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The altitudinal mobility of wild sheep at the Epigravettian site of Kalavan 1 (Lesser Caucasus, Armenia): Evidence from a sequential isotopic analysis in tooth enamel



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ABSTRACT

Kalavan 1 is an Epigravettian hunting campsite in the Aregunyats mountain chain in northeastern Armenia (Lesser Caucasus). The site lies at an elevation of 1640 m in a bottleneck that controls the descent into the Barepat Valley from the alpine meadows above. The lithic and faunal assemblages show evidence of the production of hunting weapons, the hunting and targeting of wild sheep (*Ovis orientalis*), and the constitution of animal product reserves. A seasonal occupation of the site was proposed within a model of occupation by Epigravettian hunter-gatherers that involved a search for obsidian resources in high altitude sources from the spring to the summer and settling at Kalavan 1 at the end of summer or during autumn to coincide with the migration of wild herds from the alpine meadows to the valley. A key parameter of this model is wild sheep ethology, with a specifically seasonal vertical mobility, based on observations from contemporary mouflon populations from the surrounding areas. In this study, the vertical mobility of Paleolithic wild sheep was directly investigated through sequential isotope analysis ($\delta^{18}\text{O}$, $\delta^{13}\text{C}$) in teeth. A marked seasonality of birth is suggested that reflects a physiological adaptation to the strong environmental constraints of this mountainous region. Most importantly, a recurrent altitudinal mobility was demonstrated on a seasonal basis, which confirms that wild sheep migrated from lowland areas that they occupied in the winter and then moved to higher altitude meadows during the summer. Last, low inter-individual variability in the stable isotope sequences favors a hypothesis of accumulation for these faunal remains over a short time period. Overall, this new dataset strengthens the previous interpretations for Kalavan 1 and contributes to an understanding of the pattern of occupation of mountain territories by Epigravettian communities.

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1. Introduction

The open-air site of Kalavan 1 is located at an altitude of 1640 m in the Aregunyats mountain chain on the north shore of Lake Sevan (1900 m altitude) (Fig. 1). The Paleolithic occupation was established on a late glacial alluvial terrace in the valley of the Barepat (a

tributary of the Aghstev River), at the base of a mountain slope. The excavations at Kalavan 1 revealed an Early Bronze Age necropolis (Kura-Arax culture) at the top of the stratigraphy along with Upper Paleolithic layers at the base. Over 40 m² of these Epigravettian layers have been explored over the course of several excavations (from 2006 to 2009). The occupation layer 7d3, which is dense in remains and structures, provided nearly 5400 artifacts for which over half (56.8%) are remains from hunted fauna. Seven homogeneous AMS dates placed the occupation(s) at approximately 14,000 BP [15,966–14,506 cal BC (2 sigma)] (Montoya et al., 2013; Gasparyan et al., 2014).

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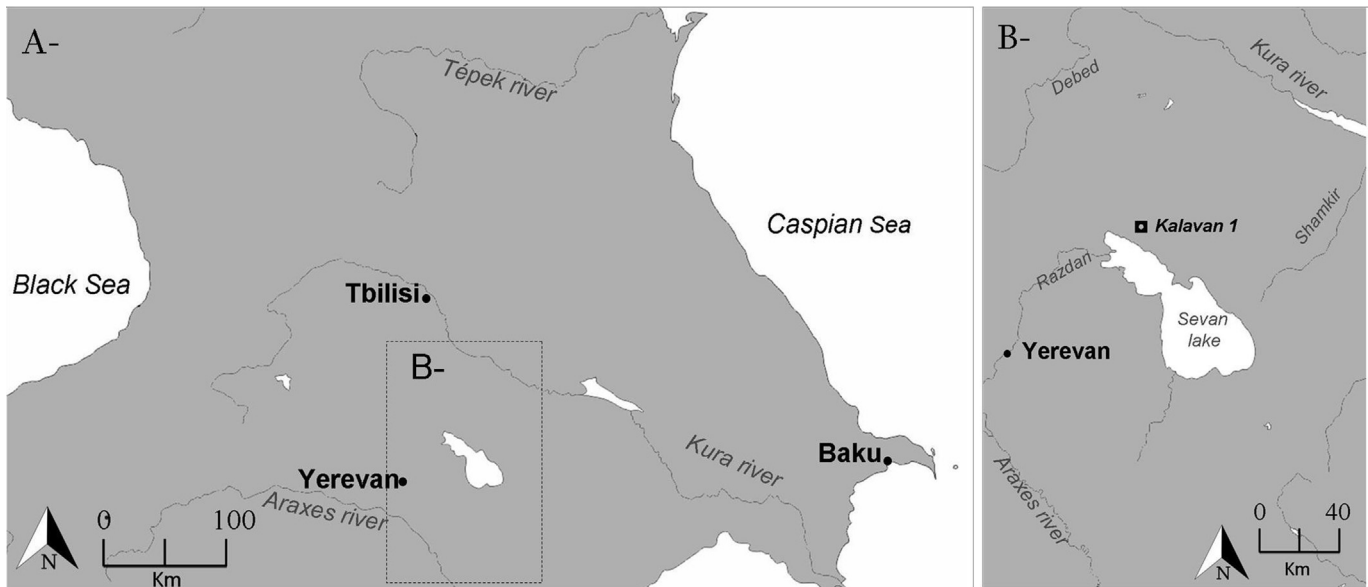


Figure 1. Map showing the location of the Kalavan 1 site in Lesser Caucasus.

Lithic and zooarchaeological analyses documented specialized hunting activity. Of over 3000 faunal remains that have been analyzed to date from layer 7, all belong to mammals, among which over 18% are caprinae, and over 80% are undetermined medium-sized mammals of similar size to the caprinae, although other species could be represented within this category, such as wild boar, wolf, or roe deer. Among the caprinae, *Ovis* dominate *Capra* (NR = 31/1). The wild sheep remains most probably belong to *Ovis orientalis gmelini*, the Armenian mouflon. The caprinae mortality profile (161 teeth) shows a predominance of mature specimens (age classes D to G, 1–6 years [Payne, 1973]) and includes no very young animals (age classes A: 0–2 months and B: 2–6 months) (Montoya et al., 2013). When we include only the wild sheep, the mortality profile (80 teeth) shows a similar tendency. This mortality may reflect the intentional selection of prey of maximum weight. However, the very poor state of preservation of the material could also produce a bias against the youngest animals. Sex ratios could not be determined due to the absence of diagnostic elements in the assemblage. Although some elements of the axial skeleton were under-represented in the assemblage, the presence of the main anatomical parts of the animals suggests hunting activity near the site (Montoya et al., 2013; Bălăşescu et al., 2016).

