



Dietary traits of the ungulates from the Middle Pleistocene sequence of Lazaret Cave: palaeoecological and archaeological implications

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Abstract

Dietary traits in ungulates from Lazaret Cave were analysed for possible changes in ecological niches throughout the marine isotopic stage (MIS) 6 sequence of the site and to investigate the duration of the occupations corresponding to the accumulation of ungulate remains by human groups. The analysis revealed changes in dietary diversity throughout the sequence related to the climatic and environmental changes of the MIS 6. These changes affected the availability of vegetal resources, competition among species, and the distribution and movement of the ungulates in the territory. Human groups were also affected by these changes, as the archaeological record of Lazaret Cave in the duration of occupations at the different levels shows. The response of the large mammal communities to persistent climatic instability is reflected in differences between the sites of southern France of the MIS 6, where species show different dietary traits.

Keywords Microwear · Mesowear · MIS 6 · Cervidae · Bovidae · Equidae

Introduction

Ungulate communities are known to be strongly influenced by climatic and environmental changes throughout the Pleistocene. These changes are ordinarily detected using the composition of mammal assemblages and, in the case of ungulates, by shifts in dietary traits (e.g. Strani et al. 2015; Strani 2021). During the marine isotopic stage 6 (MIS 6; ca. 185–130 ka), climatic and environmental variations are particularly well documented (e.g. Margari et al. 2010). In southern Europe, the MIS 6 is known for frequent and persistent millennial-scale climate instability (Wilson et al. 2021),

which affected vegetal and animal communities. The diets of large mammal communities should reflect these changes. However, studies of dietary traits based on assemblages from the MIS 6 are very scarce. In southern Europe, few studies on the paleodiet of ungulate communities are available for the MIS 6: Rigabe, Coudoulous II (level 9), Combe Grenal (levels 63 to 56), Pech de l'Azé (levels 6 to 9), Abri Suard (levels 50 to 53) (Uzunidis 2017; 2021), and Payre (level D: Rivals et al. 2009).

The present study aimed to improve our knowledge of the impact of climatic instability during the MIS 6 by analysing the dietary traits of ungulates from the Middle Pleistocene sequence of Lazaret Cave.

The Lazaret Cave is located in southern France on the Mediterranean coast by the city of Nice (43° 41' 25" N, 7° 17' 42" E) (Fig. 1). It was formed in lower Jurassic dolomite limestone; the current entrance faces southwest at 26 m a.s.l. and ca. 50 m from the coastline. The lower part of the cave sequence (Fig. 1) comprises two marine transgressive phases, complex A or lower marine beach, without fossils and ascribed to MIS 9 (Lumley et al. 2004), and complex B or upper marine beach, which is rich in coral and marine mollusks. It dates back to ca. 230 Ka, which corresponds to MIS 7 (Bahain 1993; Michel and Yokoyama 2001). These marine deposits are located under a continental fill (complex C) 6 m thick (mainly composed of clays and to a lesser extent gravel), closed off by a stalagmitic plate (complex E),

