Late and middle Pleistocene ungulates dietary diversity in Western Europe indicate variations of Neanderthal paleoenvironments through time and space

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ABSTRACT

Mesowear and microwear on enamel from 763 teeth of middle and late Pleistocene ungulates were analysed to infer the potential of dental wear analysis of faunal remains as a paleoenvironmental and paleoclimatic proxy in relation to climatic changes and diversity of vegetation available in the environment. Fossil localities including levels belonging to two glacial and two interglacial stages were selected in Germany, France, and Spain. At a temporal scale, results indicate that the dietary diversity in ungulates is higher during interglacial phases (MIS 5 and 3) than during pleniglacial phases (MIS 8 and 4). Dietary diversity is concluded to be related to climate-driven vegetation changes which during interglacials lead to increased variety of potential food items available to ungulates. At the geographical scale, during interglacials, changes in diet composition are evident along geographical gradients. The corresponding dietary gradients are proposed to be related to climate and vegetation gradients reflecting more arid climates in the Mediterranean area compared to North-Western Europe. Species consistently represented at all localities investigated are *Cervus elaphus* (Cervidae, Artiodactyla) and *Equus ferus* (Equidae, Perissodactyla). *C. elaphus* populations are found to consistently have less abrasive diets than *E. ferus* populations but dietary traits of both species varied largely, revealing a significant plasticity in the feeding adaptation of both species. Those traits are concluded to be related to differences in vegetation structure at each locality and complement the evidence that ungulates have broader dietary habits than what is usually assumed.

1. Introduction

Climate related dietary diversity in ungulate faunas was recently investigated for a middle Pleistocene succession (MIS [Marine Isotopic Stage] 14–12) in southern France (Rivals et al., 2008). The interrelationship between climate (humidity and temperature) and dietary adaptations as indicated by dental wear was studied in various levels of a single locality. We decided to expand the analysis (1) chronologically (temporally) from the middle to the late Pleistocene, from MIS 8 to MIS 3, and (2) geographically in comparing several stratigraphic (archaeological) levels from seven localities in Western and Southern Europe. We selected this set of localities recently excavated and dated, which mostly expose several archaeological levels, with a large number of ungulates species represented by abundant and well preserved material. Archaeological localities are preferred because of their good stratigraphic control and absolute dating. Employing these criteria, seven localities were selected, the geographic range of which extends from Western Europe (Germany, France) and Southern Europe (Spain).

We test whether the hypothesis that interspecific variability in dental wear signatures reflects a climatic signal is correct on a larger scale. First of all, we track changes in dietary diversity through time. We also test for differences between glacial and interglacial phases (Hypothesis 1). As already demonstrated, we expect a temperate and humid climate to lead to a broader range of resources available for the herbivorous community (Kaiser and Schulz, 2006; Kaiser and Rössner, 2007; Rivals et al., 2008). This should be reflected by a greater diversity of dietary traits represented in the community. Therefore, we expect a lower range of available resources and thus a low diversity in herbivorous feeding traits in dryer and colder environments. This hypothesis will be tested in the area of Southern France and Northern Spain only because of two reasons: (1) to exclude potential effect of latitudinal gradients and geographical differences and (2) during glacial phases areas of Northern Europe were covered with ice sheets or

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permafrost, not allowing human occupation (Speleers, 2000; Clark and Mix, 2002).

The second hypothesis concerns changes on a geographical scale. Hypothesis 2 is tested in interglacial phases using the localities from Germany, France and Spain. Diet from high latitude localities should reflect a more forested environment and more humid climate than the localities from the Mediterranean area in France and Spain where we expected a dryer climate and more open biotopes.

We employ dental wear analysis (micro- and mesowear) to infer the dietary traits of the ungulates represented in the various localities and levels. The dietary signal would allow inferences on their community structure and habitat.

2. The localities

The sites investigated are located in two main geographic areas in Western and Southern Europe (Fig. 1). The three open-air localities Salzgitter Lebenstedt, Taubach, and Wallertheim are situated in North-Western Europe. Whereas the four localities Payre, Portel-Ouest, Ermitons, and Abric Romaní are cave localities in the Mediterranean area of France (Western Europe) and Spain (Southern Europe).

2.1. Salzgitter Lebenstedt

The site of Salzgitter Lebenstedt is located approximately 50 km south-east of the town of Hannover (Germany). The site was first excavated in 1952 by A. Tode (Tode, 1953) and was opened again in 1977 (Grote and Preul, 1978) and the material is stored at the Braunschweigisches Landesmuseum at Wolfenbüttel (Germany). The site exposes a Pleistocene channel filled with Weichselian

fluvial sediments including interposed still-water deposits such as fine sand, mud and peat (Preul, 1991). The fluvial sediments are about 2 m thick and can be separated into three subunits. The archaeological material was mainly distributed in the deposits of the intermediate unit 2 and the lower unit 1. On basis of pollen and sedimentological evidences, it was suggested that the site dates to the Oerel Interstadial, dated by C14 around 58–54 ky BP (Behre and van der Plicht, 1992), i.e. the beginning of MIS 3 (Pastoors, 1996).

The fauna consist of: *Canis lupus*, *Mammuthus primigenius*, *Coelodonta antiquitatis*, *Equus ferus*, *Rangifer tarandus*, and *Bison priscus* (Gaudzinski, 2000; Gaudzinski and Roebroeks, 2000). Remains left by Neanderthals indicate a specific hunting activity on *R. tarandus* (Gaudzinski, 2000).

The dental specimens analyzed were excavated during the campaign in 1952.

2.2. Taubach

The Taubach sequence is part of a complex of travertine exposed along the slopes of the Ilm river valley close to the town of Weimar (Germany). The sequence contains a homogeneous archaeological horizon represented by a sandy travertine, the 'Knochensand' (Bratlund, 1999, 2000; Gaudzinski, 2006). Flint artefacts and mammal remains were recovered from this horizon. Analyses of small mammals (Heinrich, 1994), radiometric dates of 116 ± 19 ka (Brunnacker et al., 1983), analysis of flint artifacts (Schäfer, 1991, 1993; Schäfer et al., 2007), and the large mammal fauna support the conclusion that the Taubach travertine should be dated into the Eemian interglacial (MIS 5e) (Kahlke, 1977).

The large mammal fauna is unusually diverse and includes *Ursus arctos*, *Ursus spelaeus*, *Crocuta crocuta*, *C. lupus*, *Panthera leo* cf. *spelaea*, *Panthera pardus*, *Lynx lynx*, *Elephas* (*Palaeoloxodon*)
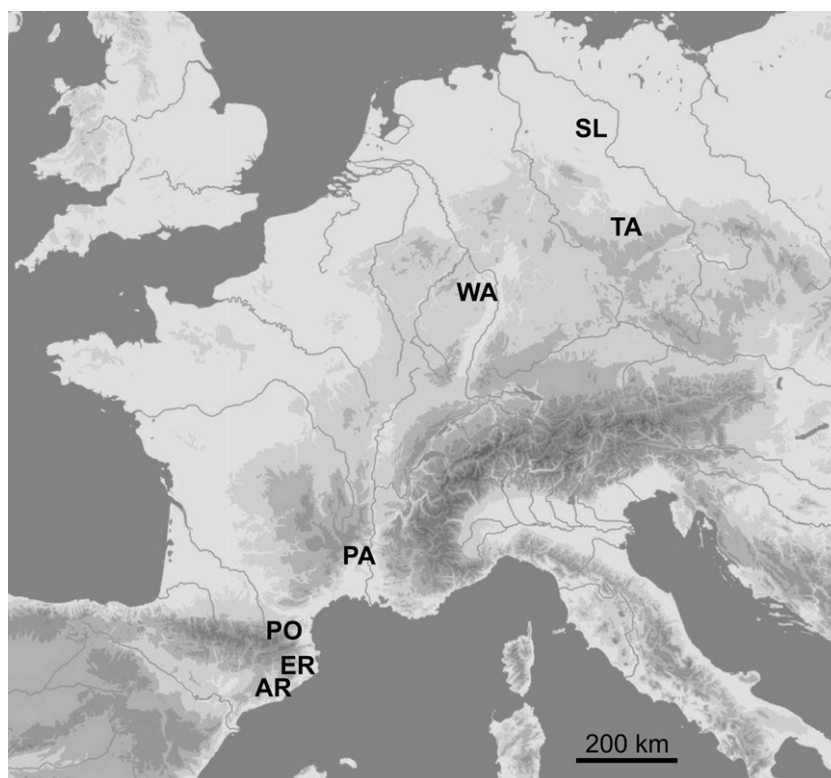

