0.44	–2.52	1.54	–2.73	4.59
NA-F196	M3	–7.81	–2.94	–6.19	1.55	–5.38	4.87	–4.94	–2.25	–3.63	0.95	–3.59	2.69
NA-F42	M2	–11.40	–6.04	–9.75	1.63	–8.72	5.36	–4.13	0.60	–1.55	1.58	–1.76	4.73
NA-F42	M3	–10.20	–5.17	–8.32	1.62	–7.69	5.03	–4.82	–0.25	–2.11	1.56	–2.54	4.57
NA-F44	M3	–10.29	–0.72	–6.67	3.05	–5.51	9.57	–4.37	0.74	–1.03	1.76	–1.82	5.11
NA-F46	M3	–10.37	–2.70	–7.23	1.93	–6.54	7.67	–5.12	1.01	–2.27	1.99	–2.06	6.13
NA-F5131	M2	–12.90	–8.20	–11.12	1.38	–10.55	4.70	–3.60	1.11	–1.50	1.80	–1.25	4.71
NA-F5518	M3	–10.22	–7.62	–9.09	0.85	–8.92	2.60	–4.25	1.11	–0.69	2.08	–1.57	5.36
NA-F5567	M3	–9.63	–6.03	–8.06	1.08	–7.83	3.60	–5.34	0.58	–3.08	1.87	–2.38	5.92
NA-F6007	M3	–9.94	–4.07	–6.91	2.18	–7.01	5.87	–4.76	1.50	–1.15	2.15	–1.63	6.26
NA-F7001	M2	–10.66	–4.40	–7.63	2.25	–7.53	6.26	–5.10	0.97	–2.02	2.02	–2.07	6.07
NA-F7001	M3	–9.66	0.55	–4.43	3.84	–4.56	10.21	–4.08	–3.14	–3.69	0.33	–3.61	0.94

**Table 3**

Cosine-modelled estimates of seasonal birth timing in Nachcharini sheep. For the two M3 specimens that met the criteria for cosine modelling (NA-F179 and NA-F5567),  $x_0/X$  values were estimated using a cosine function fitted to  $\delta^{18}\text{O}$  sequences following Balasse et al. (2012). The model was applied to trimmed sequences, excluding the final sample at 3 mm for NA-F179 and the final two samples at 4 mm and 2 mm for NA-F5567.

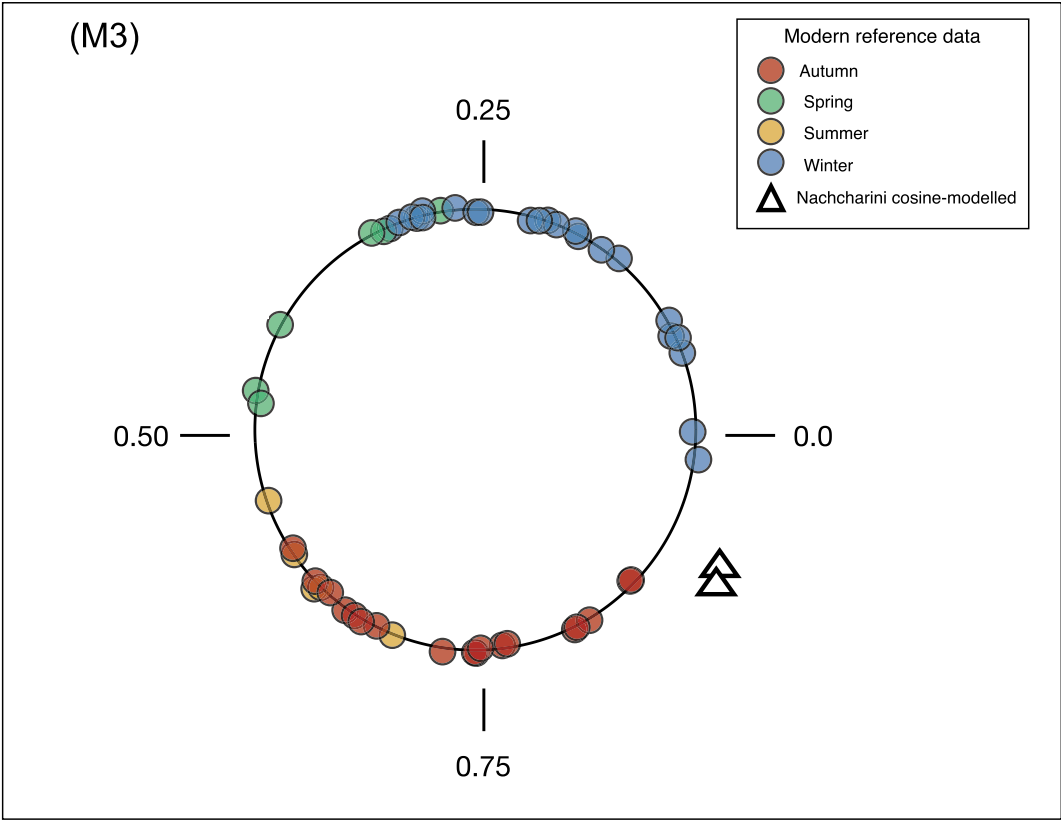
Specimen No.	Tooth	X	A	$x_0$	M	$x_0/X$	r
NA-F179	M3	20.07	2.35	18.38	–0.88	0.92	0.97
NA-F5567	M3	27.08	2.46	24.76	–3.03	0.91	0.94