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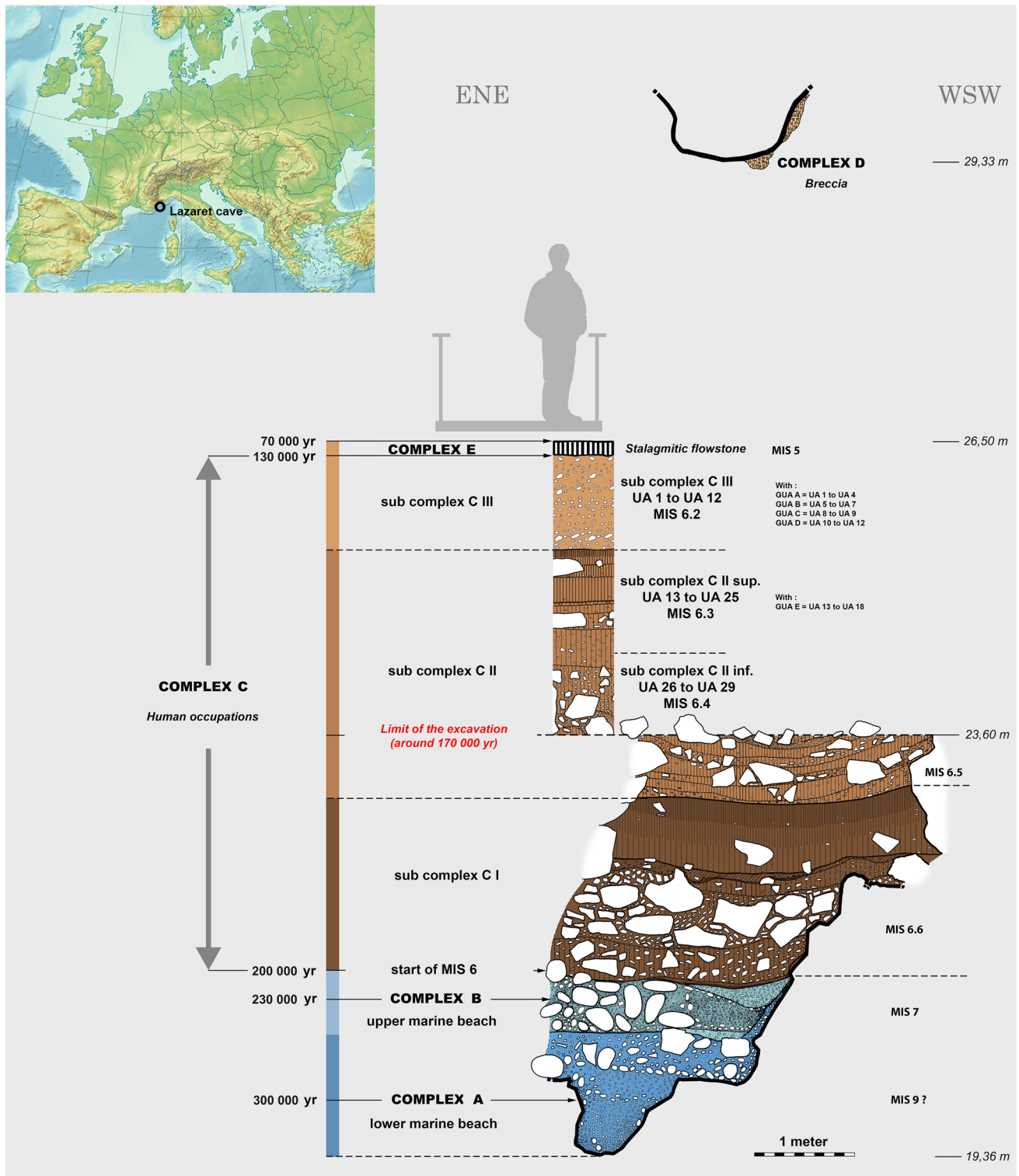


Fig. 1 Location and stratigraphic sequence of Lazaret Cave

and dating from ca. 108 to 145 Ka (Shen 1985; Michel et al. 2009). The stratigraphic complex C, dating from 220 to 130 Ka (Michel 1995; Michel et al. 2009), is divided into three stratigraphic subcomplexes, named CI, CII, and CIII. The

bottom of the continental deposits, subcomplex CI, is not yet well known, but the CII and CIII subcomplexes have been excavated and contain at least 29 archaeostratigraphic units (named UA): CII inf. (UA 29–26), CII sup. (UA 25–13), and

CIII (UA 12–1). Finally, within AU 19 to 1, five large AU (named GUA E to A), which correspond to groups of UA, have been defined.

The sedimentation process in Lazaret Cave is rather homogenous, and the archaeostratigraphy constitutes an essential and most reliable element for understanding the stratigraphy of the site (Canals 1993). These subcomplexes show a succession of hominin occupations, together with abundant lithic bifacial tools dating from the transition between the Lower and Middle Palaeolithic (e.g. Lumley et al. 2004; Hanquet et al. 2010; Valensi et al. 2007; Lumley 2019). A total of 28 human remains, which can be assigned to archaic Neanderthal forms, have been discovered in subcomplex C during excavations (Lumley 2019).

The faunal remains (large mammals, birds, small vertebrates, and gastropods) identified at Lazaret Cave indicate, in general, a cold climate and relatively humid environmental conditions, which can be related to the geographical position of the cave, which existed in a transitional zone between the French steppe and the Italian forest-grassland during MIS 6 (López-García et al. 2021). The best-represented large mammal species throughout the sequence excavated are red deer (*Cervus elaphus*) and ibex (*Capra ibex*). In terms of subsistence strategies, hominins were practising selective red deer hunting (Valensi et al. 2013). Recent studies exploring mobility in *C. elaphus* and *C. ibex* from the Lazaret Cave using multi-isotopic analysis, isoscape modelling, and spatial assignments have suggested that red deer were more likely to occupy higher elevations further from the cave in the summer and lowland areas closer to the cave site in winter; meanwhile, ibex were living nearby (Barakat et al. 2023).

The specific objectives of the present study are (1) to analyse possible changes in the ecological niches occupied by ungulates throughout MIS 6 at Lazaret Cave and (2) to investigate the duration of the occupations corresponding to the accumulation of ungulate remains by human groups in the cave.

Materials and methods

Materials

Ungulate teeth were selected from the stratigraphic subcomplexes CIII, CII inf., and CII sup. from Lazaret Cave. We selected those that were identified at the species level and whose occlusal surfaces presented facets of wear (i.e. belonging to adult individuals). All lower and upper right teeth were selected, with some left teeth added to increase the sample size when they did not belong to the same individuals as the right ones (according to tooth size and stages of wear). For subcomplex CIII, the sample was later subdivided into four sub-units (GUA A to D) to compare the

microwear patterns in *C. elaphus*. The list of specimens analysed and the raw data from tooth mesowear and microwear analyses are available at <http://dx.doi.org/10.5281/zenodo.7308555> (Rivals 2022).