Fig. 1. Location of the European sites. Salzgitter Lebenstedt (SL), Taubach (TA), and Wallertheim (WA) in Germany; Payre (PA) and Portel-Ouest (PO) in France; and Ermitons (ER) and Abric Romani (AR) in Spain.

antiquus, *Stephanorhinus kirchbergensis*, *Equus ferus taubachensis*, *Sus scrofa*, *Alces latifrons*, *C. elaphus*, *Megaloceros giganteus*, *Dama dama*, *Capreolus capreolus*, *B. priscus*, and *Bos primigenius* (Kahlke, 1958, 1977, 1984; Bratlund, 1999). The observation of cut marks on bones of most of the species and their unusually high frequencies, combined with the mortality profiles of prey animals, indicates a high degree of anthropogenic involvement in this accumulation (Bratlund, 1999). At least a large part of the faunal assemblage must have resulted from deliberate hunting of large mammals (Bratlund, 1999). The material analyzed is housed at the Forschungsstation für Quartärpaläontologie at Weimar, Forschungsinstitut und Natur-museum Senckenberg (Germany).

2.3. Wallertheim – level F

Wallertheim (Germany) is located north-west of the town of Mainz in the former flooding plains of the Wiesbach creek. The locality was first excavated by O. Schmidtgen (1927–1929). Nikolas Conard (1991–1994) excavated the six archaeological layers Wal A, B, C, D, E, and F (Gaudzinski, 1992; Conard et al., 1995). The Wal-lertheim sequence is dated from the late Eemian to the beginning of the Weichselian period based on sedimentological (Becze-Deak and Langohr, 1997) and biostratigraphical evidence (Damblon, 1997; van Kolfschoten and Thomassen, 1997; Mania, 1997; Turner, 1997; Uerpmann and Dechert, 1997) as well as thermoluminescence dates (Zöller, 1997). It is thus related to the MIS 5d.

Beside *Dama*, *Cervus*, *Bison* and *Ursus* remains of *Equus* represent the main faunal component from Wallertheim level F (Burke, 1997), which was interpreted as attritional assemblage by Gaudzinski (1995, 1999) and Levine (1983).

The material analyzed is housed at the Institut für Ur- und Frühgeschichte und Archäologie des Mittelalters, Abteilung für Ältere Urgeschichte und Quartärökologie, Universität Tübingen (Germany).

2.4. Payre – levels D, F, and G

The site of Payre is located in the middle Rhone Valley (France). Since 1990, regular excavations have taken place and have identi-fied levels with human occupations associated with numerous artefacts, fauna and some human remains (Moncel et al., 1993, 2002). The sequence is 5 m thick and has been divided into 5 main units. Only three levels where analysed (levels G, F, and D) because they contain highest numbers of fossils. The level G deposit is dated to MIS 7 by Uranium/Thorium, Electron Spin Resonance, and thermoluminescence processed on bones and teeth (Valladas et al., 2008). The level F deposit contains human occupations alternating with cave bear occupations. The U/Th, ESR and TL dates indicate MIS 7 temporal assignments. The last human occupation recorded in levels C and D during the MIS 5 (5d, 5e or end of 6) is are open-air site under a small shelter.

The fauna is composed of *U. spelaeus*, *Cuon priscus*, *Vulpes vulpes*, *P. l. spelaea*, *Felis silvestris*, *L. lynx*, *Elephas* sp., *S. kirchbergensis*, *Stephanorhinus hemitoechus*, *E. ferus*, *C. elaphus*, *C. capreolus*, *B. primigenius*, *Hemitragus bonali* (Crégut-Bonnoure, 2008; Patou-Mathis et al., 2008).

The material studied is stored at the Institut de Paléontologie Humaine, Muséum National d'Histoire Naturelle in Paris (France).

2.5. Portel-Ouest – levels F and B

The Portel-Ouest cave (Loubens, Ariège) lies at an altitude of 485 m above sea level on the northern slope of the Pyrenees. It has been excavated since 1949 by Joseph and Jean Vézian and yielded Mousterian tools (Vézian, 1989) and abundant fossil mammal material. The deposits correlate with MIS 5–2 (Gardeisen, 1999) and material was sampled from levels F and B. Level F, the oldest Mousterian level, corresponds to the end of the MIS 4. It produced the most important archaeological sample from Portel-Ouest including faunal and Neanderthal remains, stone tools and other implements. Level B is related to the end of MIS 3 and also has provided faunal remains and artefacts (Vézian, 1988).

The fauna contains: *U. spelaeus*, *C. crocuta spelaea*, *C. lupus*, *V. vulpes*, *Alopex lagopus*, *P. l. spelaea*, *L. lynx*, *F. silvestris*, *Mammuthus* sp., *C. antiquitatis*, *E. ferus*, *S. scrofa*, *R. tarandus*, *Megaloceros* sp., *C. elaphus*, *C. capreolus*, *B. primigenius*, *B. priscus*, *Capra pyrenaica*, *Capra caucasica*, and *Rupicapra pyrenaica* (Vézian, 1941; Crégut-Bonnoure, 1992; Gardeisen, 1994).

The material we analysed is stored at the Centre Européen de Recherches Préhistoriques in Tautavel (France).

2.6. Ermitons – levels IV and VI

Ermitons is located on the southern slope of the Pyrenees Mountains at 400 m above sea level. The cave has been excavated in 1970 and 1971 by A.M. Muñoz and M.L. Pericot and since 1996 by J. Maroto and his colleagues. The cave infilling is 3 m thick and contains 6 archaeological levels. Levels IV, V and VI contain lithic and faunal remains attributed to the end of the Middle Palaeolithic (MIS 3). Level IV is dated by C14 AMS to $33,190 \pm 660$ BP (Maroto Genover, 1993; Maroto et al., 1996).

The mammal fauna consists of *U. spelaeus*, *C. crocuta spelaea*, *C. lupus*, *V. vulpes*, *P. pardus*, *Lynx* sp., *Dicerorhinus* sp., *B. primigenius* or *B. priscus*, *C. pyrenaica*, and *R. rupicapra* (Maroto Genover, 1993; Maroto et al., 1996).

The material analysed is housed at the Area de Prehistoria, Universitat de Girona (Spain).

2.7. Abric Romaní – levels K, L, and M

The Abric Romaní is located in Capellades (Catalonia, Spain), at 50 km from Barcelona. The shelter is today at 317 m above sea level. The stratigraphic sequence is about 20 m thick and 27 archeological levels were identified. This sequence was dated by U-Series to 40–70 ka BP (Bischoff et al., 1988, 1994). Three levels (K, L, and M), all belonging to MIS 3 and all being recently excavated where selected. Level M is dated between 54.5 ± 1.6 and 52.2 ± 1.6 ka BP, level L between 52.2 ± 1.6 and 52.3 ± 0.6 ka BP, and level K between 52.3 ± 0.6 and 50.4 ± 0.5 ka BP (Bischoff et al., 1988).

The complete mammal faunal list of the site is composed of *Ursus* sp., *C. lupus*, *V. vulpes*, *Lynx* sp., *Hyaena* sp., *P. pardus*, *P. l. spelaea*, *S. hemitoechus*, *E. ferus*, *S. scrofa*, *C. elaphus*, *B. primigenius*, *C. pyrenaica*, and *R. rupicapra*.

The material analysed is currently stored at the Institut Català de Paleoecologia Humana i Evolució Social, Universitat Rovira i Virgili (Spain).

2.8. The "MIS groups"

The seven localities analysed were grouped into four time frames according to their absolute ages and combined with the climatic context at the site as indicated by pollens and/or ecological data derived from the mammalian assemblages (MIS 8, MIS 5, MIS 4, and MIS 3) (Fig. 2).