Figs. 4 and 5 summarize the results of our examination of birth season using cosine modelling and inter-individual differences in peak  $\delta^{18}\text{O}$  position. Of the available specimens, only two M3 teeth (NA-F179 and NA-F5567) met the criteria for cosine modelling, preserving a complete seasonal signal with well-defined  $\delta^{18}\text{O}$  maxima and minima, and strong model fits ( $r > 0.90$ ; Table 3). Fig. 4 shows the resulting  $x_0/X$  values for these individuals, plotted alongside modern domestic sheep reference data with known birth dates. Both Nachcharini specimens exhibit  $x_0/X$  values near the modern autumn range, suggesting a shift in lambing relative to spring–early summer births in contemporary wild sheep. Because most sequences did not meet the criteria for cosine modelling, we also assessed birth timing qualitatively by examining the position of  $\delta^{18}\text{O}$  maxima along the crown, without applying normalization. The M3 sequence for NA-F7001 was excluded due to low intra-tooth  $\delta^{18}\text{O}$  variation (<1‰), rendering it unsuitable for peak identification. The M3 sequence for NA-F5518 was also excluded due to insufficient length (<18 mm). Fig. 5 displays  $\delta^{18}\text{O}$  profiles for the available M2 and M3 teeth, plotted by distance from the enamel-root junction (ERJ). Despite variation in sequence length, three of the M2 profiles show  $\delta^{18}\text{O}$  maxima at broadly similar positions, suggesting birth during a comparable time of year. One specimen (NA-F5131) exhibits a peak shifted toward the ERJ, diverging from this pattern. Although the M3 sequences are generally noisier due to a greater sample size, most individuals again display peaks in a relatively similar position. Two specimens (NA-F196 and NA-F5567) deviate from this trend, with maxima occurring outside the main range. These results suggest that most Nachcharini sheep were born within a similar seasonal window, though the presence of outliers indicates some variation in birth timing. This variation may reflect genuine differences in birth seasonality but could also result from factors such as differences in sampling resolution or diagenesis. Outliers are not unexpected, given that the assemblage likely represents individuals from multiple herds accumulated over several centuries of intermittent hunting.

To assess inter-individual variation across the Nachcharini sample, we calculated  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  variability across four seasonal events identified in the M2 and M3 sequences (Table 4).  $\delta^{18}\text{O}$  maxima ranged

**Table 4**  
Optimum  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  values measured for each event across M2 (event 1 and 2) and M3 (event 3 and 4) teeth.

Specimen No.	Tooth	Event 1		Event 2		Event 3		Event 4	
		$\delta^{18}\text{O}_{\text{max}}$	$\delta^{13}\text{C}_{\text{min}}$	$\delta^{18}\text{O}_{\text{min}}$	$\delta^{13}\text{C}_{\text{max}}$	$\delta^{18}\text{O}_{\text{max}}$	$\delta^{13}\text{C}_{\text{min}}$	$\delta^{18}\text{O}_{\text{min}}$	$\delta^{13}\text{C}_{\text{max}}$
NA-F179	M3	–	–	–	–	1.3	–9.5	–3.8	–6.2
NA-F196	M2	–0.4	–9.8	–5.0	–4.4	–	–	–	–
NA-F196	M3	–	–	–	–	–2.2	–7.8	–4.9	–2.9
NA-F42	M2	0.6	–11.4	–4.1	–6.0	–	–	–	–
NA-F42	M3	–	–	–	–	–0.3	–10.2	–4.8	–5.2
NA-F44	M3	–	–	–	–	0.7	–10.3	–4.4	–0.7
NA-F46	M3	–	–	–	–	1.0	–10.4	–5.1	–2.7
NA-F5131	M2	1.1	–12.9	–3.6	–8.2	–	–	–	–
NA-F5567	M3	–	–	–	–	0.6	–9.6	–5.3	–6.0
NA-F6007	M3	–	–	–	–	1.4	–9.9	–4.8	–4.1
NA-F7001	M2	1.0	–10.7	–5.1	–4.4	–	–	–	–
NA-F7001	M3	–	–	–	–	–3.1	–9.7	–4.1	0.6
	Mean	0.6	–11.2	–4.5	–5.8	–0.1	–9.7	–4.7	–3.4
	Range	1.5	3.1	1.5	3.8	4.5	2.6	1.5	6.8