Tooth mesowear analysis

Mesowear (Fortelius and Solounias 2000) was analysed on the buccal or lingual side of the upper and lower molars, respectively, except for horses where only the lower teeth were analysed. As mesowear is dependant of the ontogenetic age of the individuals, teeth from young individuals (without wear facets) and old adult individuals (with heavy wear) were discarded (Rivals et al. 2007). Teeth with broken cusps were also discarded. The method is based on the categorization of cusp shape and relief in seven categories (from 0 to 6), ranging from high relief and sharp cusps (category 0) to blunt cusps with no relief (category 6) (Mihlbachler et al. 2011). The individual mesowear values were then averaged to obtain the mesowear score or MWS. Mesowear was analysed by a single experienced researcher (FR) to avoid inter-observer error.

Tooth microwear analysis

Tooth microwear was analysed using the low-magnification technique (Solounias and Semprebon 2002; Semprebon et al. 2004). To reduce inter-observer error, all observations and quantification were realized by a single experienced observer (FR). First, the occlusal surface of the teeth was cleaned with a cotton swab and acetone and 96% ethanol. Then, the surface was moulded using a high-resolution dental silicone (Heraeus Provil novo light, regular set), and casts were produced using transparent epoxy resin (CP Quimica, CPOX P 1060/A + CPEN 1585/B). Casts were analysed with a Zeiss Stemi 2000C stereomicroscope at 35× magnification under transmitted light. Before quantifying the microwear features, the surface was screened to identify taphonomic alterations, and these casts were discarded from the analysis (King et al. 1999; El-Zaatari 2010; Uzunidis et al. 2021). Microwear features were identified and quantified on the paracone of the upper teeth and the protoconid of the lower teeth. Two types of features were identified according to the classification proposed by Solounias and Semprebon (2002). Pits are circular or sub-circular features that appear either bright (small pits) or dark (large pits). Scratches are long microfeatures with straight and parallel sides. These features were quantified in a standard squared area of 0.16 mm² using an ocular reticule. The results obtained on the fossil samples were compared with a dataset established from extant ungulates with known diets (Solounias and Semprebon 2002; Rivals et al. 2010).

Finally, to estimate the duration of the faunal assemblages' accumulation at the Lazaret Cave, the standard deviation (SD) and the coefficient of variation (CV) computed

on the numbers of scratches were employed to quantify the variability of the microwear signal (Rivals et al. 2015). This variability recorded by microwear is related to seasonal changes in diet and relates to the duration of the accumulation events (i.e. hunting events in this case). The SD and CV values are plotted on a bivariate heat map to classify each assemblage in three categories: event lasting one season or less, events longer than a season, and separate events that occurred during different non-contiguous seasons (i.e. either spring and autumn or winter and summer).

Results

Tooth mesowear

The mesowear values for the ungulates from the Lazaret Cave fell between $MWS = 2.2$ and $MWS = 3.3$ (Table 1; Fig. 2). In comparison with modern ungulates with known diets, they fit within the range of grass-dominated mixed feeders and pure grazers (Fig. 2). When samples of the same species were compared throughout the sequences (i.e. for *C. ibex* and *C. elaphus*), the MWS values for CII inf., CII sup., and CIII were not significantly different (ANOVA; *C. ibex*; $F = 0.5707$; $p = 0.577$; *C. elaphus*; $F = 0.3822$; $p = 0.6848$). At a higher stratigraphic resolution, within subcomplex CIII, some significant changes were observed for *C. elaphus* (ANOVA; $F = 9.996$; $p = 0.0002$). The lowest MWS values were found in the lower units GUA C and D, while the highest were reported for GUA A and B (Table 2). The

difference in mesowear scores was significant between GUA B and C (Tukey's $Q = 5.146$; $p = 0.0073$). There was a shift from low to high abrasive diets through subcomplex III. *C. elaphus* was a browser or browse-dominated mixed feeder in GUA D and shifted to a grazer or grass-dominated mixed feeder in GUA B and A.

Tooth microwear

Tooth microwear was performed on 70 samples presenting enamel surfaces without any taphonomic alteration. The horse *Equus caballus* was present in the three stratigraphic subcomplexes, but the sample size was significant for CII sup. only. For subcomplexes, CII inf. and CIII, the sample size was too small ($N = 1$). The horse from subcomplex CII sup. revealed a high number of scratches, a mixture of fine and coarse scratches, and an absence of gouges (Table 1). In comparison with extant ungulates, the sample falls amongst the confidence ellipse of the extant grazers (Fig. 3), indicating a highly abrasive diet.

