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High-resolution paleoenvironmental context for human occupations during the Middle Pleistocene in Europe (MIS 11, Germany)

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ABSTRACT

High-resolution paleoecological proxies, such as stable isotopes or tooth microwear in large mammals, are often used for their potential to deliver information about the paleodietary traits of individuals and populations at the time of death. Such proxies are of interest in high resolution sites because they provide accurate data regarding the diet of large herbivores as well as the habitats that were available at the time of formation of the site, and by inference can detect seasonality in the formation of the assemblages. The integration of two techniques, tooth mesowear and microwear, applied to Middle Pleistocene assemblages of large herbivores from Steinheim and Heppenloch did not indicate seasonality at any of the two sites, most likely due to low resolution and time averaging of the dietary signal. However, the combination of the two proxies was highly informative for reconstructing the paleodiets of the large herbivores. The two paleodietary proxies provided consistent results that permitted us to propose a reconstruction of the paleodiets and habitats available at each site.

1. Introduction

Multi-proxy studies are becoming increasingly common for reconstructing the paleoenvironmental context of human occupations during the Pleistocene. The recent trend in such studies is to integrate a large number of environmental proxies to make paleoenvironmental reconstructions as accurate as possible. A further trend involves the development of high-resolution proxies to improve the quality of data in high-resolution stratigraphic contexts (Vaquero, 2008; Carbonell i Roura, 2012). For example, in recent years, the paleodiets of large mammals (herbivores in particular) have been determined using various proxies for habitat reconstruction at archaeological sites. These proxies range from low temporal resolution (e.g. overall morphology) to high resolution (e.g. dental microwear). Today, in archaeological contexts, the trend is to discard solely morphology-based approaches (e.g. molar hypsodonty) which only give clues about evolutionary trends within a lineage, and to base interpretations on high-resolution proxies such as stable isotopes or tooth microwear which provide a snapshot of the diet and resources exploited by an individual (Davis and Pineda Munoz, 2016). This paper is intended to evaluate a combination of dietary proxies for reconstructing paleoenvironments during the hominin occupation of Europe in the Middle Pleistocene. Multi-proxy approaches are valuable because they take into account differences in scale measured by different proxies including the large temporal and geographical variability inherent in such various methods, which may result in discrepancies in results. Rather than an inconvenience, these discrepancies among proxies reveal the significance of diet at different scales of analysis and their respective potential for comprehensive paleohabitat reconstructions (Davis and Pineda Munoz, 2016; Sánchez-Hernández et al., 2016).

Tooth microwear and mesowear are often used together, as the integration of the two techniques provides information about the habitat exploited at the time of death (Rivals and Semprebon, 2012; Rivals et al., 2015a), but also about the existence of seasonal patterns of occupations at the sites (Rivals et al., 2015b; Sánchez-Hernández et al., 2016).

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The main objective of this paper is to test whether the integrated analysis of tooth mesowear and microwear is able to provide accurate information about habitats and to detect the existence of seasonal patterns in two Middle Pleistocene sites where the temporal resolution is low. The results obtained from the sites selected, Steinheim and Heppenloch, will be compared with data published on coeval assemblages from the UK (Clacton, Hoxne, and Swanscombe) also correlated with MIS 11 (Schreve, 2001; Schreve and Bridgland, 2002; Ashton et al., 2008; Kahlke et al., 2011; van Asperen, 2013; Rivals and Lister, 2016).

2. Materials and methods

2.1. Materials

We studied the large herbivore assemblages from two Middle Pleistocene localities correlated with MIS 11, Steinheim and Heppenloch. The fossil material from these two sites is stored in the collections of the Staatliches Museum für Naturkunde Stuttgart (SMNS) in Germany.

The Steinheim fossil locality, situated on a fluvial terrace of the River Murr, is well known for the discovery of a skull of an ancient hominin in 1933, originally named *Homo steinheimensis*, but often listed as *Homo heidelbergensis*. The Middle Pleistocene fauna was correlated to MIS 11 (Schreve and Bridgland, 2002; van Asperen, 2013). This study is based on the sampling of the assemblage corresponding to one of the four subdivisions defined by Adam (1954) - the *antiquus*-gravels (*antiquus*-Schotter) named after *Palaeoloxodon antiquus*. The large mammal assemblage includes *Palaeoloxodon antiquus*, *Stephanorhinus kirchbergensis*, *Stephanorhinus hemitoechus*, *Equus ferus*, *Bos/Bison*, *Megaloceros giganteus antecedens*, *Cervus elaphus* and *Dama dama*. Two other taxa, *Mammuthus trogontherii* and *Coelodonta antiquitatis*, were sampled but excluded from this analysis because they belong to the upper part of the sequence correlated to the Rissian complex (Saalian) (Ziegler and Dean, 1998; Adam, 1954).