**Fig. 4.** Circular chart showing the distribution of cosine-modelled  $x_0/X$  values for M3 teeth. Coloured circles represent modern reference sheep with known birthdates; the colour of each marker indicates season of birth (blue = winter, green = spring, yellow = summer, red = autumn). Modern reference data include the breeds Ouessant  $\times$  Lande de Bretagne ( $n = 24$ ; Balasse et al., 2020), North Ronaldsay ( $n = 4$ ; Balasse and Ambrose, 2005), Merino d’Arles ( $n = 9$ ) and Lacaune ( $n = 17$ ; Balasse et al., 2023), and Corsican ( $n = 1$ ; Fabre et al., 2023).  $x_0/X$  values for Nachcharini specimens are shown as open triangles with black borders.

from 0.6 ‰ to 2.1 ‰, minima from –5.3 ‰ to –3.6 ‰, and intra-tooth amplitudes from 1.5 ‰ to 4.5 ‰. In contrast,  $\delta^{13}\text{C}$  maxima ranged from 0.6 ‰ to –8.2 ‰ and minima from –9.7 ‰ to –12.9 ‰, with amplitudes up to 6.8 ‰. These values were compared to reference datasets from modern domestic sheep from the Orkney Islands in northern Scotland and southern France (Balasse et al., 2009, 2012; Blaise and Balasse, 2011), as well as to Late Pleistocene wild sheep from Kalavan 1 (Tornerio et al., 2016a). While inter-individual  $\delta^{18}\text{O}$  variability in the Nachcharini sheep was broadly similar to that observed in these comparative datasets,  $\delta^{13}\text{C}$  variation was considerably greater. Rather than indicating an extended accumulation period, the elevated  $\delta^{13}\text{C}$  variability more likely reflects dietary heterogeneity, shaped by

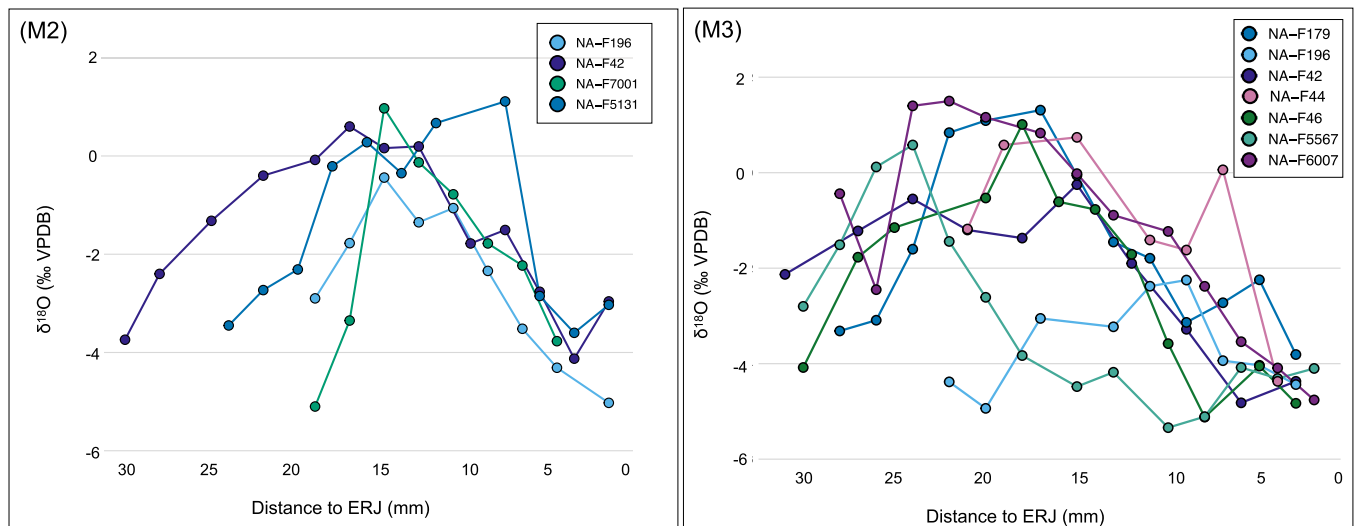
environmental differences across the altitudinal gradient exploited by the Nachcharini sheep. This interpretation is consistent with a logistical hunting strategy focused on animals that were seasonally available near the site, and it aligns with broader evidence for intermittent use of Nachcharini inferred from the archaeological context.