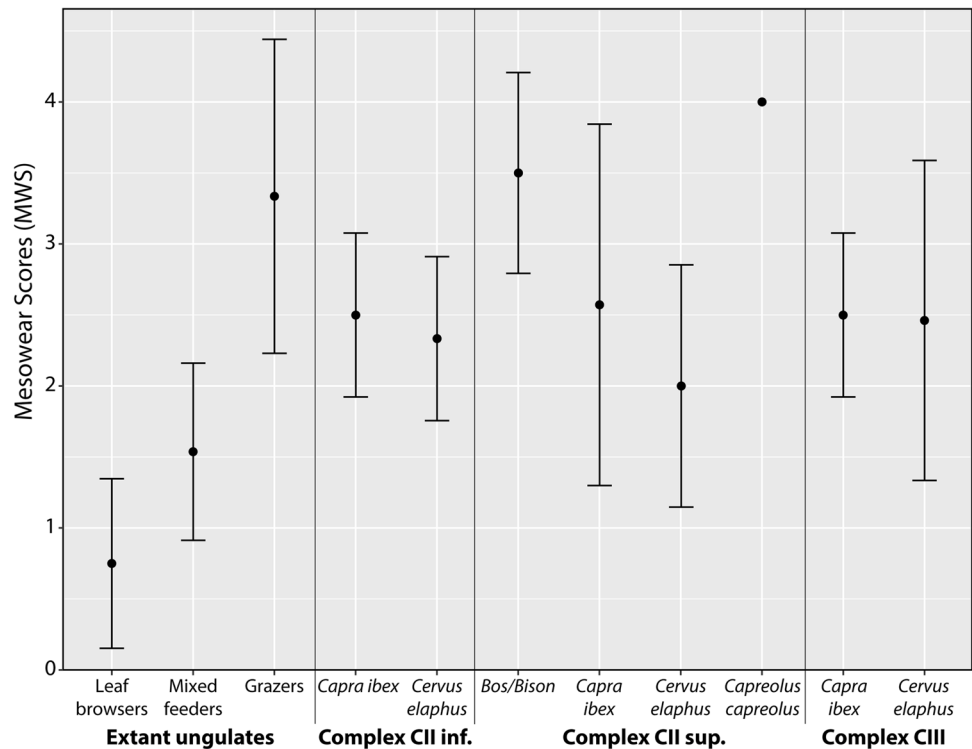
The red deer *C. elaphus* showed moderately low values of scratches and pits in all three subcomplexes (Table 1). There was no significant difference amongst the three samples, and they all encompass a wide range extending from leaf browsing to mixed feeding (Fig. 3). They may have belonged either to browsers or browse-dominated mixed feeders. The samples from subcomplex CIII sorted by the four GUA revealed no change in terms of total numbers of pits and scratches, but there were some differences in terms of the proportion of large pits, gouges, and cross scratches (Table 2). The results

Table 1 Summary of the mesowear and microwear results for the ungulates from Lazaret Cave

	Mesowear		Microwear							
	<i>N</i>	MWS	<i>N</i>	Npit	Nscr	%LP	%G	SWS	%XS	%HC
C III										
<i>Capra ibex</i>	6	2.17	5	26.60	16.70	80.00	20.00	1.20	0	0
<i>Cervus elaphus</i>	26	2.50	23	12.80	15.59	82.61	30.43	1.26	21.74	13.04
<i>Equus caballus</i>	-	-	1	11.00	23.00	-	-	1.00	-	-
C II supérieur										
<i>Bos/bison</i>	3	3.33	2	15.00	16.50	-	-	1.00	-	-
<i>Capra ibex</i>	8	2.75	10	21.40	17.70	60.00	40.00	1.00	0	0
<i>Capreolus capreolus</i>	-	-	2	12.75	10.00	-	-	2.00	-	-
<i>Cervus elaphus</i>	14	2.21	14	13.93	14.57	64.29	14.29	1.29	35.71	7.14
<i>Equus caballus</i>	-	-	5	11.30	24.30	60.00	0	1.20	0	0
C II inférieur										
<i>Capra ibex</i>	4	2.50	4	14.50	19.00	75.00	0	1.00	0	0
<i>Cervus elaphus</i>	3	2.33	3	12.00	14.00	100	0	1.00	33.33	0
<i>Equus caballus</i>	-	-	1	12.50	27.00	-	-	1.00	-	-

Abbreviations: *N*, number of specimens; MWS, mesowear score; Npit, mean number of pits; Nscr, mean number of scratches; %LP, percentage of individuals with large pits; %G, percentage of individuals with gouges; SWS, scratch width score; %XS, percentage of individuals with cross scratches; %HC, percentage of individuals with hypercoarse scratches

Fig. 2 Mesowear scores (MWS) for the ungulates from Lazaret Cave compared with the dietary categories in extant ungulates (i.e. leaf browsers, mixed feeders, and grazers). Error bars correspond to the standard error of the mean (± 1 SEM) for each sample



confirm the mixed feeding diet reported for the entire sample from CIII, but the differences in some qualitative variables suggest the consumption of different plant parts.