(1) The MIS 8 is represented by the levels G and F from Payre. In these two levels mammal assemblages indicate a cold and dry climate leading us to assign these two levels to the glacial MIS 8 (Moncel et al., 2002).
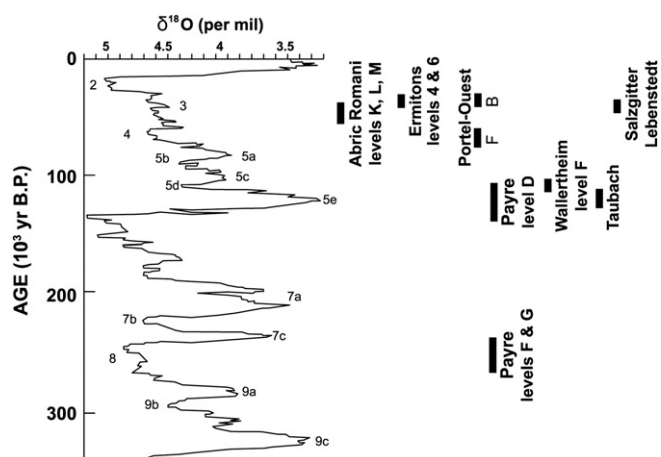
Fig. 2. Isotopic curve (Shackleton and Pisias, 1985) for the Marine Isotope Stages sampled (MIS 9–MIS 1). Chronological position of the various localities and levels are indicated by vertical black bars. Localities are positioned according to their geographic location, from South to North.

(2) The MIS 5 corresponds to Taubach (MIS 5e), Wallertheim (MIS 5d), and to the level D from Payre (MIS 6–5d), with dates ranging from the beginning of the MIS 5 (5e and 5d), or possibly to the end of the MIS 6 for level D at Payre. At Payre level D, various proxies indicate a temperate environment (Moncel et al., 2002), which represents more likely the assignment to the beginning of MIS 5 rather than to the end of MIS 6. All three levels correspond to the Eemian period where paleoenvironmental studies are indicating the presence of a so called "mosaic environment" (Caspers et al., 2002; Gaudzinski, 2006; Brauer et al., 2007).

(3) The MIS 4 is represented by level F from Portel-Ouest. Pollen and mammals reveal cold and dry environmental conditions (Marquet et al., 1998; Renault-Miskovsky and Girard, 1998).

(4) The MIS 3 is represented by Salzgitter Lebenstedt, Portel-Ouest level B, Ermitons, and Romaní levels K, L, and M. Climate is known to have quite fluctuated during the MIS 3 (REF), however, at those levels pollens and micromammals indicated rather temperate climate conditions including a Mediterranean influence and semi-open landscapes with arboreal pollens always present (Burjachs and Julià, 1994; El Hazzazi, 1998; Marquet et al., 1998; Kalai et al., 2001).

3. Methods

All available isolated upper and lower second molars (M2 or m2), and tooth rows containing M2 or m2 were sampled. Only adults individuals were selected to prevent discrepancy due to the age structure of the population following the methodology after Fortelius and Solounias (2000), Solounias and Semprebon (2002), and Rivals et al. (2007a). All specimens were carefully screened and those showing poor preservation of occlusal enamel surfaces or indication of taphonomic alterations were discarded from analysis. The whole occlusal surface of the teeth was moulded using a high-precision polyvinylsiloxane dental impression material. These molds were used for making clear epoxy casts.

Mesowear analysis was performed to characterize dietary traits of ungulates following the protocol developed by Fortelius and Solounias (2000). Mesowear and its application to extinct species is discussed further by Kaiser et al. (2000), Kaiser and Solounias (2003), Kaiser and Fortelius (2003), Franz-Odendaal et al. (2003), and Kaiser and Rössner (2007). Mesowear describes the prolonged

type of cumulative dental wear that represents a comparatively long period of an individual animal's lifetime. The method reduces ungulate tooth wear to two variables: occlusal relief and cusp shape. Occlusal relief is classified as high or low, depending on how high the cusps rise above the valley between them. The second mesowear variable, cusp shape, includes three attributes: sharp, round, and blunt according to the degree of facet development. A mesowear score (Rivals et al., 2007a; Croft and Weinstein, 2008; Kaiser et al., in press), based on the upper second molar (M2), was computed for each fossil sample (i.e. each species in a given level). Individual molar cusp shape and relief scores were converted to a single mesowear score as follows: a combination of high relief and sharp cusps was assigned a score of 0; a combination of high relief and rounded cusps was assigned a score of 1; a combination of low relief and rounded cusps was assigned a score of 2; a combination of low relief and sharp cusps was assigned a score of 2.5; a combination of low relief and blunt cusps was assigned a score of 3. Mesowear scores for each individual within a sample were then averaged to obtain an average mesowear score for that sample similar used like the first application in Rivals et al. (2007a) and Semprebon and Rivals (2007). Because mesowear is sensitive to the age of individuals (Fortelius and Solounias, 2000; Rivals et al., 2007b; Schulz et al., 2007), teeth from young and old adult individuals were discarded from the sample. The intra-observer and inter-observer errors are known to be not significant (Kaiser et al., 2000). For reducing inter-observer errors, mesowear scoring was done by only one investigator (ES).

Microwear analysis was performed following the low-magnification procedure developed by Solounias and Semprebon (2002). Microwear features observed on the occlusal enamel surfaces are the result of single occlusal events, and thus reflect diets within a much shorter time frame (Walker et al., 1978) than mesowear, perhaps days or even hours before the death of the individual. High-resolution epoxy casts were examined at $35\times$ magnification using a Leica MZ16 stereomicroscope. Examination of microwear was done on the second enamel band of the paracone of the upper second molar or alternatively the protoconid of the lower second molar. Relative pit sizes and scratch textures were assessed on the basis of differential light refraction properties as outlined by Solounias and Semprebon (2002) and Semprebon et al. (2004). Counts of pits and scratches were made on a standard 0.16 mm^2 area on each tooth. Typical grazers have the highest numbers of scratches and the lowest numbers of pits; typical leaf browsers have lower numbers of scratches and more disparate numbers of pits. Semprebon et al. (2004) have validated the robustness of the low-magnification light microscopy microwear method when applied to different measurement sites and for intra-observer and inter-observer errors which were reported to be not significant. Nevertheless in our study, to exclude inter-observer error, all the data acquisition was made by a single investigator (FR).

4. Results

A total of 1016 teeth (or tooth rows) were moulded. Among them, after screening to exclude specimens damaged by taphonomical processes, our sample consists of 763 specimens which were analysed for mesowear and 512 for microwear. Tables 1, 2, 3, and 4 summarize the basic statistics for meso- and microwear data for each locality and/or level grouped into the four MIS time frames, MIS 8, MIS 5, MIS 4, and MIS 3, respectively.

4.1. Dietary diversity and changes through time

MIS 8 samples from Payre levels G and F have mesowear scores ranging from 0.9 (C. elaphus) to 2.5 (H. bonali), i.e. a range of 1.6 (Fig. 3).

Table 1
Summary statistics for the samples from Marine Isotopic Stage 8. N = number of tooth specimen sampled, MWS = mesowear score value, NP = number of pits, NS = number of scratches, %LP = percentage of large pits, STS = scratch texture score value (0 = fine scratches, 1 = mixed scratches, 2 = coarse scratches), %CS = percentage of cross scratches, M = mean, SD = standard deviation.