The study of the lithic “chaîne opératoire” sheds light on the management of lithic raw material and hunter gatherers’ socio-economic behavior. The Paleolithic group acquired obsidian from sources that are located to the west and the south of Lake Sevan, at high elevations (1500 m to nearly 3000 m; Fig. 1; Chataigner and Gratuze, 2014a,b). These deposits were accessible only after the snowmelt, during the mildest season (the end of spring to the end of summer). Judging by their size and weight, most of the obsidian blades were probably produced directly by or near the raw material sources. This seems to be confirmed by the absence of any lithic sub-products of the chaîne opératoire of the blades at Kalavan 1. However, some small blocks of obsidian with blade toolkits were introduced at the site. These small blocks of obsidian, in addition to some local raw materials, were dedicated to the production of bladelets for hunting weaponry (backed bladelets and micro-gravettes). Treatment of animal skins at the site is suggested by the presence of an ochred area in association with a concentration of

stone tools (end scrapers) that are usually devoted to this task (Montoya et al., 2013; Bălăşescu et al., 2016).

Over all, the faunal assemblage and the whole lithic collection that has been recovered at Kalavan 1 reflect the production of hunting tools, the hunting and targeting of wild sheep and the butchering of caprinae carcasses to provide animal products (meat and skin). This Paleolithic occupation most likely occurred specifically at the time of the wild sheep migrations through the Barepat Valley.

A key parameter of this model is wild sheep ethology – more specifically, their vertical mobility. Today, the Armenian mouflon’s distribution is limited to northwestern Iran and the Zangesur mountains that define the border between Nakhchivan (Azerbaijan) and southern Armenia (Syunik province [Valdez, 2008; Khorozyan et al., 2009; Talibov et al., 2009]). The Armenian mouflon preferentially lives in open spaces, inhabiting medium to high altitude mountain steppes and grasslands, with vertical mobility tuned to the seasonal cycle: the winter is spent in the midlands to lowlands, while in the summer, most individuals move to high elevation alpine meadows. It is likely that the present day Armenian mouflon has been gradually moved from the lowlands to middle slope elevation pastures due to the increasing presence of livestock, which has led to competition for space and overgrazing (Talibov et al., 2009). It is supposed that wild sheep were hunted at Kalavan while spending winter under milder conditions at lower elevation sites in the Kura River Basin, below 500 m altitude. The spring migration towards the alpine meadows could have led them through the Agstev River Valley, which is connected to the Getik River Valley and the Barepat Valley, where Kalavan 1 is situated (Fig. 2). At the campsite, located at an intermediate elevation in a bottleneck on the way from the valley to the alpine meadows, the hunting of wild sheep could have occurred either at the time of the spring or the autumn migration (upward and downward migration, respectively). The autumn migration would have provided the hunters with fatter animals with higher quality skin.

The model for the wild sheep altitudinal mobility builds on observations of modern populations and implies similar vertical movements for the late Pleistocene wild sheep. This prerequisite can be directly tested on the archaeological specimens themselves,

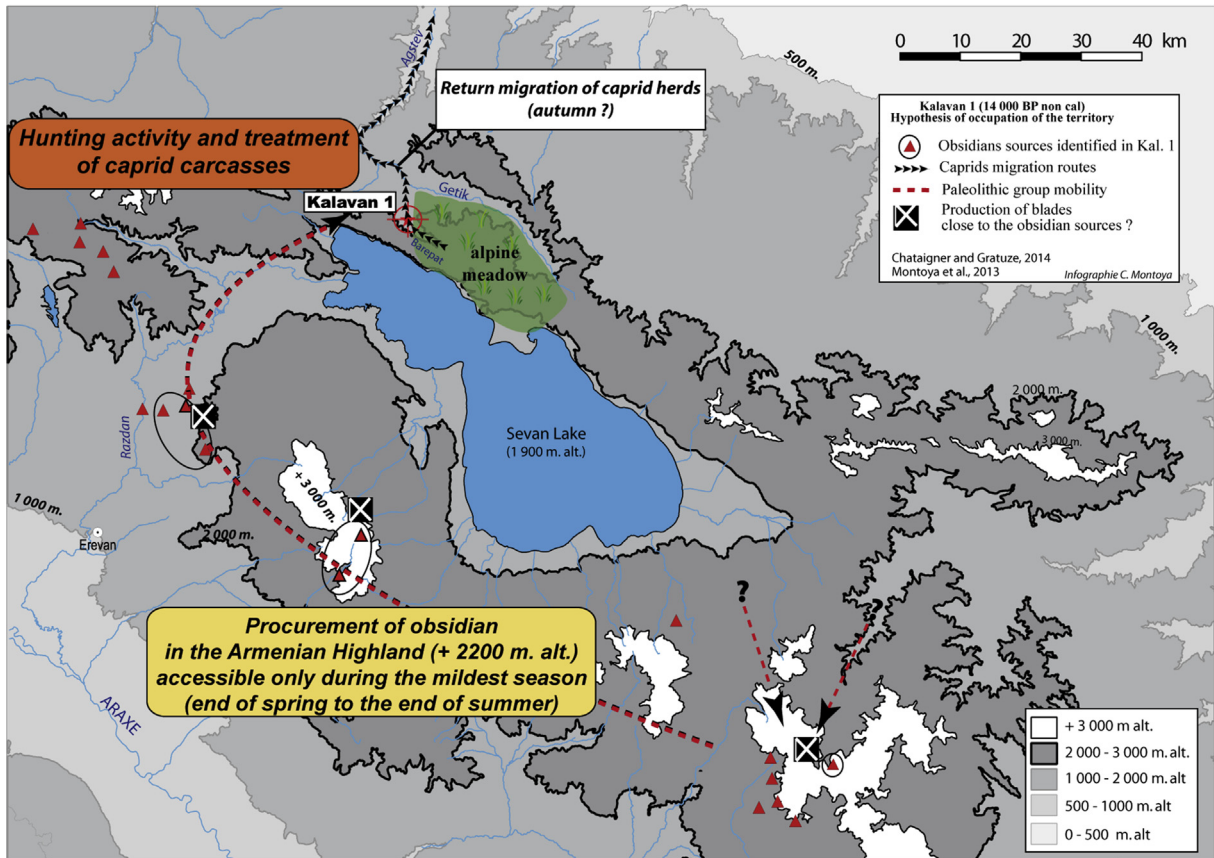


Figure 2. Map showing the scheme of the seasonal occupation model of the territory proposed from Kalavan 1 and its surroundings (Re-drawn from Chataigner and Gratuzé, 2014a,b) (©Computer graphics C. Montoya).

through sequential stable isotope analysis of tooth enamel. The objective of this study is to determine whether the stable isotopic signals that were retrieved from the wild sheep teeth from Kalavan 1 could be interpreted in terms of paleoethology, focusing particularly on mobility. The site of Kalavan 1 provides unique evidence for a human re-colonization of the Lesser Caucasus high mountains after the Last Glacial Maximum. Any information that is related to the wild game ethology and environment would be valuable in documenting the subsistence strategy of these Upper Paleolithic hunter-gatherers.