The roe deer *Capreolus capreolus* exhibited a small number of scratches associated with a low variability as reflected by the standard deviation, while the variability in the number of pits was very high (Fig. 3).

The ibex *C. ibex* exhibited an increase in the number of pits and a decrease in the number of scratches from CII inf. to CIII (Table 1) and an increase in the variability of the values as reflected by the standard deviation (Fig. 3).

The large bovids were represented by two individuals, both in CII sup.: an aurochs, *Bos primigenius*, and an unidentified large bovid classified as *Bos/Bison*. The two individuals had very different microwear patterns. The aurochs, with a low number of scratches, was categorised as a leaf

browser, while the *Bos/Bison* was categorised as a mixed feeder.

The results from the three stratigraphic subcomplexes reveal that most of the species were mixed feeders. When the minimum number of individuals (MNI) was taken into account, the assemblage was dominated by mixed feeders (Table 3), comprising between 87.5 and 94.1% of the assemblage. The other dietary categories were much less common. Grazers were present in all assemblages (between 1.5 and 13%) and leaf browsers only in subcomplex CII sup.

There were some differences in terms of the variability of microwear signals between and amongst species (Table 4). In CII inf., only *C. ibex* provided significant results, indicating a seasonal accumulation of remains due to its position in zone A (Fig. 4A). In CII sup., *C. ibex* falls in zone B, indicating an occupation that lasted longer than one season

Table 2 Summary of the mesowear and microwear results for the ungulates from the GUA from subcomplex CIII at Lazaret Cave

	Mesowear		Microwear							
	N	MWS	N	Npit	Nscr	%LP	%G	SWS	%XS	%HC
GUA A	7	3.00	7	14.64	15.64	85.71	42.86	1.29	0	0
GUA B	6	3.50	5	10.60	14.20	60.00	40.00	1.20	60.00	0
GUA C	6	2.00	5	10.90	17.50	80.00	20.00	1.40	0	60.00
GUA D	7	1.57	6	14.08	15.08	100	16.67	1.17	33.33	0

Abbreviations: N, number of specimens; MWS, mesowear score; Npit, mean number of pits; Nscr, mean number of scratches; %LP, percentage of individuals with large pits; %G, percentage of individuals with gouges; SWS, scratch width score; %XS, percentage of individuals with cross scratches; %HC, percentage of individuals with hypercoarse scratches