## 5. Discussion

### 5.1. Altitudinal migration

Sequential stable isotope analysis of wild sheep tooth enamel showed a sinusoidal pattern of negative covariation between  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$





**Fig. 5.** Stable oxygen ( $\delta^{18}\text{O}$ ) isotope sequences for M2 (left) and M3 (right) teeth from Nachcharini sheep. The y-axis shows  $\delta^{18}\text{O}$  values, and the x-axis shows sampling position along the tooth crown, measured as distance from the enamel-root junction (ERJ). Each line represents a different individual, with colours distinguishing specimens as noted in the legend. Most sequences show a clear sinusoidal pattern, with  $\delta^{18}\text{O}$  maxima occurring at relatively similar positions along the tooth crown, suggesting broadly consistent timing of birth. A few outliers exhibit inter-individual variation in birth timing.

values in most individuals, consistent with seasonal altitudinal migration (Figs. 2 and 3). While the number of individuals analyzed in this study is relatively low, the consistent pattern observed suggests a systematic behavioural strategy. We interpret the inverse sequences of stable isotope values as evidence of animal movements between alpine,  $\text{C}_3$ -dominant meadows during the summer and midland to lowland mixed  $\text{C}_3/\text{C}_4$  valleys during the winter. This interpretation has previously been proposed to describe the mobility patterns of both wild (Fisher and Valentine, 2013; Tornero et al., 2016a) and domestic caprines (Makarewicz, 2017; Makarewicz et al., 2017; Tornero et al., 2018). Due to physiological differences between  $\text{C}_3$  and  $\text{C}_4$  plants, the relative abundance of each plant type varies along an altitudinal gradient. Typically,  $\text{C}_3$  plants dominate at higher elevations, leading to an overall decrease in the mean  $\delta^{13}\text{C}$  values of plant communities with increasing altitude (Tieszen et al., 1979). The  $\delta^{13}\text{C}$  sequences of wild sheep from Nachcharini suggest summer grazing in highland  $\text{C}_3$ -dominated environments (i.e., when  $\delta^{18}\text{O}$  values were most enriched), and winter foraging in lower elevation zones where mixed  $\text{C}_3/\text{C}_4$  vegetation was accessible (i.e., when  $\delta^{18}\text{O}$  values were most depleted). All individuals in this study showed minimum  $\delta^{13}\text{C}$  values (i.e., winter values) below the threshold for pure  $\text{C}_3$  diets in water-stressed environments ( $\sim -7\text{‰}$ ; Cerling et al., 1997; Wang et al., 2008). There was considerable inter-individual variation in maximum  $\delta^{13}\text{C}$  values (i.e., summer values; Table 2), likely reflecting flexibility in the relative proportion of  $\text{C}_3$  and  $\text{C}_4$  plants consumed while grazing at lower elevations. Most individuals exhibit enriched  $\delta^{13}\text{C}$  maxima, approaching or exceeding  $-5\text{‰}$ , indicating seasonal intake of  $\text{C}_4$  vegetation. While a small number of values exceed the conventional threshold for pure  $\text{C}_4$  diets ( $\sim -2\text{‰}$ ; Cerling et al., 1997), some of these may reflect diagenetic alteration (e.g., NA-F44-M3 and NA-F7001-M2) and should be interpreted cautiously. Nonetheless, the overall trend suggests that  $\text{C}_4$  plants were sufficiently abundant in winter foraging zones to contribute measurably to diet. These intra-annual  $\delta^{13}\text{C}$  shifts provide further support for seasonal foraging across altitudinal zones.