2. Principles

A sequential analysis of stable oxygen and carbon isotope compositions of enamel was performed on wild sheep dental remains. Because enamel is not remodeled after the completion of mineralization, this protocol allows for the reconstruction of individual stable isotope histories over the time of tooth formation. In sheep, the formation of the second and third molars covers over two years in early life (Weinreb and Sharav, 1964). Stable oxygen and carbon isotopes are incorporated into the enamel through eating and drinking (Land et al., 1980; Lee-Thorp and van der Merwe, 1987). They are inherited from the plants and water in the ecosystem, whose $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values depend on environmental and climatic factors, some of which may be influenced by seasonality (Rozanski et al., 1993; Kohn et al., 1996; Kohn and Welker, 2005). These signals thus help us to assess mobility on a seasonal scale.

The oxygen isotope ratios in the mineral fraction of vertebrate skeletons are linked to that of body water. The oxygen isotope composition of body water results from the balance between ingested water (mainly drinking water in the case of the Armenian mouflon) and water that is lost during excretion and transpiration. In large mammals from temperate Europe, $\delta^{18}\text{O}$ values in skeleton bioapatites are strongly related to that of local meteoric water (Land et al., 1980; D'Angela and Longinelli, 1991), the oxygen isotopic composition of which is affected by climatic and geographic factors, including ambient temperature and altitude. At high and middle latitudes, at a given location, seasonal changes in ambient temperature lead to higher $\delta^{18}\text{O}$ values in meteoric water during the warmer seasons and lower $\delta^{18}\text{O}$ values during the colder seasons (Gat, 1996).

Considering the hypothesis of vertical mobility for wild sheep, the altitude effect should also be taken into account, with increasingly low $\delta^{18}\text{O}$ values as elevation gets higher, due to a gradual removal of moisture from uplifted air masses with a preferential removal of ^{18}O during condensation (Rozanski et al., 1993). The gradients in precipitation $\delta^{18}\text{O}$ values versus altitude vary according to local conditions on the order of 1–3‰/km (Confiantini et al., 2001; Longinelli and Selmo, 2003). Additionally, at high elevation sites, melt water from surface snow (accumulated over winter at the time of the year when $\delta^{18}\text{O}$ values are the lowest) and also potentially from glacial ice (deposited in colder times over the Last Glacial Maximum and with considerably lower $\delta^{18}\text{O}$ values [Bhatia et al., 2011]), would provide wild sheep with ^{18}O -depleted water in spring and summer (Fisher and Valentine, 2013). Consequently, the expected vertical trajectories of wild sheep with

summer pasturing in the highlands and wintering in lowlands could counterbalance seasonal trends in $\delta^{18}\text{O}$ values at the local scale, leading to a reduction of the annual amplitude of variation in $\delta^{18}\text{O}$ values that are recorded in tooth enamel on an annual scale. The likelihood of these effects leading to a reversal of the pattern of seasonal variations in $\delta^{18}\text{O}$ values on an annual scale, with the lowest $\delta^{18}\text{O}$ values corresponding to summer and the highest to winter, is difficult to evaluate given the uncertainties in (1) the relative contribution of the different potential water sources at high elevation sites – spring/summer precipitations, snow melt, glacial ice melt, (2) and how much those would be ^{18}O -depleted compared to water sources in the valley in winter.

Carbon isotopes in enamel bioapatite reflect $\delta^{13}\text{C}$ values of food plants (Lee-Thorp and van der Merwe, 1987; Cerling et al., 1993). Wild sheep are mainly grazers, although they may also feed on shrubs. The grassy component in their diet should reflect changes between summer and winter ranges, even though the plants' relative availability may be biased by food preferences. At the time of occupation of Kalavan 1, in the prevailing cold and dry conditions of the Late Glacial period, the site was surrounded by a steppe environment (Montoya et al., 2013). Only C_3 plants are expected in the subalpine and alpine meadows. Today, the dry steppe to semi-desert environments of the Kura Valley provide habitats to many C_4 plants (R. Hovsepyan, pers. comm). C_4 grasslands have also been documented in the lowlands of northeastern (Akhani and Ziegler, 2002; Akhani and Ghasemkhani, 2007) and northwestern Iran (Hatami and Khosravi, 2013). In these areas, the presence of C_4 Chenopodiaceae has been identified until late autumn although the proportion of C_4 plants dramatically drops in the winter, some may survive on protected parts of the ground and between rocks. The occurrence of C_4 plants in the region in the Late Glacial time is unknown. Although C_4 ecosystems existed during the Last Glacial Maximum on a global scale (at a time when they were favored by climate and reduced CO_2 levels [Ehleringer, 2005]), favorable pluviometric and temperature conditions for the development of C_4 plants were essentially found at low latitudes. In the middle latitudes, inversely, the relative abundance of C_4 plants increased from the Last Glacial Maximum to the Holocene – during the Late Glacial period – concomitantly with the increase in temperature (Rao et al., 2012). Therefore, although it is not expected that the availability of C_4 plants would have been higher at the time of occupation of Kalavan 1, whether it was similar to the present day or significantly lower is difficult to determine.

In modern environments, C_3 and C_4 plants have $\delta^{13}\text{C}$ values averaging, respectively, 26.5‰ (Kohn, 2010) and –12.5‰ (Vogel et al., 1978; Winter, 1981). These $\delta^{13}\text{C}$ values must be corrected for the fossil fuel effect when they are applied to pre-industrial ecosystems (+1.5‰; Friedli et al., 1986; Marino and McElroy, 1991). Moreover, both atmospheric CO_2 concentrations and $\delta^{13}\text{C}$ values rose from the last glacial period to the Holocene (Marino et al., 1992). In Western Europe, the residual effect led to higher $\delta^{13}\text{C}$ values for plants by 1.5–3‰ in the last glacial period (Hatté et al., 1998). In Late Glacial time, within the transitional phase between full glaciation and the Holocene, the amplitude of this change would have been lower, and we may consider that pre-industrial plants' $\delta^{13}\text{C}$ values are reasonable approximations for vegetation at the time of the occupation of Kalavan 1, although the fact that they might have been slightly higher must be kept in mind. Using an enamel-diet ^{13}C -enrichment factor of +14.1‰ (Cerling and Harris, 1999), the expected mean value for a pure C_3 diet should be close to –11.3‰ in enamel. According to the review by Kohn (2010), the $\delta^{13}\text{C}$ values of C_3 plants extremely rarely exceed –23‰ in modern environments, including those that thrive under a wide range of mean annual precipitation (1–3700 mm/yr), mean annual temperature (–13.5 to 28.4 °C) and altitude (–391 to 4900 m). Consequently the value of –7.7‰ in

enamel may be considered as the absolute cut-off value for a pure C_3 diet in pre-industrial times. This estimation is similar to the value of –7 to 8‰ that was given in Cerling et al. (1997).