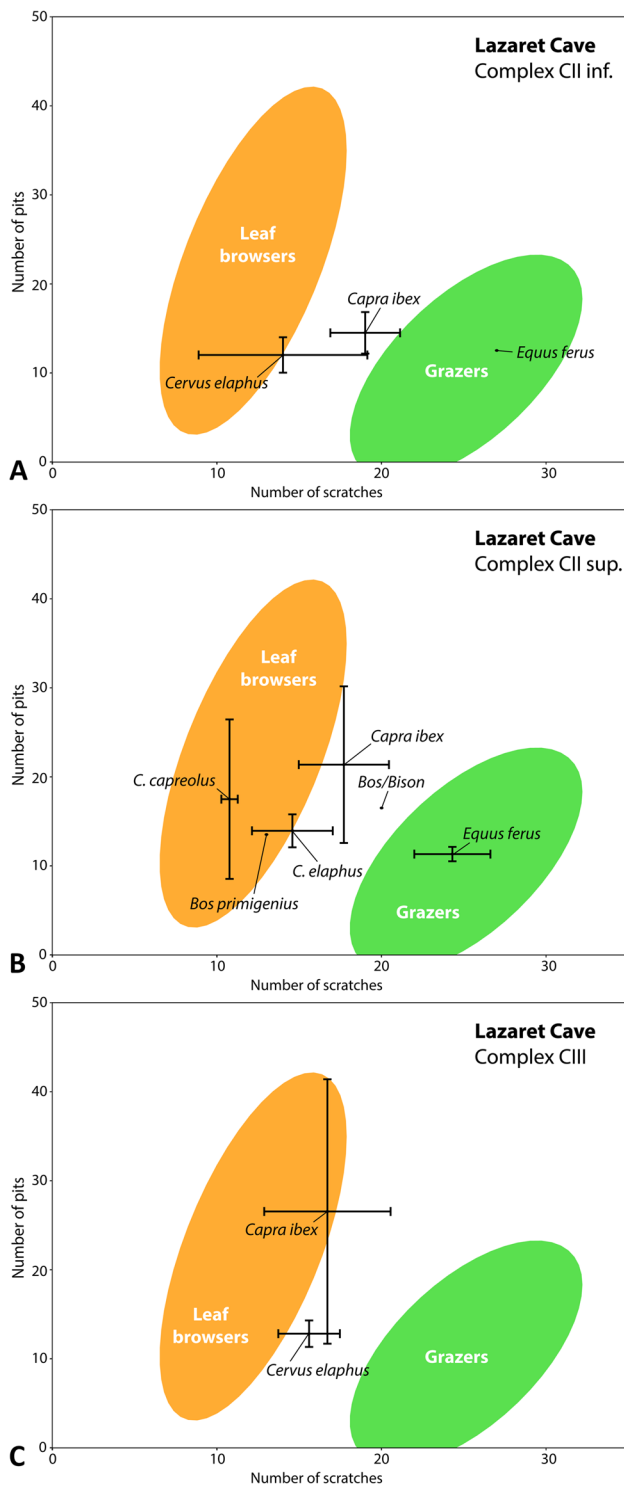


Fig. 3 Bivariate plot of the number of pits and scratches for the ungulates from Lazaret Cave. Error bars correspond to standard error of the mean (± 1 SEM) for each sample. Plain ellipses correspond to the Gaussian confidence ellipses ($p=0.95$) on the centroid for the extant leaf browsers (LB) and grazers (G) based on the reference database from Solounias and Semperebon (2002)

(Fig. 4B). *Equus caballus* falls in zone A, indicating a seasonal occupation. *C. elaphus* did not provide significant results. In CIII, *C. ibex* and *C. elaphus* fall in zone B, indicating an accumulation that lasted longer than one season (Fig. 4C). Due to its larger size, the sample of *C. elaphus* can be divided in four GUA (Table 5; Fig. 4D). The data for GUA B were not significant because they fell on the boundary between zones B and C. The samples from GUA A and C fell into zone B, indicating an accumulation that lasted longer than one season, while that from GUA D indicates at least two events in non-consecutive seasons (e.g. spring and fall or summer and winter).

Discussion

Paleoenvironmental implications

The ungulate assemblages from the three subcomplexes studied were dominated by mixed feeders, which comprised between 87.5 and 94.1% of the individuals (based on the minimum number of individuals). The grazers and leaf browsers, when present, comprised between 1.5 and 13% of the ungulates. Thus, all three assemblages were dominated by eurytopic species, mainly *C. ibex* and *C. elaphus*, that is species that could tolerate a wide range of habitats or ecological conditions. The results support the wide diversity of habitats available in the surroundings of the cave, as paleoenvironmental analyses based on the small and large mammals have shown (Valensi and Abbassi 1998; Valensi et al. 2007; Hanquet et al. 2010; López-García et al. 2021). Our results are very similar to those from other sites from MIS 6 in southern France. At some sites, ungulate communities were dominated up to 80% by mixed feeders, such as at Rigabe (Uzunidis 2017, 2021). The other sites where dental wear data are available were dominated more or less equally by mixed feeders and grazers. This was also the case for level D from Payre (Rivals et al. 2009), level 9 from Coudoulous II, levels 63 to 56 from Combe Grenal, levels 6 to 9 from Pech de l'Azé, and levels 50 to 53 from Abri Suard (Uzunidis 2017; 2021). Even if the taxonomic composition of the fauna varied between these sites, the dietary traits of the ungulates from the Lazaret Cave were nevertheless similar, especially in the case of Rigabe; both corresponded to the coldest period of the MIS 6, and both probably contained low-growing plants, shrubs, and small trees associated with some open grass areas, characteristic of the sclerophyll Mediterranean forest (Hanquet et al. 2010).

When comparing the three subcomplexes from the Lazaret Cave, dietary diversity appeared to be higher in subcomplex CII sup., where grazers, mixed feeders, and browsers

Table 3 Minimum number of individuals (MNI) and percentage of leaf browsers (LB), mixed feeders (MF), and grazers (G) in the three assemblages from Lazaret Cave

	MNI				Percentages		
	LB	MF	G	Total	LB	MF	G
CIII		111	7	118	0	94.1	5.9
CII sup	4	62	1	67	6.0	92.5	1.5
CII inf		7	1	8	0	87.5	13

were present. This suggests that a greater diversity of vegetal resources was available to the ungulates in subcomplex CII sup. than in the other subcomplexes. By contrast, Valensi and Abbassi (1998) detected no environmental change throughout the sequence. A study of the small vertebrate assemblages revealed cold conditions for subcomplexes CII inf. and CIII and slightly warmer conditions for CII sup. (López-García et al. 2021), but the differences were reported as not significant. Our results accord with Valensi et al.'s (2007) study of the large mammal assemblages from subcomplexes CII and CIII, which were dominated by *C. elaphus* and *C. ibex* (Valensi et al. 2007). The subcomplex CII sup. comprised more temperate species (e.g. *Bos primigenius* and *Capreolus capreolus*) than subcomplex CIII, which contains the cold-adapted *Rangifer tarandus* and *Bison priscus* (Valensi et al. 2007). Environmental changes were also found in the bird and reptile assemblages (Hanquet et al. 2010) and the gastropods (Valensi et al. 2007). All paleoenvironmental proxies that analysed faunal assemblages provided consistent indications of a cold and humid climate. The cooling reported from CII sup. to CIII was observed through all faunal groups, except the rodents.