While enamel  $\delta^{18}\text{O}$  sequences from Nachcharini followed the expected sinusoidal pattern associated with seasonal variation in temperature and humidity (i.e., enriched values in summer and depleted values in winter), the amplitude of variation was considerably reduced relative to modern meteoric water in the Anti-Lebanon Mountains, which exhibits an annual range of approximately  $9.5\text{‰}$  (Koeniger et al., 2016). In contrast, the Nachcharini wild sheep showed a mean enamel  $\delta^{18}\text{O}$

amplitude of  $4.7\text{‰}$ , with individual values ranging from  $0.9\text{‰}$  to  $6.3\text{‰}$ . This attenuation likely reflects the combined effects of several overlapping factors. Most fundamentally, the dampened signal may result from time-averaging associated with enamel mineralization and the resolution of the sampling protocol. Because enamel mineralization in sheep occurs over a period of 5 to 6 months, variations in the stable isotope composition of environmental inputs, including diet, climate, and ingested water, are not recorded instantaneously. Instead, enamel  $\delta^{18}\text{O}$  values reflect a time-averaged signal that is attenuated in amplitude relative to the original environmental variation (Zazzo et al., 2005, 2010; Green et al., 2025). Further, in this study, sequential samples were collected from the outer enamel surface at approximately 2 mm intervals. This sampling protocol may have compounded the effects of time-averaging by integrating isotopic signals over longer periods of crown formation, further contributing to the reduced  $\delta^{18}\text{O}$  amplitude.

Additional sources of isotopic signal dampening could include seasonal movement across altitudinal zones, which would have exposed animals to muted temperature extremes and isotopically depleted water sources at higher elevations. The Beqaa Valley, located at approximately 800 masl and roughly 24 km southwest of Nachcharini Cave (Fig. 1), may have served as a lower-elevation winter grazing zone, while highland meadows near the cave, at around 2100 masl, were likely used in spring and summer. The altitudinal gradient in meteoric  $\delta^{18}\text{O}$  values in this region is estimated at  $-0.14\text{‰}$  per 100 m (Koeniger et al., 2016), meaning that migration along this elevation range could result in a seasonal reduction of approximately  $2\text{‰}$  in  $\delta^{18}\text{O}$  values. Further dampening may also have resulted from the ingestion of snowmelt during early summer, which is further depleted in  $\delta^{18}\text{O}$  due to its origin in cold-season precipitation (Bhatia et al., 2011). While sheep are predominantly non-obligate drinkers (Makarewicz, 2017), they may at times rely on available water sources such as streams and rivers (Dwyer, 2021; Bunyaga et al., 2023), and the isotopic composition of these sources could influence the  $\delta^{18}\text{O}$  values recorded in tooth enamel. It is important to note, however, that while reduced  $\delta^{18}\text{O}$  amplitude is often associated with vertical mobility (Isaakidou et al., 2019), this pattern is not universal, as demonstrated in both archaeological and modern contexts (Knockaert et al., 2018; Lazzarini et al., 2021).

Comparable isotopic patterns to those observed at Nachcharini have been reported for Epigravettian wild sheep at Kalavan 1, a high-altitude ( $\sim 1640$  masl) hunting camp in the Lesser Caucasus Mountains of Armenia, where inverse  $\delta^{13}\text{C}$ - $\delta^{18}\text{O}$  covariation in enamel sequences was

linked to seasonal movement between highland meadows in summer and lowland valleys in winter (Tornerio et al., 2016a). Tornerio et al. (2016a) evaluated whether the ingestion of snowmelt-derived water during summer, combined with altitude effects, could dampen  $\delta^{18}\text{O}$  signals and potentially reverse the expected seasonal pattern driven by temperature. This scenario would require substantial input from  $^{18}\text{O}$ -depleted meltwater during periods of grazing in the highlands. However, the authors did not favour this scenario, citing the large  $\delta^{18}\text{O}$  amplitudes observed (up to 10 ‰) and the unexpectedly high  $\delta^{13}\text{C}$  values (−8‰ to −6‰) during the presumed summer period, which were inconsistent with the pure  $\text{C}_3$  diet expected in alpine zones. We interpret the Nachcharini data in a similar way.  $\delta^{18}\text{O}$  amplitudes are relatively high (up to 6.3 ‰), and most individuals show  $\delta^{13}\text{C}$  maxima  $\geq$  −5‰ (Table 2), consistent with the seasonal intake of  $\text{C}_4$  plants, which would be unexpected in alpine environments. Thus, while the consumption of  $^{18}\text{O}$ -depleted meltwater and altitude-related effects may have contributed to dampening the temperature signal in the Nachcharini sheep, we do not believe these factors were sufficient to reverse it. Taken together, Kalavan 1 and Nachcharini offer rare isotopic baselines for seasonal altitudinal mobility in unmanaged wild sheep. These data provide valuable reference points for understanding caprine ecology and mobility prior to the emergence of animal management.