Variations of moderate amplitude (1–2‰) have been documented on a seasonal scale for C_3 plants' $\delta^{13}\text{C}$ values, the highest values occurring in dry seasons and/or during the summer and the lowest in wet seasons and/or during the winter (Smedley et al., 1991; Hartman and Danin, 2010). In the case of vertical mobility towards higher elevations in the summer, the altitude effect on plant $\delta^{13}\text{C}$ values may also apply. Carbon isotope discrimination during the photosynthesis of C_3 plants was found to decrease with increasing altitude, due to changes in temperature and atmospheric pressure, although a substantial genotypic component to this variation was also shown (Körner et al., 1988, 1991). In the study area, the bottom of the Kura Valley lies at 300 m, while the alpine meadows are situated at an altitude of 2100–2200 m, although during cold episodes of the Upper Pleistocene alpine meadows would have been lower (Adler and Tushabramishvili, 2004). In Körner et al. (1988), a linear regression between altitude and plant carbon isotope values shows an increase of 1.5‰ from 400 m to 2500 m above sea level. An increase of comparably modest amplitude could therefore be expected in the $\delta^{13}\text{C}$ values of the alpine meadows compared to the valley pastures. The extent to which this pattern would be counterbalanced by differences in the relative abundance of C_3/C_4 at high and low elevations would depend on the relative abundance of C_4 in the lowlands in winter.

3. Materials and methods

3.1. Level 7, paleosurface 7d3

Taphonomic and geomorphological analyses of the Paleolithic layer 7 have shown disturbances, including bioturbation, light runoff and vertical dispersion (approximately 10 cm), which are probably linked to repeated seasonal freezing-melting phenomena alternatively compressing and decompressing the soil (Montoya et al., 2013). However, a colluvial phenomenon from the mountain slope allowed for a quick burial of the paleosurface 7d3. The latter appears to be well preserved, with several anthropic structures, among which three hearths, lithic concentrations, ochred areas and three heaps of faunal remains were found (Montoya et al., 2013). The tooth remains that were analyzed in this study are from the two principal faunal concentrations from paleosurface 7d3 (FG 23–24 and H32 [Fig. 3]).

3.2. The sampled specimens

Six lower tooth rows were selected for stable isotope analysis (Table 1). Considering laterality, wear stage and morphology, they all belong to different individuals. From the tooth eruption and wear patterns, they were attributed to Payne's age classes 2–3 to 4–6 years (Payne, 1973). They all contained a second (M2) and a third molar (M3) except (KAL Ovis 01), for which only the M3 was analyzed because M2 was missing.

3.3. Sampling procedures

Sequential sampling was performed on the buccal side of the teeth, on the anterior lobe of the M2 and on the middle lobe of the M3 (Supplementary Online Material [SOM] 1). Each sample is located in the tooth crown using its distance from the enamel root junction (ERJ).

Enamel powders weighing 4–9 mg were treated for 4 h in 0.1 M acid acetic (0.1 ml/mg sample). Over treatment, the weight loss was approximately $28 \pm 4\%$. Pre-treated enamel samples weighing

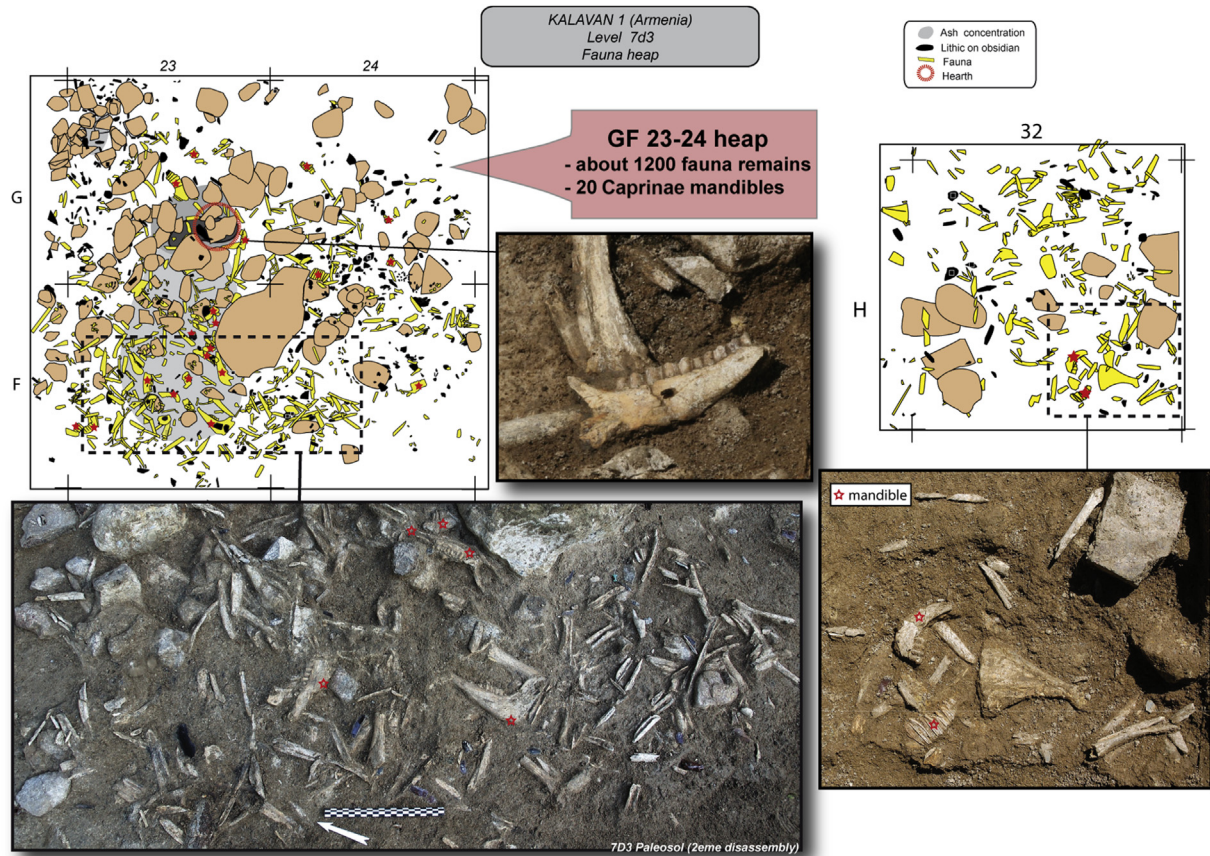


Figure 3. Spatial distribution of the mandible remains in paleosurface 7d3 (©Computer graphics C. Montoya).

~600 μg were analyzed on a Kiel IV device interfaced to a Delta-V Advantage IRMS. Samples were reacted under vacuum with orthophosphoric acid [H_3PO_4] at 70° C in individual vessels. The accuracy and precision of the measurements were checked using our laboratory calcium carbonate standard (Marbre LM normalized to the international standard NBS 19). Over the period of analysis of these bioapatite samples, 68 Marbre LM gave a mean $\delta^{13}\text{C}$ value of $+2.05 \pm 0.02\text{‰}$ (1σ) (expected value $+2.13\text{‰}$) and $\delta^{18}\text{O}$ value of $-1.64 \pm 0.04\text{‰}$ (1σ) (expected value -1.83‰). The mean analytical precision within each run was calculated from 7 to 8 measurements of Marbre LM in each analytical series, with averages of $0.03 \pm 0.01\text{‰}$ for $\delta^{13}\text{C}$ values and $0.08 \pm 0.02\text{‰}$ for $\delta^{18}\text{O}$ values. The results are expressed in V-PDB.