Locality	Species		Mesowear		Microwear						
			N	MWS	N	NP	NS	%LP	STS	%CS	NS/NP ratio
Payre – F	Bos primigenius	M	5	1.8	6	25.33	25.17	16.7	0.7	83.3	0.99
		SD		1.1		2.11	1.94				
	Hemitragus bonali	M	–	–	4	22.38	23.50	25.0	1.0	100.0	1.05
		SD		–		6.84	3.03				
	Capreolus capreolus	M	11	2.2	5	20.90	26.90	0.0	0.8	100.0	1.29
		SD		1.1		4.53	1.47				
	Cervus elaphus	M	10	1.3	12	18.13	21.00	0.0	1.0	83.3	1.16
		SD		1.0		2.30	2.11				
	Equus ferus	M	24	2.1	9	20.72	19.44	22.2	1.1	77.8	0.94
		SD		0.9		3.00	3.80				
	Stephanorhinus kirchbergensis	M	3	1.3	3	26.33	20.00	33.3	1.0	100.0	0.76
		SD		–		–	–				
Payre – G	Bos primigenius	M	7	1.7	10	22.55	25.60	20.0	0.9	80.0	1.14
		SD		1.0		2.43	1.63				
	Hemitragus bonali	M	5	2.5	2	15.25	28.00	0.0	1.0	50.0	1.84
		SD		0.9		–	–				
	Capreolus capreolus	M	3	0.0	2	19.75	24.25	0.0	1.0	50.0	1.23
		SD		–		–	–				
	Cervus elaphus	M	9	0.9	10	17.40	21.10	40.0	1.4	80.0	1.21
		SD		0.9		3.63	3.83				
	Equus ferus	M	11	2.4	3	26.00	19.00	33.3	1.0	33.3	0.73
		SD		0.8		–	–				
Total			88		66						

Species scores of the two samples widely overlap (F entirely within the range of G), which indicates a highly similar spectrum of mesowear signatures in the species represented in the two levels at Payre. Microwear variables indicate a narrow range of variation, both in the numbers of scratches and pits (Fig. 4). All fossil samples plot in between the major areas of extant browsers and grazers. As also observed in mesowear signatures, samples of the two levels (F and G) widely overlap. The scratch/pit ratio of the microwear signature

Table 2
Summary statistics for the samples from Marine Isotopic Stage 5. N = number of tooth specimen sampled, MWS = mesowear score value, NP = number of pits, NS = number of scratches, %LP = percentage of large pits, STS = scratch texture score value (0 = fine scratches, 1 = mixed scratches, 2 = coarse scratches), %CS = percentage of cross scratches, M = mean, SD = standard deviation.

Locality	Species		Mesowear		Microwear						
			N	MWS	N	NP	NS	%LP	STS	%CS	NS/NP ratio
Payre – D	Bos primigenius	M	7	1.7	10	23.95	25.50	40.0	1.0	100.0	1.06
		SD		0.9		4.66	2.61				
	Hemitragus bonali	M	4	0.8	13	19.58	27.54	30.8	1.1	84.6	1.41
		SD		0.5		2.58	5.42				
	Capreolus capreolus	M	3	0.7	5	25.30	27.40	0.0	1.0	40.0	1.08
		SD		–		2.77	3.97				
	Cervus elaphus	M	14	1.6	17	15.47	20.03	11.8	0.9	88.2	1.29
		SD		1.0		2.80	2.58				
	Equus ferus	M	8	2.8	7	18.71	20.79	28.6	1.1	85.7	1.11
		SD		0.5		4.19	3.15				
	Stephanorhinus kirchbergensis	M	–	–	7	19.36	17.57	85.7	1.1	100.0	0.91
		SD		–		2.19	1.40				
	Rupicapra rupicapra	M	2	0.3	3	26.67	22.33	33.3	1.0	66.7	0.84
		SD		–		–	–				
Taubach	Bison priscus	M	18	1.0	22	27.70	17.09	72.7	1.0	81.8	0.62
		SD		0.2		5.75	4.13				
	Capreolus capreolus	M	10	0.5	8	22.25	11.44	12.5	1.0	50.0	0.51
		SD		0.4		3.17	1.18				
	Cervus elaphus	M	14	0.6	14	23.50	13.11	78.6	1.1	57.1	0.56
		SD		0.4		4.71	1.43				
	Elephas (P.) antiquus	M	–	–	17	11.82	13.56	35.3	1.3	82.4	1.15
		SD		–		3.03	1.56				
	Equus ferus	M	12	1.9	9	19.39	12.72	55.6	1.0	44.4	0.66
		SD		1.2		5.05	1.94				
	Sus scrofa	M	–	–	17	26.56	14.88	88.2	0.9	94.1	0.56
		SD		–		2.33	2.97				
Wallertheim – F	Equus ferus	M	14	1.5	13	22.96	28.08	53.8	0.5	7.7	1.22
		SD		0.7		5.60	2.87				
Total			106		162						

Table 3
Summary statistics for the samples from Marine Isotopic Stage 4. N = number of tooth specimen sampled, MWS = mesowear score value, NP = number of pits, NS = number of scratches, %LP = percentage of large pits, STS = scratch texture score value (0 = fine scratches, 1 = mixed scratches, 2 = coarse scratches), %CS = percentage of cross scratches, M = mean, SD = standard deviation.

Locality	Species		Mesowear		Microwear						
			N	MWS	N	NP	NS	%LP	STS	%CS	NS/NP ratio
Portel-Ouest – F	Bos/Bison	M	14	1.3	25	16.92	23.06	20.0	0.9	64.0	1.36
		SD		0.5		2.69	2.46				
	Capra caucasica	M	3	1.0	7	22.36	18.57	42.9	0.9	0.0	0.83
		SD		–		2.50	2.57				
	Cervus elaphus	M	24	0.8	21	22.90	18.79	23.8	1.0	28.6	0.82
		SD		0.4		6.45	2.76				
	Equus ferus	M	31	2.0	27	16.52	21.96	0.0	1.1	18.5	1.33
		SD		0.8		3.72	3.91				
	Rangifer tarandus	M	34	1.4	30	23.23	25.35	3.3	1.1	60.0	1.09
		SD		0.6		4.89	3.10				
	Rupicapra pyrenaica	M	–	–	2	21.25	22.25	50.0	1.0	0.0	1.05
		SD		–		–	–				
Total			106		112						

Table 4
Summary statistics for the samples from Marine Isotopic Stage 3. N = number of tooth specimen sampled, MWS = mesowear score value, NP = number of pits, NS = number of scratches, %LP = percentage of large pits, STS = scratch texture score value (0 = fine scratches, 1 = mixed scratches, 2 = coarse scratches), %CS = percentage of cross scratches, M = mean, SD = standard deviation.