Within subcomplex III, the mesowear analysis of the assemblages from the four GUA was carried out for *C. elaphus*. Changes in mesowear scores indicated an increase in the abrasiveness of the diet through the sequence of subcomplex CIII, and this was especially significant between

Table 4 Variability values for the numbers of scratches for the ungulates from Lazaret Cave

	N	CV	SD
C III			
<i>Capra ibex</i>	5	0.26	4.30
<i>Cervus elaphus</i>	23	0.29	4.49
C II supérieur			
<i>Capra ibex</i>	10	0.24	4.33
<i>Cervus elaphus</i>	14	0.32	4.59
<i>Equus caballus</i>	5	0.11	2.59
C II inférieur			
<i>Capra ibex</i>	4	0.11	2.12
<i>Cervus elaphus</i>	3	0.32	4.44

Abbreviations: N, number of specimens; SD, standard deviation of the number of scratches; CV, coefficient of variation of the number of scratches

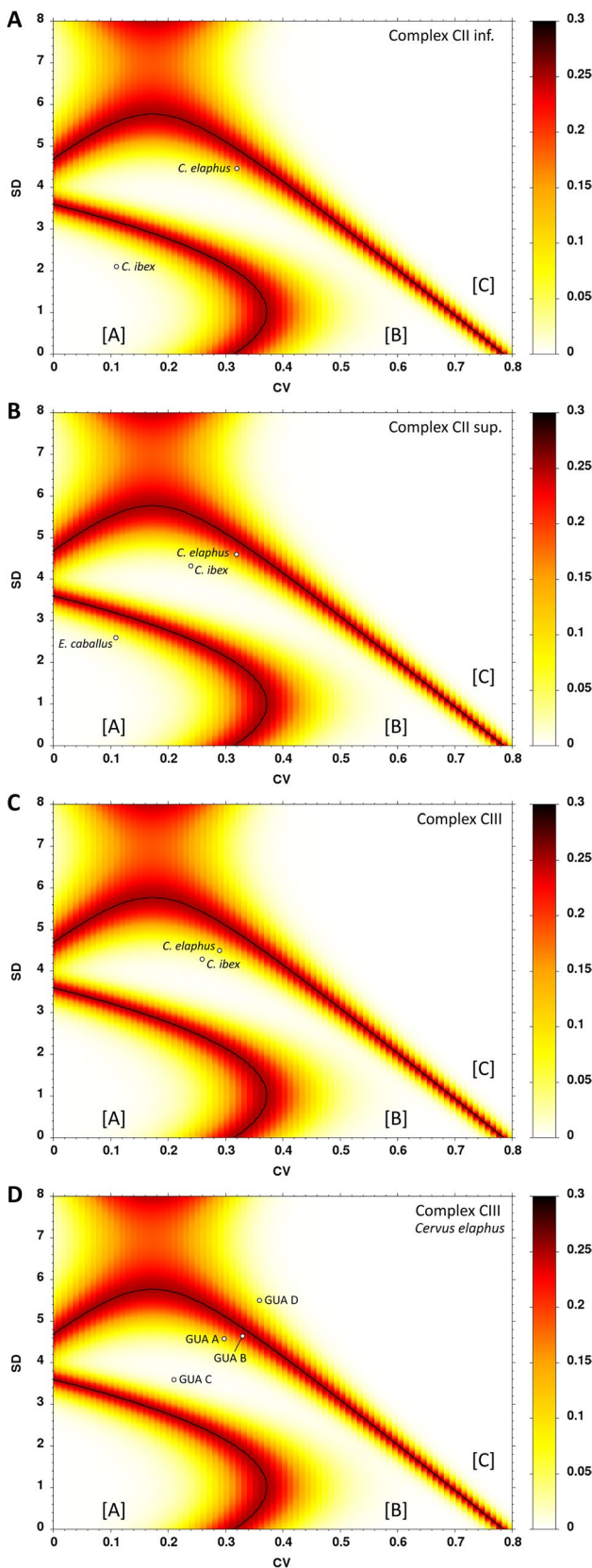
GUA C and B, suggesting an increase of grasses in the red deer diet and, correspondingly, either a slow opening of the habitat and changes to colder conditions throughout the formation of subcomplex CIII or a change in diet due to competition with other herbivore mammals. The climatogrammes based on the ecological and climatic preferences of the large mammals did not detect significant changes, especially regarding the opening of the habitat (Hanquet et al. 2010). Nevertheless, the climatogramme method has limitations, and it is very difficult to provide evidence of the interstadial periods in a refuge zone. The data do not always fit together and often seem contradictory. Thus, the first hypothesis can be ruled out. The increase in grass shows a dietary change that was certainly related to a displacement of the ecological niche of the red deer or greater (perhaps seasonal) mobility of red deer populations, as strontium and oxygen isotope analysis has shown (Barakat et al. 2023).