4. Results

The results from the stable carbon and oxygen isotope measurements are shown in Fig. 4. The sequences of the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values along the tooth crown show a pattern that is close to a sinusoidal variation, which reflects seasonal rhythmicity. The $\delta^{18}\text{O}$ values range from 0.8‰ to -10.4‰ in the M2s (with an amplitude

of intra-tooth variation from 6.9‰ to 10.2‰) and from -0.7‰ to -11.0‰ in the M3s (with an amplitude of intra-tooth variation from 6.4‰ to 10‰). The $\delta^{13}\text{C}$ values range from -6‰ to -10.4‰ (with an amplitude of intra-tooth variation from 2.1‰ to 3.8‰) in the second molars and from -6.5‰ to -10.2‰ in the third molars (with an amplitude of intra-tooth variation from 2.3‰ to 3.3‰).

Over the (M2-M3) sequence, five landmarks are observed that correspond with optimum (highest or lowest) $\delta^{18}\text{O}$ values (Fig. 5). Because the timing of the formation of the M2 and M3 overlaps in sheep (Weinreb and Sharav, 1964), event 2 may be represented twice, occurring both on the lowest (the latest formed) part of the M2 crown and on the highest (the earliest formed) part of the unworn M3 crown. This only occurs in KAL Ovis 04, which is the youngest specimen (Payne's E stage) with very slight tooth wear on the M3. In other individuals, tooth wear caused the loss of event 2 in the M3 (see SOM 1). The sequences that were measured over the M2 and M3 span two complete annual cycles. The optimum $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values for each event are given in Table 2.

Intra-tooth variations in the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences are opposed, in contradiction to what would be expected for seasonal changes in pasture $\delta^{13}\text{C}$ values on a local scale, whether it is due to

Table 1
Wild sheep specimens included in this study.

Sample	Year	Square	Inventory no	Side	Dental stage (Payne, 1973)	Age
KAL Ovis.01	2008	G23	481	Left	F	3–4 years
KAL Ovis.02	2009	F23	3324	Right	F	3–4 years
KAL Ovis.03	2009	E22	3384-170	Left	F	3–4 years
KAL Ovis.04	2009	H32	3387-170	Right	E	2–3 years
KAL Ovis.05	2008	F23	456-457	Right	F	3–4 years
KAL Ovis.06	2008	G23	526	Right	G	4–6 years

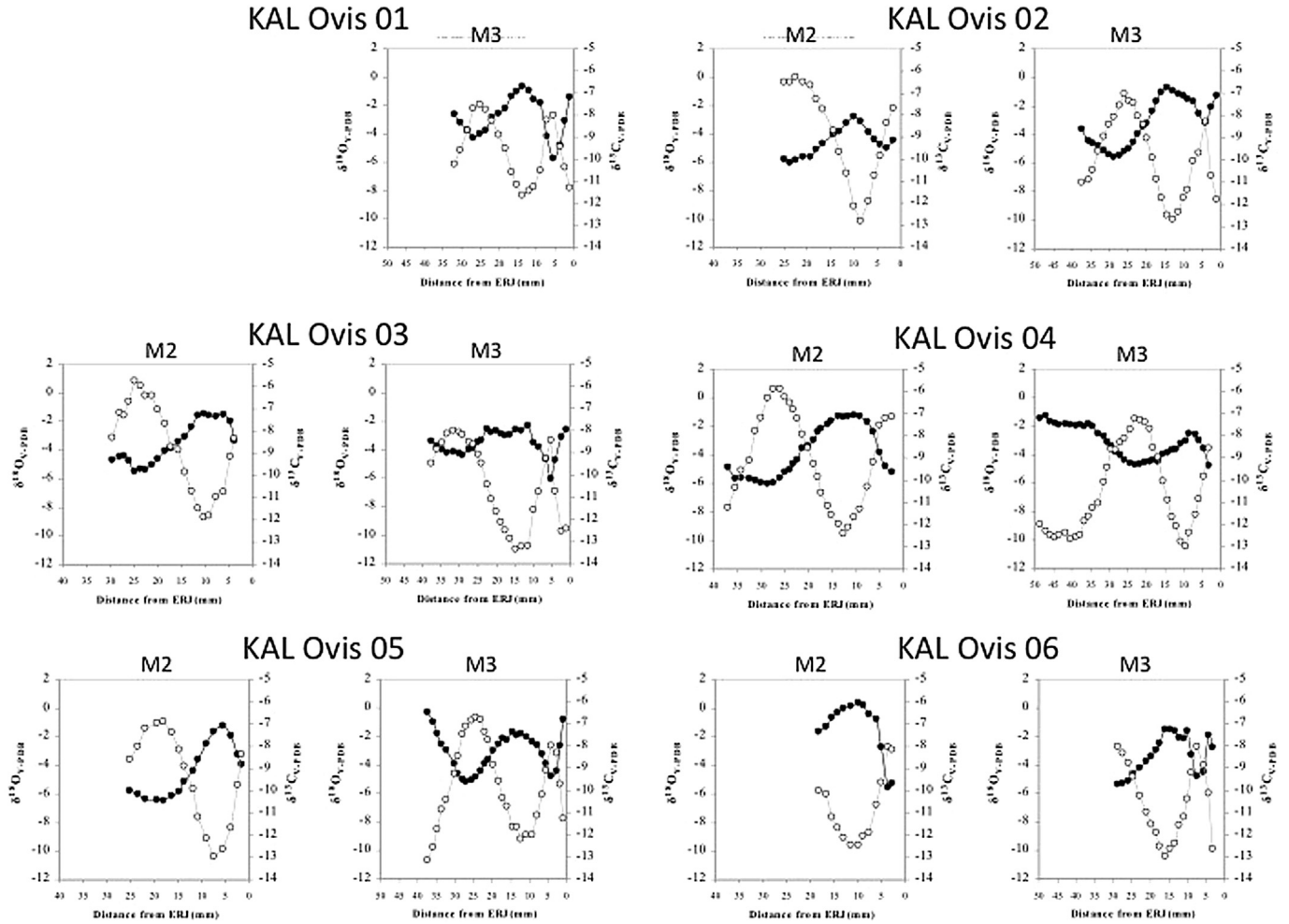


Figure 4. Results from the sequential analysis of carbon ($\delta^{13}\text{C}$) and oxygen ($\delta^{18}\text{O}$) isotope composition in second (M2) and third molars (M3).