### 5.2. Timing and duration of the birth season

Estimating the timing of birth in archaeological wild sheep offers insight into their ecology, seasonal mobility, and broader life history patterns. In seasonal environments, timing parturition with periods of resource abundance enhances offspring survival and supports the energetic demands of lactation. To investigate birth seasonality at Nachcharini, we applied the cosine model developed by Balasse et al. (2012) and qualitatively evaluated the positions of  $\delta^{18}\text{O}$  maxima within the enamel sequences. Of the available specimens, only two M3 teeth (NA-F179 and NA-F5567) met the criteria for cosine modelling and produced  $x_0/X$  values consistent with births in autumn (Fig. 4 and Table 3). While limited in number, these results suggest a possible shift in the timing of lambing relative to modern wild sheep in Europe and western Asia, which typically give birth between spring and early summer (Geist, 1974; Bunnell, 1982; Bon et al., 1995; Khorozyan et al., 2009; Özü, 2009). This pattern is unexpected and lacks a clear ecological explanation or modern analogue. One possible explanation is that later births may have allowed lambs additional time to mature before migrating to alpine meadows in the late spring and early summer. However, this scenario is difficult to reconcile with the behaviour of modern wild sheep, which also undertake seasonal migrations but predominantly give birth in spring. These findings should therefore be interpreted with caution, particularly given the reliance on reference data derived from modern domestic sheep. Although domestic sheep (*Ovis aries*) retain the same tooth eruption sequence as their wild relatives (Geiger et al., 2020) (*O. vignei*, *O. orientalis*, *O. ammon*, *O. gmelini musimon*), domestication has accelerated several key life history traits, including earlier sexual maturity, shorter gestation, higher reproductive output, and reduced breeding seasonality (Asdell, 1964; Schaller, 1977; Rosa and Bryant, 2003; Castelló, 2016). These changes may also influence when enamel formation occurs and how quickly it progresses, introducing potential bias when applying models based on domestic sheep to archaeological wild populations.

To broaden the analysis beyond the two cosine-modelled  $x_0/X$  values, we qualitatively assessed the position of  $\delta^{18}\text{O}$  maxima within the M2 and M3 sequences of the Nachcharini sheep. The position of  $\delta^{18}\text{O}$  maxima was broadly similar in most individuals, suggesting a relatively consistent birth season. However, a few individuals deviate from this pattern, indicating some degree of reproductive variability (Fig. 5). In seasonal environments, the timing of birth is a critical life history trait shaped by selection to align late gestation and early lactation with periods of peak forage quality, thereby enhancing offspring survival and

maternal recovery (Ofstedal, 1985; Bunnell, 1982; Festa-Bianchet, 1988; Albon & Langvatn, 1992). These pressures are especially pronounced in montane ungulates that undertake seasonal altitudinal migration, where the combination of brief growing seasons and the physiological stress of migration reinforces tight birth synchrony (Clutton-Brock et al., 1987; Gaillard et al., 1993; Côté & Festa-Bianchet, 2001). Modern wild sheep in Europe and western Asia typically give birth between February and early June (Geist, 1974; Bunnell, 1982; Bon et al., 1995; Khorozyan et al., 2009; Özü, 2009), with lambing timed to precede altitudinal migration from lowland valleys to alpine summer pastures. For example, European mouflon (*Ovis gmelini musimon*) inhabiting the Alps, Pyrenees, and Massif Central follow this pattern, moving to higher elevations (~1500–2000 masl) in late spring and early summer, descending to mid-elevations in autumn and early spring, and overwintering at lower elevations (~500–1000 masl) (Dubois et al., 1993; Bourgoignie et al., 2008). After lambing in the spring, lactating females with young often occupy rocky, mid-altitude habitats before ascending to alpine pastures (Bon et al., 1995). Considering the evidence for vertical mobility and the relatively consistent  $\delta^{18}\text{O}$  maxima across most individuals, it is likely that the Nachcharini sheep experienced ecological and physiological constraints on reproductive timing similar to those observed in modern migratory montane ungulates.