| Locality	Species		Mesowear		Microwear						
			N	MWS	N	NP	NS	%LP	STS	%CS	NS/NP ratio
Abric Romani – K	Cervus elaphus	M	14	1.1	15	11.10	23.57	0.0	66.7	60.0	2.12
		SD		0.9		2.43	8.63				
	Equus ferus	M	11	2.7	9	10.22	30.56	0.0	11.1	33.3	2.99
		SD		0.3		2.21	3.84				
	Bos primigenius	M	2	1.3	–	–	–	–	–	–	–
		SD		–		–	–				
Abric Romani – L	Cervus elaphus	M	9	1.2	5	11.60	20.30	20.0	60.0	80.0	1.75
		SD		0.8		1.39	6.18				
	Equus ferus	M	6	2.5	5	12.60	27.40	0.0	20.0	0.0	2.17
		SD		0.8		7.07	7.80				
	Bos primigenius	M	2	1.8	2	10.25	21.25	0.0	50.0	100.0	2.07
		SD		–		–	–				
Abric Romani – M	Cervus elaphus	M	20	1.0	19	9.63	27.82	5.3	26.3	63.2	2.89
		SD		0.6		2.04	4.65				
	Equus ferus	M	15	2.4	13	11.92	34.23	0.0	0.0	61.5	2.87
		SD		0.8		3.13	4.37				
	Bos primigenius	M	3	1.7	3	7.67	36.83	0.0	0.0	66.7	4.80
		SD		–		–	–				
Portel-Ouest – B	Capra caucasica	M	3	0.7	3	21.83	18.33	0.0	1.0	0.0	0.84
		SD		–		–	–				
	Cervus elaphus	M	2	1.0	3	10.67	24.17	0.0	0.7	0.0	2.27
		SD		–		–	–				
	Rupicapra pyrenaica	M	13	1.1	5	23.80	18.80	20.0	1.4	0.0	0.79
		SD		1.1		3.44	2.46				
Salzgitter–Lebenstedt	Bison priscus	M	8	0.9	3	30.17	15.17	66.7	1.3	0.0	0.50
		SD		0.4		–	–				
	Equus ferus	M	13	1.7	5	26.70	15.80	20.0	1.0	80.0	0.59
		SD		0.8		9.18	2.77				
	Rangifer tarandus	M	342	1.2	82	29.12	10.87	47.6	0.9	4.9	0.37
		SD		0.8		6.62	2.11				
Ermitons – IV	Capra pyrenaica	M	–	–	3	23.17	18.67	100.0	1.0	0.0	0.81
		SD		–		–	–				
	Rupicapra pyrenaica	M	–	–	4	12.75	19.38	0.0	1.0	25.0	1.52
		SD		–		1.71	5.88				
Ermitons – VI	Capra pyrenaica	M	–	–	6	18.08	18.75	83.0	1.0	16.7	1.04
		SD		–		3.50	3.24				
	Rupicapra pyrenaica	M	–	–	4	16.63	22	25.0	1.0	25.0	1.32
		SD		–		2.63	5.07				
Total			463		189						
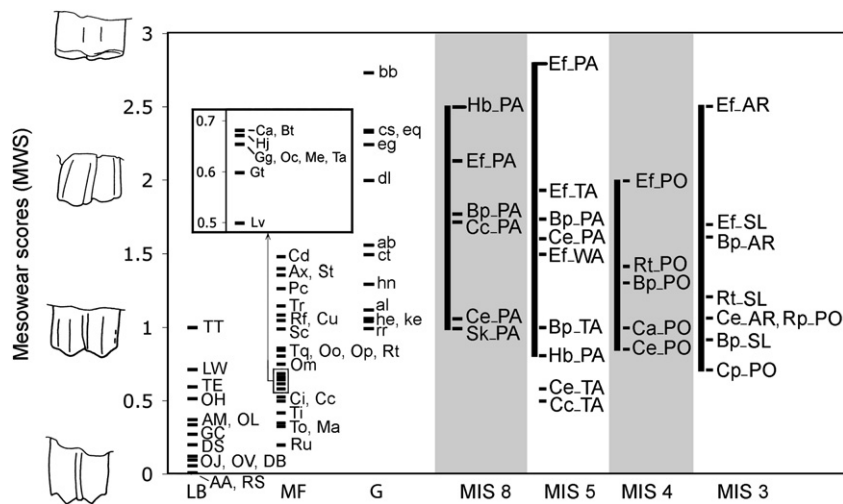
Fig. 3. Mesowear scores based on the extant reference species from Fortelius and Solounias (2000) and the middle and late Pleistocene samples grouped by the Marine Isotope Stages (MIS 8, 5, 4 and 3). Data and captions for the extant samples are taken from Fortelius and Solounias (2000). Extant taxa are classified as leaf browsers (LB), mixed feeders (MF) and grazers (G). Captions for the fossil samples are composed of the species abbreviation (*Bison priscus* or *Bos primigenius* (Bp), *Capra caucasica* (Ca), *Capreolus capreolus* (Cc), *Cervus elaphus* (Ce), *Stephanorhinus kirchbergensis* (Sk), *Elephas* (*Paleoloxodon*) *antiquus* (Ea), *Equus ferus* (Ef), *Hemitragus bonali* (Hb), *Rangifer tarandus* (Rt), *Rupicapra rupicapra* (Rr), *Rupicapra pyrenaica* (Rp) and *Sus scrofa* (Ss)) followed with the locality abbreviations (Abric Romani = AR levels K, L and M, Payre = PA levels D, F and G, Portel-Ouest = PO levels B and F, Salzgitter-Lebenstedt = SL, Taubach = TA and Wallertheim = WA level F) and the stratigraphic level abbreviation (single letter). Vertical black bars correspond to the range covered by the samples.
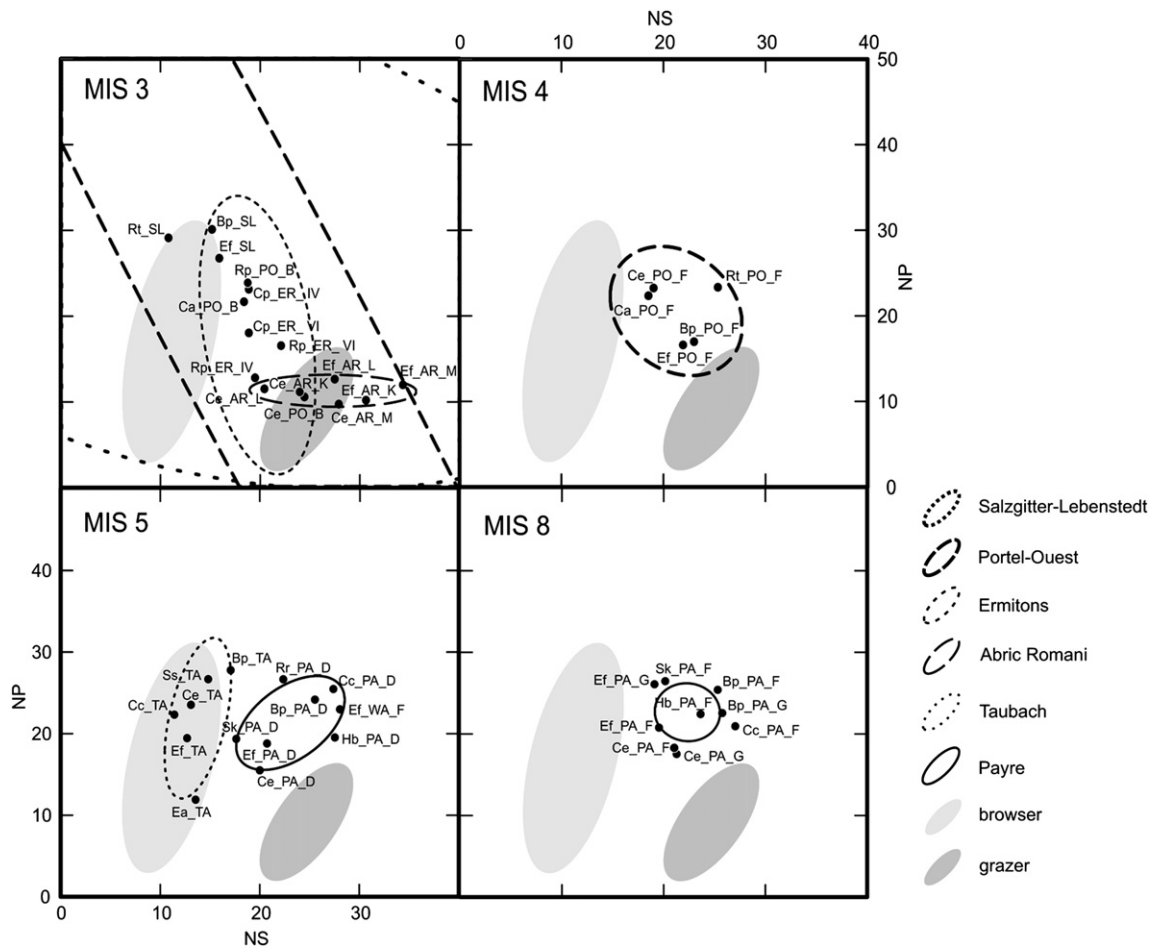
Fig. 4. Bivariate diagrams based on microwear signatures of extant reference species from Solounias and Semprebon (2002) and the middle and late Pleistocene samples grouped by the Marine Isotope Stages (MIS 8, 5, 4 and 3). Grey areas indicating Gaussian confidence ellipses ($p = 0.95$) on the centroid of the grazer/browser sample adjusted by sample size. NS = number of scratches, NP = number of pits. For abbreviations of fossil samples see caption of Fig. 3.

(Fig. 5) indicates a rather short range of 0.56 between *E. ferus* and *C. capreolus* at the extremes.

MIS 5 samples from Payre, Taubach, and Wallertheim have mesowear scores ranging from 0.5 (*C. capreolus*) to 2.8 (*E. ferus*), i.e. a range of 2.3. Excluding localities from Northern Europe this range is 2.1 (Fig. 3). The range of the mesowear scores in MIS 5 is the largest of all time frames investigated. Score ranges of the Payre (Level D) samples from and Taubach are overlapping. There is no overlap between the Taubach and Payre samples in the microwear signatures of the faunas (Fig. 4). *E. ferus*, the only species available from Wallertheim, plots within the confidence ellipse of Payre. Both microwear variables (pits and scratches) show a wider range of variation compared to MIS 8. The scratches/pits ratios of the MIS 5 samples (Fig. 5) range from 0.51 (*C. capreolus*) to 1.41 (*H. bonali*) and ranges over 0.9 units. It is two times wider than the range for the pleniglacial MIS 8. When considering only localities from Southern Europe the range reduces to 0.57.