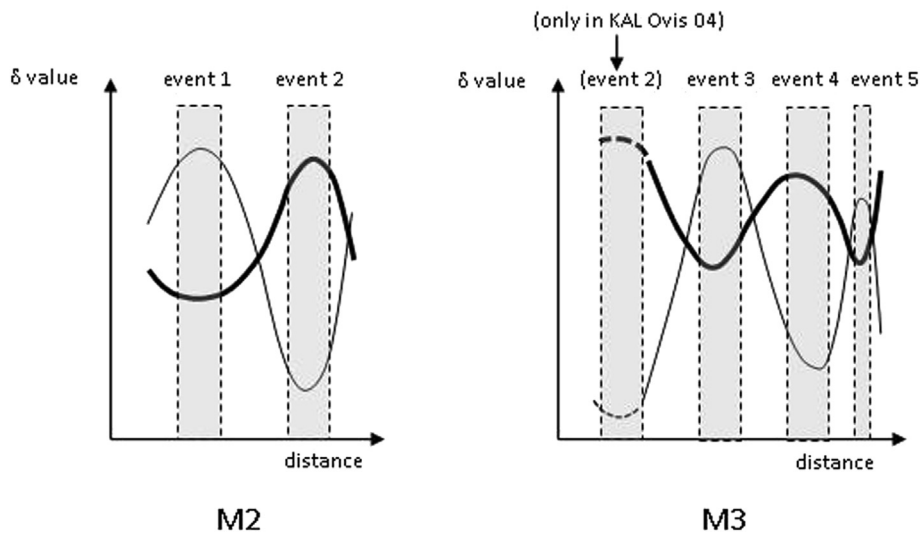


Figure 5. Schematic representation of variations of the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ (bold curve) values along the second (M2) and third (M3) molar crown, and the location of climatic events as reflected in the $\delta^{18}\text{O}$ values.

Table 2
Optimum $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values measured for each event (as defined in Fig. 6).

Sample	M2				M3					
	Event 1		Event 2		Event 3		Event 4		Event 5	
	$\delta^{18}\text{O}_{\text{max}}$	$\delta^{13}\text{C}_{\text{min}}$	$\delta^{18}\text{O}_{\text{min}}$	$\delta^{13}\text{C}_{\text{max}}$	$\delta^{18}\text{O}_{\text{max}}$	$\delta^{13}\text{C}_{\text{min}}$	$\delta^{18}\text{O}_{\text{min}}$	$\delta^{13}\text{C}_{\text{max}}$	$\delta^{18}\text{O}_{\text{max}}$	$\delta^{13}\text{C}_{\text{min}}$
KAL Ovis 01	–	–	–	–	–1.9	–9.0	–8.3	–6.7	–2.7	–10.0
KAL Ovis 02	0.0	–10.2	–10.2	–8.1	–1.2	–9.9	–9.9	–6.7	–3.1	–8.3
KAL Ovis 03	0.8	–9.8	–8.7	–7.2	–2.7	–9.1	–11.0	–7.8	–3.3	–10.2
KAL Ovis 04	0.6	–10.1	–9.5	–7.1	–1.5	–9.3	–10.4	–7.9	–	–
KAL Ovis 05	–0.9	–10.4	–10.4	–7.1	–0.7	–9.6	–9.2	–7.4	–2.6	–9.3
KAL Ovis 06	–	–	–9.6	–6.0	–	–	–10.4	–7.2	–2.7	–9.3
Mean	0.1	–10.1	–9.7	–7.1	–1.6	–9.4	–9.9	–7.3	–2.9	–9.4
Range	1.7	0.6	1.7	1.0	2.0	0.9	2.7	1.2	0.7	1.9

the changing relative proportions of C_3/C_4 plants, or to changes in plant $\delta^{13}\text{C}$ values. In both cases, this would lead to higher $\delta^{13}\text{C}$ values during the warmer seasons. The opposing pattern that was observed in the wild sheep from Kalavan 1 most probably reflects vertical mobility. Similarly, opposed variations were measured in mountain sheep (*Ovis canadensis*) from a western North America site that dated to the Fremont period (ca AD 1100 to 1350; Fisher and Valentine, 2013).

Given the uncertainties that are exposed above concerning the $\delta^{18}\text{O}$ values of summer water sources in high elevation sites and the occurrence of C_4 plants in the Kura Valley in the Late Glacial period, two scenarios may be proposed to explain the opposing variations that are observed in the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences:

- (1) In the first scenario, the lower $\delta^{18}\text{O}$ values would reflect summer temperatures and water sources from high elevations. The altitude effect would lower the $\delta^{18}\text{O}$ values in summer precipitations, while snow melt could also contribute with ^{18}O -depleted water, both factors acting in opposition to the seasonal temperature effect. However, it must be noted that these combined factors could lead to a significant reduction in the amplitude of variation on the annual scale, but probably not to the point of reversal of the pattern. Considering the high amplitude of intra-tooth variation (up to 10‰), a reversal of the pattern (i.e., the lowest values $\delta^{18}\text{O}$ corresponding to the summer instead of the winter seasons) would imply a significant contribution of considerably depleted water in the summer, potentially from the melting of glacial ice. In this scenario, events 2 and 4 would reflect summertime in the alpine meadows. The associated high $\delta^{13}\text{C}$ values (that comprised between -8 and -6 ‰) are sometimes higher than the absolute cut off values for a pure C_3 diet (-7.7 ‰), even though only C_3 plants can thrive at these elevations. In this scenario, slightly higher $\delta^{13}\text{C}$ values for plants in the Late Glacial period may be argued to explain this difference.
- (2) In the second scenario, glacial ice melt did not contribute significantly to the summer water source at high elevation sites, and the combined effect of altitude and contribution of snow melt is not important enough to reverse the seasonal pattern in the $\delta^{18}\text{O}$ values due to the temperature effect. In this scenario, events 1, 3 and 5 reflect summertime, while events 2 and 4 reflect wintertime. The higher $\delta^{13}\text{C}$ values in the winter (over the cut off value for a pure C_3 diet) reflect the occurrence of small amounts of C_4 plants in the Kura Valley – C_4 Chenopodiaceae, which are typical fodder plants, may have been preferentially grazed by the wild sheep – while the C_4 plants were absent at the high elevations sites in summer. In summertime, the $\delta^{13}\text{C}$ values that comprised between -10 and -9 ‰, may reflect a modest altitude effect.

5. Discussion

5.1. A systematic pattern of vertical mobility

The pattern of vertical mobility is observed in all specimens and, at least, over two consecutive years (M2–M3). Although the number of analyzed individuals is low, within this sample seasonal vertical mobility may be seen as a systematic behavioral pattern. Modern Armenian mouflons migrate from the lowlands to spend the summer in the high mountains in search of more abundant food. They return to the lowlands in autumn and spend the winter there, escaping from the harsh conditions and scarcity of vegetal resources. Similar reasons must have driven the vertical mobility that has been observed in the Late Glacial wild sheep.