The comparison with Late Pleistocene wild sheep from Kalavan 1 further highlights the connection between birth timing and altitudinal migration. At Kalavan 1, the positions of  $\delta^{18}\text{O}$  maxima in M2 and M3 sequences from six individuals were closely aligned, indicating a relatively constrained birth season (Tornerio et al., 2016a). A broadly similar pattern is visible in the Nachcharini sequences, where  $\delta^{18}\text{O}$  maxima from most individuals also fall within a relatively narrow range, although the presence of a few outliers may suggest greater inter-individual variation. Taken together, the results from both sites indicate a pattern of seasonal lambing likely shaped by the timing of altitudinal migration. These findings not only clarify the seasonal behaviours of ancient wild sheep but also highlight the ecological knowledge and strategic mobility of the hunters who targeted them. Although the Nachcharini sample is relatively small, it contributes to a growing body of research using  $\delta^{18}\text{O}$  sequences to reconstruct the timing of birth in archaeological caprines (Balasse et al., 2003, 2017, 2020; Tornerio et al., 2016a, 2018, 2020; Hadjiloumimis et al., 2019; Sierra et al., 2021; Fabre et al., 2023). More broadly, seasonal birth patterning in archaeological wild sheep offers insight into how montane ungulates have responded to environmental variability over long time-scales. As anthropogenic climate change increasingly threatens alpine ecosystems (Dainese et al., 2024), these long-term records provide important baselines for evaluating species' resilience and informing effective conservation strategies.

### 5.3. Short duration of wild sheep accumulation at Nachcharini

Both the faunal and lithic assemblages from Nachcharini Cave support its interpretation as a seasonal hunting camp, used intermittently over a limited timeframe. New radiocarbon dates place the primary occupation within the early PPNA, between approximately 11,000 and 11,600 cal BP (Rhodes, 2025), though these dates offer only broad chronological resolution. Dense concentrations of wild sheep remains suggest targeted hunting and intensive butchery activities (Rhodes et al., 2020). The lithic assemblage also points to short-term use, as indicated by the limited number of retouched flakes, absence of bifacial tools, variable Khiam point morphology, and reuse of debitage (Yerkes et al., 2003; Kaufman and Nadel, 2007). Taken together, these features indicate a specialized occupation focused on the repeated seasonal exploitation of wild game.

To evaluate whether the stable isotope data support a temporally constrained wild sheep assemblage, we examined inter-individual variation in  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values in the M2 and M3 sequences of the Nachcharini sheep. While these sequences do not yield absolute dates,

comparing values across individuals can indicate whether animals experienced similar climatic and environmental conditions during tooth formation, suggesting they lived, and were likely hunted, within a limited number of years. Following [Tornero et al. \(2016a\)](#), we identified seasonal “events” based on recurring  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  maxima and minima, and calculated variability in both peak values and amplitude ([Table 4](#)). In the Nachcharini sheep,  $\delta^{18}\text{O}$  maxima and minima varied between 1.5 ‰ and 1.7 ‰, with amplitudes ranging from 1.5 ‰ to 4.5 ‰. These values fall within, or slightly above, the range observed in modern domestic sheep raised under environmentally consistent conditions (i.e., foraged in the same pastures and drank from the same water sources), such as those from Rousay in the Orkney Islands of northern Scotland and from subalpine southern France ([Balasse et al., 2009, 2012; Blaise and Balasse, 2011](#)). Sheep from Rousay showed  $\delta^{18}\text{O}$  variability of 1.9 ‰ (maxima), 1.1 ‰ (minima), and 1.3 ‰ (amplitude), while those from southern France ranged from 1.5 ‰ (maxima) and 1.2 ‰ (minima) in M2s to 2.5 ‰ (maxima) and 1.6 ‰ (minima) in M3s. Comparable variability was also reported for Late Pleistocene wild sheep at Kalavan 1, with maxima and minima ranging from 0.7 ‰ to 2.7 ‰, and amplitude from 0.7 ‰ to 3.7 ‰. This similarity suggests that Nachcharini sheep experienced broadly consistent seasonal climatic conditions during enamel formation, supporting the view that the assemblage accumulated over a relatively short period (~ 600 years).