Archaeological implications

The variability in microwear signals points to differences in seasonality amongst species and stratigraphic units. However, as only a few of the present samples provided significant results, it is not possible to infer the type of occupation for each unit. Also, the findings can only be used to initiate a discussion of differences in hunting patterns amongst species.

In subcomplex CII inf., the remains of Alpine ibex, *C. ibex*, accumulated during a seasonal event or various successive events. These events may have occurred during various years but always each time at the same season. For the red deer, the duration appeared to be longer, but the variability value was not significant. The combined study of these two species from UA 29 using dental eruption and wear and cementum analysis indicate that hunting of red deer and ibex occurred from late autumn to the beginning of summer, with two peaks: the first one in autumn and early winter and the second one in spring (Roussel et al. 2021). There were clear differences in the timings of human occupations amongst the various archaeological units within subcomplex CII inf., suggesting a significant variability in hominin behaviour.

In subcomplexes CII sup. and CIII, the remains were accumulated in the cave during events that lasted more than one season, or during shorter events (maybe seasonal) at different seasons. In subcomplex CII sup., the remains of



◀ **Fig. 4** Boundary lines with an error probability (heat map) based on standard deviations (SD) and coefficient of variation (CV) values of microwear data used for the classification of the Lazaret Cave samples into short events (region A), long-term events (region B), or two separate short events (region C)

horses corresponded to seasonal occupations that might have occurred either at the same time as one of the occupations when the ibex was hunted or at a different time of the year. Strontium and oxygen isotope analyses have been conducted on a limited sample ($N=4$) from UA 25 to determine animal movements and seasonality (Barakat et al. 2023). The results support the hypothesis that red deer were seasonally mobile and most probably hunted in autumn and winter when they were in areas close to the cave (Barakat et al. 2023). Occupational patterns during the formation of subcomplex CII sup. were strongly related to the seasonal availability of the game.

In subcomplex CIII, the red deer was certainly hunted at the same time as the Alpine ibex, (i.e. during various seasons throughout the year). Nevertheless, there were some differences within subcomplex CIII if the GUA are taken into account (though for GUA A, C, and D only, because the results were not significant for GUA D). The GUA A and C followed the same pattern as previously described for the entire unit CIII (i.e. an accumulation throughout various seasons of the year), while the results for the GUA D indicate two different seasons of accumulation. As was the case with the underlying subcomplex CII sup., the procurement of large mammals and the occupation of the site were driven by seasonal changes.

The results are difficult to interpret or even discuss because few samples generated significant results. Nevertheless, differences in variability of the microwear patterns provide evidence of distinct differences in the types of occupations of the cave throughout the stratigraphic sequence, from short seasonal occupations to longer occupations during fewer seasons. It is also important to emphasise that the combination

Table 5 Variability values for the numbers of scratches for *Cervus elaphus* from the GUA from subcomplex CIII at Lazaret Cave

<i>C. elaphus</i>	<i>N</i>	<i>CV</i>	<i>SD</i>
GUA A	7	0.29	4.57
GUA B	5	0.33	4.66
GUA C	5	0.21	3.59
GUA D	6	0.36	5.48

Abbreviations: *N*, number of specimens; *SD*, standard deviation of the number of scratches; *CV*, coefficient of variation of the number of scratches

of analytical techniques improved the resolution and accuracy of the results. In this case, data obtained on juvenile individuals (through tooth eruption and wear and cementum analysis) and adult individuals (cementum analysis, strontium and oxygen isotopes, and tooth microwear) are consistent.

Conclusions

The analysis of the dietary traits of the ungulates from the Lazaret Cave revealed changes in dietary diversity throughout the sequence related to the climatic and environmental changes of MIS 6. These changes affected the availability of vegetal resources, the competition between species, and the distribution and movement of ungulates in the territory. Human groups were also affected by these changes, as indicated by the duration of occupations at the different levels. The response of the large mammal communities to frequent and persistent climatic instability is reflected in differences amongst and between the sites of southern France of the MIS 6, where species show different dietary traits according to the environmental conditions.

Author contribution FR: conceptualization, data collection, formal analysis, data curation, and writing original draft; JC: conceptualization and samples selection; ED: conceptualization and samples selection. All authors read and approved the final manuscript.

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Data availability Datasets related to this article can be found at <http://dx.doi.org/10.5281/zenodo.7308555>, an open-source online data repository hosted at Zenodo (Rivals 2022).

Code availability The R code to obtain the bivariate plots of microwear features is available at <https://doi.org/10.5281/zenodo.2587575> (Rivals 2019).

Declarations

Competing interests The authors declare no competing interests.

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Conflict of interest The authors declare no competing interests.

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