5.2. A marked seasonality of birth

The sequences of the $\delta^{18}\text{O}$ values that were measured in all of the individuals' M2 and M3s are compared in Figure 6. The great similarity between individuals in the position of optimum values in tooth crowns suggests a strong seasonality of birth (Bryant et al., 1996; Fricke and O'Neil, 1996; Balasse et al., 2003). A constrained season of births goes together with seasonal mobility over a wide range because long distance altitudinal mobility would increase the vulnerability of lactating females and young animals. This constraint may, therefore, influence the timing of births, so when mobility is initiated, both females and young mouflons are strong enough to endure the experience. This would also imply a reduction in the birth period. The reproductive cycle of modern Armenian mouflons is indeed strongly tuned to their pattern of altitudinal mobility. The rutting season occurs in the lowland areas between mid-October and the end of November, with the peak activity in the first part of November when adult females and males are less dispersed. The females give birth in early spring in the lowland areas before the migration to the high altitudes; although some of them may spend the summer at the valley bottom if the young calves or mothers fail to reach adequate weight before the migration (Dinnik, 1910; Sarkisov, 1944; Vereshchagin, 1959; Valdez, 2008; Khorozyan et al., 2009; Talibov et al., 2009).

5.3. Specimens accumulated over a short period of time

The faunal assemblage that was recovered at Kalavan 1 may have been the result of hunting events that were conducted over a limited number of episodes. The archaeological evidence at the site argues for seasonal, short-term occupations. The spatial distribution and volume of the archaeological vestiges, the documented steps in knapping activities, the weak thermo-alteration of the hearth soils and stone surfaces, and the absence of important rearrangement of the fireplaces all suggest a relatively brief

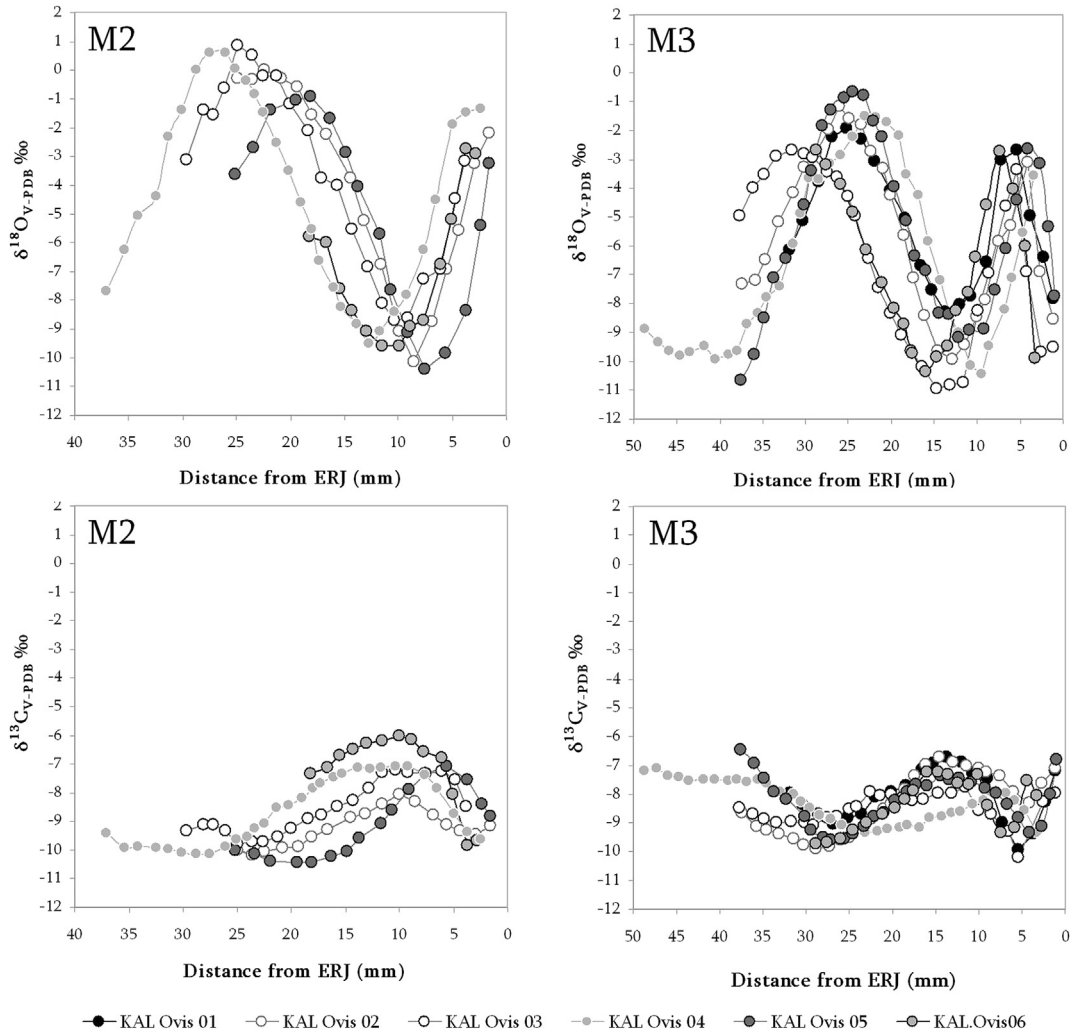


Figure 6. Sequential $\delta^{18}\text{O}_{\text{V-PDB}}$ and $\delta^{13}\text{C}_{\text{V-PDB}}$ values in all second and third molars.

occupation of the site (Bălăşescu et al., 2016; Montoya et al., 2013). The densest concentration (GF 23–24 in 7d3 layer) was composed of a compact and homogeneous mound of fauna remains in an ashy, sedimentary matrix. No intercalated solifluxion flow in the fauna heaps was observed during the excavation, while this phenomenon was clearly identified within the 7d2 layer.

The $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values that were measured in all of the specimens are compared in Figure 6. Events 1 to 5 (as referred to in Fig. 5) span a two-year sequence of time. In all five of the individuals, this sequence spans the same period of life. Considering that the attributed ages at death are close to each other (2–3 years for KAL Ovis 04; 3–4 years for KAL Ovis 01, Ovis 02, Ovis 03 and Ovis 05; 4–6 years for KAL Ovis 06; Table 1) and considering the extreme case of a unique hunting event, the sequences that are measured in these specimens may refer to the same years for KAL Ovis 01, Ovis 02, Ovis 03 and Ovis 05 and to very close years for the remaining two sheep. In this case, and supposing minimal inter-annual variability in environmental $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ signals over a four year time period, a great similarity would be expected in the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ values. Although similar stable isotope values would not necessarily demonstrate close contemporariness between individuals, great dissimilarity would invalidate the hypothesis.