Mesowear scores of MIS 4 samples from Portel-Ouest (level F) range from 0.8 (*C. elaphus*) to 2.0 (*E. ferus*), i.e. a range of 1.2 (Fig. 3). This is the smallest mesowear range observed. Also the range of microwear variables (0.54) is the smallest (Fig. 5). All samples plot between the two confidence ellipses of extant browsers and grazers (Fig. 4) with only very little overlap of the Portel-Ouest sample.

During MIS 3, mesowear scores of the samples from Portel-Ouest (level B), Abric Romaní, Ermitons, and Salzgitter Lebenstedt are ranging from 0.7 (*C. caucasica*) to 2.7 (*E. ferus*), i.e. a range of 2.0 (Fig. 3). Exclusion of Salzgitter Lebenstedt (Northern Europe) does not change this range. Microwear signatures in MIS 3 show comparatively largest scattering, confidence ellipses are overlapping (Fig. 4). Scratch/pit ratios covers a range of 2.62 (2.2 when excluding Salzgitter Lebenstedt). This is largest range observed (Fig. 5).

Mesowear scores recorded cover a broad range of levels in food abrasiveness, ranging from low abrasion levels as typical of browsers to very high levels as in grazers (Fig. 3). The range covered by mesowear scores is changing through time. During the glacial phases of the Pleistocene (MIS 8 and 4) the range is significantly smaller than during the interglacial phases (MIS 5 and 3).

Microwear as well as mesowear signals reveal a broad variety of dietary traits in the fossil species. The range of diversity, observed based on the scratch variable, is also different in the various time frames considered. However the microwear ratio does not reveal a change between the MIS 8 and 5 considering localities from France and Spain only. The number of scratches was identified as a key to interpret the microwear signal (Solounias and Semprebon, 2002; Semprebon and Rivals, 2007; Rivals et al., 2009). Similar to mesowear signatures, also microwear scratch/pit ratios (Fig. 5) indicate that the diversity in dietary traits was higher during warm interglacial periods (MIS 5 and 3) as compared to cold glacial periods (MIS 8 and 4).

Interglacial phases are of interest because we investigate samples from different geographic areas. In MIS 5e, we observe a significant difference between the samples from Payre (level D) and Taubach, in microwear signatures (Fig. 4) but not so in meso-wear signatures (Fig. 3). The sample from Wallertheim is not included here because it belongs to the MIS 5d, which correspond to a colder period within the interglacial stage. The North European Taubach samples indicate browsing dietary traits for almost all species. At Payre, microwear signatures as indicated by confidence ellipses (Fig. 4) correspond to mixed feeding traits in all species as indicated by the position of the ellipses between the browsing and grazing reference species.

A latitudinal gradient is observed in the microwear signature of MIS 3 samples (Fig. 5). From North to South, from Salzgitter Lebenstedt, via Portel-Ouest and Ermitons, to Abric Romaní in the South, scratches/pits ratios increase.

4.2. Dietary traits of E. ferus and C. elaphus

Among all ungulates analysed, *C. elaphus* and *E. ferus* are the most frequently preserved species at all sites. That abundance in most of the localities and from different time frames is used to investigate the variability of their dietary signals.

Consistently mesowear scores recorded for *C. elaphus* are lower than those of *E. ferus* which range from 0.6 to 1.6, and from 1.7 to 2.8 respectively (Fig. 6). The overlap between the two species is very small. This indicates a higher level of abrasion control in the tooth wear equilibrium of *E. ferus*. In both species the mesowear signatures cover a wide range of feeding traits. Within the range of mesowear scores, the local variation is 1.1 in *E. ferus* and 1.0 in
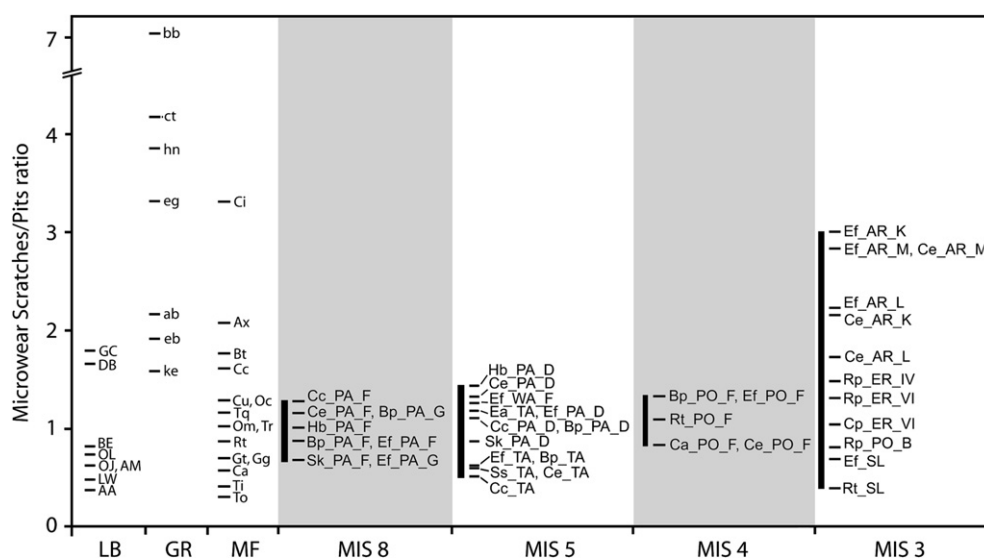

Fig. 5. Microwear pits/scratches ratio based on microwear signatures of extant reference species from Solounias and Semprebon (2002) and the middle and late Pleistocene samples grouped by the Marine Isotope Stages (MIS 8, 5, 4 and 3). Data and captions for the extant samples are taken from Fortelius and Solounias (2000). Extant taxa are classified as leaf browsers (LB), mixed feeders (MF) and grazers (G). For abbreviations of the fossil samples please see the caption of Fig. 3. Vertical black bars correspond to the range covered by the samples from Western and Southern Europe.
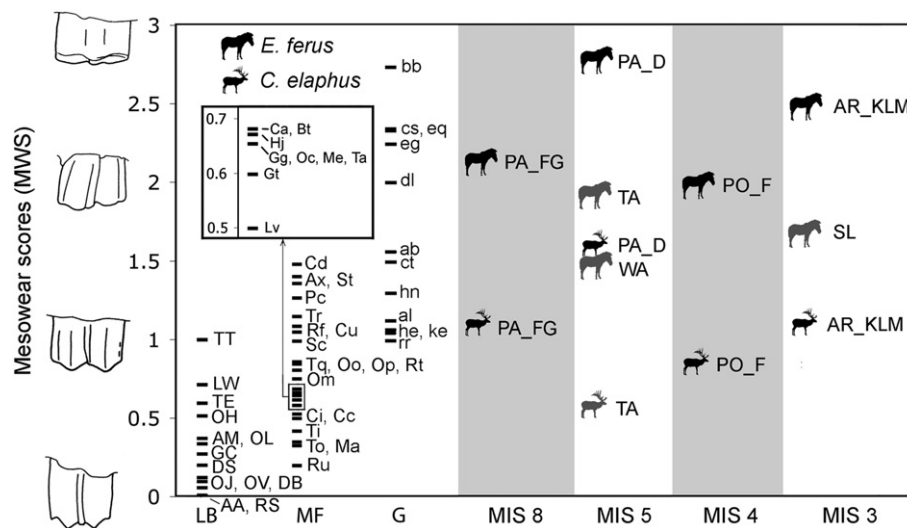
Fig. 6. Mesowear scores based on the extant reference species from Fortelius and Solounias (2000) and the middle and late Pleistocene samples of *Equus ferus* and *Cervus elaphus*. Data and captions for the extant samples are taken from Fortelius and Solounias (2000). Extant taxa are classified as leaf browsers (LB), mixed feeders (MF) and grazers (G). Captions for the fossil samples are composed of the locality abbreviations (Abric Romani = AR levels K, L and M, Payre = PA levels D, F and G, Portel-Ouest = PO levels B and F, Salzgitter-Lebenstedt = SL, Taubach = TA and Wallertheim = WA level F). Black silhouettes indicate samples from French and Spanish localities, grey ones from German localities.