In contrast, inter-individual variation in  $\delta^{13}\text{C}$  values among the Nachcharini sheep was substantially greater than in the modern and Late Pleistocene reference sets. Across the four seasonal events recorded in M2 and M3 sequences ([Table 4](#)),  $\delta^{13}\text{C}$  maxima and minima varied from 0.8 ‰ to 2.4 ‰, and amplitude reached up to 6.8 ‰. Even after excluding sequences with possible diagenetic alteration (i.e., NA-F44 M3, NA-F6007 M3, NA-F42 M3/M2, NA-F196, NA-F46 M3),  $\delta^{13}\text{C}$  variation remained elevated, ranging from 3.4 ‰ to 4.1 ‰ for maxima/minima and 3.3 ‰ for amplitude. These values exceed the ranges reported for sheep on Rousay (1.2 ‰ maxima, 1.4 ‰ minima, 1.1 ‰ amplitude) and at Kalavan 1 (0.6 ‰ to 1.2 ‰ for maxima/minima; 1.2 ‰ to 1.9 ‰ amplitude). While elevated  $\delta^{13}\text{C}$  variation could suggest a longer accumulation period, the relatively constrained  $\delta^{18}\text{O}$  values do not support this interpretation. Instead, we interpret the higher  $\delta^{13}\text{C}$  variation as a signal of dietary heterogeneity linked to local environmental diversity.

Unlike the  $\text{C}_3$ -dominated vegetation on Rousay, the landscape surrounding Nachcharini Cave likely featured diverse plant communities structured along altitudinal and microclimatic gradients. Even in the Kura Valley near Kalavan 1, Late Pleistocene vegetation is thought to have been predominantly  $\text{C}_3$ , with limited  $\text{C}_4$  presence ([Tornero et al., 2016a](#)). By contrast, the Anti-Lebanon Mountains and Beqaa Valley likely supported a heterogeneous plant assemblage that included mid- and low-elevation areas with  $\text{C}_4$  grasses and mixed  $\text{C}_3/\text{C}_4$  forbs, due to warmer, drier conditions and extended growing seasons ([Ehleringer et al., 1997; Makarewicz and Tuross, 2006](#)). Wild sheep foraging across these ecologically varied zones, potentially exhibiting individual differences in movement and dietary preference, would have consumed vegetation with highly distinct isotopic signatures. This environmental heterogeneity could account for the pronounced  $\delta^{13}\text{C}$  differences among individuals, even if they lived within a relatively short time span. In sum, the stable isotope results align with archaeological and faunal data suggesting short-duration, seasonally patterned use of Nachcharini Cave by PPNA hunters.

## 6. Conclusions

Sequential stable carbon ( $\delta^{13}\text{C}$ ) and oxygen ( $\delta^{18}\text{O}$ ) isotope analysis of wild sheep teeth from Nachcharini Cave was used to reconstruct patterns of seasonal mobility, reproductive timing, and faunal accumulation during the PPNA. The results indicate that the animals undertook seasonal altitudinal migrations, making them locally available during only part of the year, likely from late spring through summer. This seasonal

presence would have required hunters to possess detailed ecological knowledge and to strategically time site use in accordance with herd movements. Cosine-modelled results tentatively suggest births occurred in autumn, but this pattern appears ecologically implausible given the behaviour of modern wild sheep. A more reliable signal emerges from the consistent placement of  $\delta^{18}\text{O}$  maxima across individuals, which points to a relatively consistent and seasonally patterned birth period. This pattern, in correlation with evidence for altitudinal migration, aligns with the reproductive timing of modern wild sheep, where births are closely tied to forage availability and seasonal movement between ecological zones. The low degree of inter-individual variation in  $\delta^{18}\text{O}$  values among the Nachcharini sheep suggests a relatively short-term accumulation of remains, consistent with episodic hunting during a limited seasonal window. In contrast, the greater variation in  $\delta^{13}\text{C}$  values points to dietary and environmental heterogeneity, likely reflecting foraging across diverse plant communities within the regional landscape.

Although the subsistence strategies of PPNA groups in the central Levant remain poorly documented, the Nachcharini assemblage provides rare evidence for targeted caprine hunting at high elevation. Isotopic data indicate a strategy of seasonal movement adapted to the migratory behaviour of prey and the environmental constraints of montane landscapes. These findings underscore the ecological knowledge required to anticipate herd movements and align hunting with resource availability. Nachcharini Cave thus offers insight into how task-specific groups organized seasonal mobility and hunting in a challenging alpine setting, reflecting continuity with Epipaleolithic practices even as broader Neolithic transformations were underway. By documenting the use of a marginal ecological zone peripheral to major PPNA settlements, our study contributes to a more nuanced understanding of subsistence practices across the Levant and challenges rigid distinctions between foraging and farming in early Neolithic societies.

## CRedit authorship contribution statement

**L.C. Eastham:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **S. Rhodes:** Writing – review & editing, Investigation.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jasrep.2025.105366>.

## Data availability

All data supporting the findings of this study are available within the Manuscript and [Supplementary materials](#).



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