Inter-individual variability is not solely a matter of the vegetal environment and climate that defines the isotopic history;

individual feeding behavior, metabolism and physiology (tooth growth and mineralization rate) also influence the integration of the input signal in enamel and, consequently, the final maximum and minimum values of the sequence. For this reason, inter-individual variability within a pool of individuals with the same stable isotope history may exist. Elements for comparison may be found in modern reference studies. Two reference sets of domestic sheep were considered. The first one consists of 10 modern sheep that were raised on the island of Rousay (Orkney archipelago, Scotland [Balasse et al., 2009, 2012]). All of the specimens were born a few weeks apart, were raised in the same cohort, grazing on the same terrestrial pasture with access to the same water sources, and they were slaughtered on the same day. In these specimens' M2s, in which the isotopic sequences encompassed a winter and a summer event, inter-individual variability was 1.9‰ and 1.1‰, respectively, in optimal $\delta^{18}\text{O}$ values ($n = 10$ [Balasse et al., 2012]) and 1.2‰ and 1.4‰, respectively, in optimal $\delta^{13}\text{C}$ ($n = 6$ [Balasse et al., 2009]). The difference in the amplitude of variation was 1.3‰ for the $\delta^{18}\text{O}$ values, and 1‰ for the $\delta^{13}\text{C}$ values. In the second reference set (Blaise and Balasse, 2011), inter-annual variability over four years is introduced. This set includes eight sheep that were raised in the subalpine region of Southern France. The sheep were born between 1998 and 2001 and slaughtered in May 2004. They grazed on the rangelands near the farm all year round and

Table 3
Amplitude of the $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ sequences during recorded events.

Sample	Amplitude in $\delta^{18}\text{O}$				Amplitude in $\delta^{13}\text{C}$			
	Events 1 to 2	Events 2 to 3	Events 3 to 4	Events 4 to 5	Events 1 to 2	Events 2 to 3	Events 3 to 4	Events 4 to 5
KAL Ovis 01	–	–	6.4	5.6	–	–	2.3	3.3
KAL Ovis 02	10.2	9.0	8.7	6.8	2.1	1.8	3.2	1.6
KAL Ovis 03	9.5	6.0	8.3	7.7	2.6	1.9	1.3	2.4
KAL Ovis 04	10.1	8.0	8.9	–	3.0	2.2	1.4	–
KAL Ovis 05	9.5	9.7	8.5	6.5	3.3	2.5	2.2	2.0
KAL Ovis 06	–	–	–	7.7	–	–	–	2.1
Max	10.2	9.7	8.9	7.7	3.3	2.5	3.2	3.3
Min	9.5	6.0	6.4	5.6	2.1	1.8	1.3	1.6
Range	0.7	3.7	2.5	2.1	1.2	0.7	1.9	1.7

were provided with water from a source near the town. In the M2s, where the isotopic sequences encompassed a summer and a winter event, inter-individual variability in optimal $\delta^{18}\text{O}$ values was 1.5‰ ($n = 5$) and 1.2‰ ($n = 3$), respectively; in the M3s, in which the isotopic sequences also encompassed a summer and a winter event, inter-individual variability in the optimal $\delta^{18}\text{O}$ values was 2.5‰ ($n = 5$) and 1.6‰ ($n = 6$), respectively.

In the Kalavan 1 mouflon, the inter-individual variability in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values that were recorded in the different summer and winter events are shown in Table 3. In the $\delta^{18}\text{O}$ values, inter-individual variability is 1.7‰, 1.7‰, 2‰, 2.7‰ and 0.7‰ in events 1, 2, 3, 4 and 5, respectively, while in $\delta^{13}\text{C}$, it is 0.6‰, 1‰, 0.9‰, 1.2‰ and 1.9‰, respectively. The inter-individual variability in the amplitude of variation between two successive events is 0.7‰, 3.7‰, 2.5‰ and 2.1‰ in $\delta^{18}\text{O}$ values and 1.2‰, 0.7‰, 1.9‰ and 1.7‰ in $\delta^{13}\text{C}$ values between events 1 to 2, 2 to 3, 3 to 4 and 4 to 5, respectively (Table 3). All of these indicators of inter-individual variability are of similar magnitude to those observed in the modern reference sets of sheep that were born in the same year or a few years apart, which supports the hypothesis that these sheep had similar environmental life histories and were possibly born within a short time period. This is in agreement with the hypothesis of a short time accumulation of sheep remains at the campsite.

6. Conclusions

Although a larger sample size would be desirable, the outcomes of this study are significant for the paleoethology of ancient wild sheep populations from northeastern Armenia (Lesser Caucasus region) during Late Glacial times. They contribute indirectly to the understanding of the pattern of occupation of mountain territories by Epigravettian communities. On the paleoethological side, for the first time, vertical mobility on a seasonal scale was demonstrated for the wild sheep that were recovered at Kalavan 1. This was reflected in opposed variation in the $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ sequences, which suggests that winter was spent in the lowlands and summer on the highland meadows. The pattern of vertical mobility in Late Glacial wild sheep is similar to the one that was described for modern Armenian mouflons and may have been driven by similar reasons, pushing wild sheep towards higher elevation in summer in search of better pastures and pushing them downwards with the arrival of winter and reduced accessibility to highland meadows because of the snow cover. Additionally, a strong seasonality of birth for Late Glacial wild sheep was suggested, in agreement with the strong constraint that was represented by the pattern of a wide range in seasonal mobility.

From a methodological point of view, uncertainties remain in the interpretation of the $\delta^{18}\text{O}$ sequences: would vertical mobility, in this context, lead to a reversal of the otherwise expected temperature-controlled pattern? This particular point should be

addressed in the future as it would be relevant to any study that investigates the summer attendance at high elevation sites where glacial ice melt may contribute to the water pool. This interpretation would also directly influence determination of wild sheep birth season from $\delta^{18}\text{O}$ sequences in teeth.

On the archaeological side, the pattern of seasonal altitudinal mobility of the wild sheep that were recovered at Kalavan 1 suggests that their availability near the site was restricted to certain times of the year during bi-annual migrations. The hunter-gatherers of Kalavan 1 scheduled wild sheep exploitation at specific periods of the year when the animals were crossing the altitudinal location of the site, which implies an awareness of wild herd mobility strategies. Further, a low inter-individual variability in the stable isotope sequences does not contradict other archaeological evidence in favor of the accumulation of these faunal remains over a short period of time. This new dataset strengthens the previous interpretations at Kalavan 1, which presents this hunting camp site within a wider and complex strategy of exploitation of the mountainous territories by Epigravettian communities, involving the acquisition of obsidian resources at high elevation sites after the thawing of the snow cover in spring to summer and carcass butchering for the collection of stores of animal products at Kalavan 1 (Montoya et al., 2013; Bălăşescu et al., 2016, Fig. 2). This integrative study of animal behavior and the socio-economy of Epigravettian hunter-gatherers builds a picture of how two mobile trajectories met at Kalavan 1: a logistic nomadism by Paleolithic communities on the one hand and the seasonal altitudinal migration of wild sheep herds on the other.

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Supplementary Online Material

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