C. elaphus. The range of traits encapsulated in the observed variation could be best explained as embracketing what could be called the dietary adaptation of the species. For both species the biggest diversity of feeding traits is observed during the interglacial MIS 5.

Microwear signatures also indicate a broad range of food resources used by the two species, from low to high proportion of grass in the diet (Fig. 7A and B). Different from the mesowear signature, there is a clear overlap in the microwear signature of the samples of the two species. *E. ferus* covers a broader range in the scratches variable than *C. elaphus*. *E. ferus* populations thus are concluded to have included a slightly higher level of grass in their diets as compared to *C. elaphus* populations. For *E. ferus*, where more samples are available for comparison, the diversity of feeding traits is higher during the two interglacial phases (MIS 5 and 3) as compared to two pleniglacial periods (MIS 8 and 4).

5. Discussion

The Western and Southern European localities we sampled show a large variability in the diets of all species covering a large range within the ungulate dietary spectrum. This variability reveals significant variation in the composition of the diet that is proposed to correspond to variation in the proportions of more or less abrasive food sources in the habitat of these faunas. Variation largely reflects changes through time regarding these biomechanical properties of plant foods and would also be related to the presence of exogenous grit or dust on the vegetation (Williams and Kay, 2001). Using the microwear approach, the presence of exogenous material was evidenced in arid environments which lead to a "dirty browsers" signature, as indicated by a comparatively higher abundance of pits in the scar spectrum as compared to scratches (Semprebon and Rivals, 2007). Thus, dental wear signatures allow inference on vegetational structure and composition as well as environmental humidity (Kaiser and Schulz, 2006; Kaiser and Rössner, 2007; Semprebon and Rivals, 2007; Schulz, 2008).

5.1. Dietary diversity and changes through time (testing hypothesis 1)

The four localities from France and Spain which represent 10 archaeostratigraphic complexes indicate that the dietary diversity

as revealed by the range of dietary traits recorded (Fig. 8) is higher during interglacial phases (MIS 5 and 3) than during pleniglacial phases (MIS 8 and 4). Dietary diversity is thus concluded to be related to climate-driven vegetation changes which during interglacials lead to increased variety of potential food items available to ungulates. This relationship between dietary diversity and climatic changes confirms the hypothesis put forward by Rivals et al. (2008) on a longer chronological scale and on a broader geographical setting.

The diversity in dietary traits should correspond to the diversity in vegetation available in the local environment around the site. This diversity should be immediately reflected by the pollen record. However, pollen was not always preserved or studied for the sites investigated. When published, the pollen data do not always include the complete list of plant taxa, and thus inference on plant biodiversity as a potential food source is not always possible based on the pollen record. Based on the pollen record from lacustrine sediments it was evidenced that the vegetational diversity in Central Italy during the late Quaternary was generally higher during the interglacial and forested periods than in open landscape during glacial periods (Magri, 1999; Magri and Sadori, 1999). To our knowledge, such data are not available for other parts of Western and Southern Europe. It is difficult to conclude on generalized patterns at the scale of the entire European continent. It is known that vegetational composition is more complex and also sensitive to climatic changes in the Mediterranean area than in North-Western Europe (Follieri et al., 1998).

5.2. Dietary diversity and changes through space (testing hypothesis 2)

During interglacial phases (MIS 5 and 3), Northern Europe was free of glacial ice or permafrost and more likely populated by game and also by Neanderthals (Hublin, 2002; Richter, 2006; Finlayson and Carrión, 2007). Thus it is possible to compare localities from Northern and Southern Europe to test the hypothesis that a latitudinal gradient of food availability should have existed during MIS 5 and MIS 3.

Dental microwear revealed that all MIS 5e ungulate species from Payre (level D) indicate mixed feeding traits whereas all Taubach ungulates show exclusively browsing traits. In MIS 3, a gradient
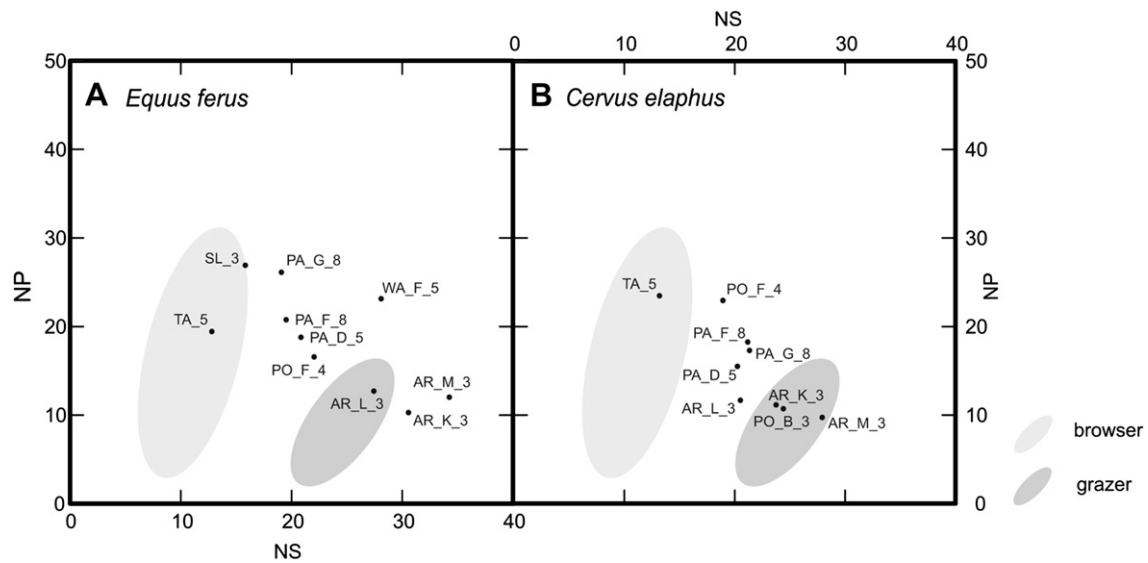
Fig. 7. Bivariate diagrams based on microwear signatures of extant reference species from Solounias and Semprebon (2002) and the middle and late Pleistocene samples of *Equus ferus* (A) and *Cervus elaphus* (B). Grey areas indicating Gaussian confidence ellipses ($p = 0.95$) on the centroid of the grazer/browser sample adjusted by sample size. Captions for the fossil samples are composed of the locality abbreviations (Abric Romani = AR levels K, L and M, Payre = PA levels D, F and G, Portel-Ouest = PO levels B and F, Salzgitter-Lebenstedt = SL, Taubach = TA and Wallertheim = WA level F) and the number for the Marine Isotope Stages (MIS 8, 5, 4 and 3).

toward more grazing is observed from North to South in the four localities sampled. However that latitudinal gradient in microwear signatures is not statistically supported for Portel-Ouest and Salzgitter Lebenstedt populations. In the MIS 5e, and at a lesser extant in the MIS 3, changes in diet composition are evident along geographical gradients. The corresponding dietary gradients are thus proposed to be related to climate and vegetation gradients i.e. probably to more arid climates in the Mediterranean area compared to North-Western Europe during interglacial stages (van Andel, 2002; Barron and Pollard, 2002; Pollard and Barron, 2003). The models developed by the previous authors are assuming the existence of a vegetation gradient ranging from temperate grassland in Southern Europe to evergreen forest in North-Western Europe (Barron and Pollard, 2002). Such latitudinal gradients are known in mammalian communities of Western Europe for the Miocene Climatic Optimum, where mammals reflect a more arid

climate in the localities from South-Western Europe (Costeur and Legendre, 2008).

That latitudinal gradient evidenced in microwear signatures, however, is not consistent with mesowear signatures. Mesowear is known to be less sensitive to seasonal changes because it records the diet on a longer time frame than microwear. The absence of latitudinal gradient in mesowear signals is thus interpreted as to reflect the less sensitive nature of mesowear in terms of subtle local conditions.

The obvious difference between the two differently scaled dietary proxies strongly indicates that the temporally higher resolving microwear signature encapsulated a signal not resolved by the mesowear signature. Most likely this is a seasonality signal. It is therefore most likely, that the gradient resolved by the microwear signal reflects seasonal changes in Neanderthal hunting and occupation behaviour at a site, rather then a rough climatic signal,
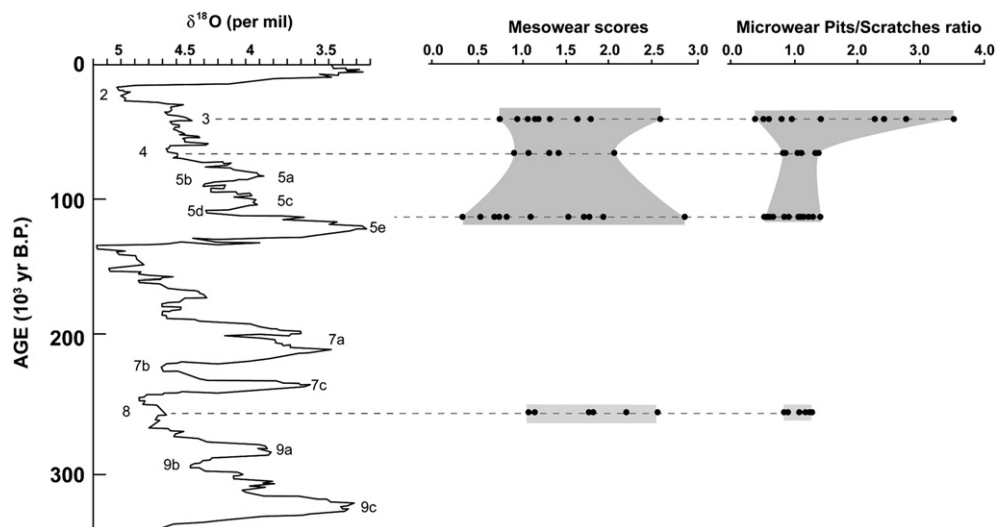

Fig. 8. Isotopic curve (Shackleton and Pisias, 1985) for the Marine Isotope Stages (MIS) sampled (MIS 9–MIS 1) combined with the mesowear score values and microwear pits/scratch ratio of the fossil samples from MIS 8, 5, 4, and 3. Grey areas indicating changes in wear signatures interpreted as width and diversity of dietary adaptations.

which would also be reflected by the mesowear signature as has been shown by Kaiser and Schulz (2006) and Kaiser and Rössner (2007). Intra-site seasonality may vary, such as at Abric Romaní in the various levels (Fernández-Laso et al., in press), and such changes are not reflected by our microwear data. It appears that the general climatic signal recorded in microwear is stronger than the seasonal signal. A strong seasonality signal, however, is encapsulated in intra specific variability (or stability) of variable scores but not generally is reflected by the sample average (Rivals et al., 2009).

It is thus surprising to find microwear to be more sensitive to that geographic gradient than mesowear. However, a latitudinal climate gradient is not the only alternative to explain the observed variability pattern. Climate is known to be highly variable during interglacials. Instabilities are reported in MIS 3 with the cooling cycles called Heinrich events (Heinrich, 1988; Maslin et al., 1995), but also in the MIS 5 (Lambeck et al., 2002). Several climatic changes are evidenced, with cold periods approaching temperatures in Europe equivalent to the last glacial maximum and warm periods having temperatures only a few degrees below Holocene values (Barron and Pollard, 2002). However, the model developed by Barron and Pollard (2002) indicates that Southern Europe was always dryer, independent from temperatures considered in the model. The pollen evidence at each locality confirms a dryer climate for Southern Europe in all periods of the MIS 5 or 3. It is thus more likely that intra specific dietary variability as observed based on dental microwear may be regarded a humidity proxy rather than indicating temperature. However it is not possible to conclude whether the variability is to be related to local or seasonal changes, or to changes on a longer temporal scale.

5.3. Dietary traits of E. ferus and C. elaphus

Comparing the most frequent species, C. elaphus and E. ferus, we observe that their local dietary traits range from low to high abrasion levels in the diet, i.e. from browse-dominated to graze-dominated diets. This is certainly related to the different metabolic adaptations of both species (Hofmann, 1985 for C. elaphus, Kuntz et al. (2006) for E. ferus przewalskii). Compared to other Cervidae C. elaphus has rather brachyodont teeth (index of hypsodonty = 1.96 for C. elaphus canadensis in Janis, 1988) and is classified a mixed (intermediate) feeder Janis and Ehrhardt (1988), whereas E. ferus is hypsodont (index of hypsodonty = 5.7 for E. ferus przewalskii after Janis, 1988) and is usually assumed a grazer. It is interesting to note that in the fossil record we analysed, whatever their degree of hypsodonty, the two species cover a broad range of dietary traits. Their mesowear signatures cover a wide range, and their microwear signals are overlapping from browse-dominated to graze-dominated diets. The overlap in mesowear for the two species is very small, at the contrary to what is observed for the microwear where the two species overlap totally. The fact that microwear overlap is larger than in mesowear is probably related to the fact that microwear records seasonal fluctuation. Thus the large variability in the diets for C. elaphus and E. ferus is probably due to the combined (superimposed) effects of climate and seasonality.

During the MIS 5, C. elaphus and E. ferus from Taubach have less abrasive diets than populations of the same species at Payre level D, but more abrasive diets than those from Wallertheim. In MIS 3 times E. ferus from Salzgitter Lebenstedt the level of abrasion is lower than at Abric Romaní levels K, L, and M. Samples from Germany on one side and France and Spain on the other side (Taubach and Payre, and Salzgitter Lebenstedt and Abric Romani) consistently indicate less abrasive diets for the German sites. This was trend was also identified based on data of the entire herbivore community. In the MIS 5, the Wallertheim sample of E. ferus does not support this trend. Both Payre and Taubach were dated to the

MIS 5e interstadial, the Eemian, the warmest period of the MIS 5. Wallertheim (level F) was dated to the stadial MIS 5d, which corresponds to a period of cooling during the MIS 5 interglacial. Thus, it is probable that the discrepancy observed for the Wallertheim sample is related to climate-driven vegetational differences between MIS 5e and 5d.

It was expected to find C. elaphus to have less abrasive diets than E. ferus, but it is interesting to note that in the Pleistocene, the dietary traits of those two species varied significantly, including a certain degree of overlap in the MIS 5 revealing a large plasticity in the adaptation of those species. Those traits are thus more obviously rather related to differences in vegetation structure as related to each local setting as to a specific "dietary adaptation" of the individual species. The physiological adaptation would then just delimit the breath of variability and thus delimit the "dietary" niche, however to would not influence the signal within the range of variability which should rather be related to food availability. This approach of using intra specific variability in the dental wear signatures of local populations was pioneered by Kaiser (2003) who first inferred habitat setting of Miocene horses. Later the approach was also employed for other fossil species like R. tarandus in Western Europe (Rivals and Solounias, 2007), B. priscus and B. antiquus in Northern America (Rivals et al., 2007a), B. primigenius in Northern Europe (Schulz and Kaiser, 2007) and for extant species like Equus quagga in Sub-Saharan Africa (Kaiser and Schulz, 2006). It thus is evident that ungulates have broader dietary habits than what is usually assumed for paleoenvironmental reconstructions.

6. Conclusion

Dietary traits of the two most common species in our samples, C. elaphus and E. ferus show a large plasticity in their adaptations. Such variability was known for other extant and fossil species, and was considered as exceptions to the uniformitarian rules. However, such exceptions are more common than commonly acknowledged. The broad range of dietary habits ungulates display, if populations from different environments, times and climates are investigated impressively deem for testing assumptions on stable dietary traits commonly employed in classical paleoenvironmental reconstructions using the principle of taxonomic uniformitarianism. Population based dietary analysis through meso- and microwear seems to be a good alternative to those classical methods. Analysis of dietary traits in middle and late Pleistocene ungulates revealed some significant changes in dietary diversity through time (glacials vs. interglacial phases). The diversity appears to be higher during interglacials and must be related to a higher diversity in vegetation elements during the interglacials (forested periods) as compared to glacial periods when open landscapes prevailed. It was also observed that dietary diversity reflects a latitudinal gradient during interglacials MIS 5e and 3. This gradient indicates more forested habitats in Northern Europe as compared to the south. Dental wear analysis is thus again confirmed to be an even more powerful tool for detecting and tracking paleoenvironmental changes through time and space.

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