The Heppenloch locality is a cave which infilling has been attributed to the German Holsteinian interglacial (Adam, 1975) and correlated with the MIS 11 (Kahlke et al., 2011). The large mammal assemblage that was sampled in this study includes *Stephanorhinus hemitoechus*, *Equus ferus*, *Bos/Bison*, *Cervus elaphus* and *Capreolus capreolus*.

2.2. Tooth mesowear analysis

Mesowear analysis, first introduced by Fortelius and Solounias (2000), is a method of categorizing the gross dental wear of ungulate molars by evaluating the relief and sharpness of cusp apices in ways that are correlated with the level of abrasiveness in a species' diet. A diet with low levels of abrasion (high attrition) maintains sharpened apices on the buccal cusps as the tooth wears. In contrast, high levels of abrasion, associated with a diet of siliceous grass, results in more rounded and blunted buccal cusp apices. Mesowear was scored macroscopically from the buccal side of upper molars and lingual side of lower molars, preferably the paracone of upper M2 (Fortelius and Solounias, 2000) of all ungulate species. Other molars (both upper and lower M1 and M3) were used to increase sample size. Unworn (and marginally worn) teeth, extremely worn teeth, and those with broken or damaged cusp apices were omitted from mesowear analysis (Rivals et al., 2007). In this study, the standardized method introduced by Mihlbachler et al. (2011) was employed. The method is based on seven cusp categories (numbered from 0 to 6), ranging in shape from high and sharp (stage 0) to completely blunt with no relief (stage 6). The average value of the mesowear data from a single sample of fossil dentition corresponds to the 'mesowear score' or MWS (Mihlbachler et al., 2011). Dental mesowear analysis was conducted by a single experienced researcher (FR) to reduce inter-observer error, following the recommendations of Loffredo and DeSantis (2014).

2.3. Tooth microwear analysis

Microwear features of dental enamel were examined using a stereomicroscope on high-resolution epoxy casts of teeth following the protocol developed by Solounias and Semprebon (2002) and Semprebon et al. (2004). In the present study, all the data were collected by a single experienced observer (FR). The occlusal surface of each specimen was cleaned using acetone and then 96% alcohol. The surface was moulded using high-resolution silicone (vinylpolysiloxane) and casts were created using clear epoxy resin. All casts were carefully screened under the stereomicroscope. Those with badly preserved enamel or taphonomic defects (features with unusual morphology and size, or fresh features made during the collecting process or during storage) were removed from the analysis, following King et al. (1999). Casts were observed under transmitted light with a Zeiss Stemi 2000C stereomicroscope at 35 × magnification using the refractive properties of the transparent cast to reveal microfeatures on the enamel. Microwear scars (i.e., elongated scratches and rounded pits) were quantified on the paracone of the upper teeth or the protoconid of lower teeth in a square area of 0.16 mm^2 using an ocular reticule. We used the classification of Solounias and Semprebon (2002) and Semprebon et al. (2004) which basically distinguishes pits and scratches. Pits are microwear scars that are circular or sub-circular in outline and thus have approximately similar widths and lengths, while scratches are elongated microfeatures that are not merely longer than wide, but have straight, parallel sides. Using average scratch and pit data, it is possible to discriminate between the dietary categories of leaf browsers (i.e., eating woody and non-woody dicotyledonous plants), grazers (i.e., eating grass), and mixed feeders.

3. Results

The summary data from the mesowear and microwear analyses are provided in Tables 1 and 2. The raw data have been published in Mendeley Data (Rivals, 2018) and are available at: https://doi.org/10.17632/vkpz5tv84x.2.

3.1. Steinheim

A total of eight species were sampled from the Steinheim fossil assemblage, one proboscidean, three perissodactyls, and four artiodactyls.

The mesowear values (Table 1) ranged from MWS = 1.33 for *Cervus elaphus* to 4.14 for *Stephanorhinus hemitoechus*. Such values cover the dietary spectrum from browsers and browse-dominated mixed feeders to grazers (Fig. 1). The microwear values of pits and scratches (Fig. 2A) show that our 7 samples cover the dietary spectrum from browsers to grass-dominated mixed feeders. There is no pure grazer, only *Stephanorhinus hemitoechus* overlaps slightly with the grazing ecospace. The values also show a significant overlapping among ungulates in terms of microwear patterns (Fig. 2A).

The straight-tusked elephant, *Palaeoloxodon antiquus*, was analysed only through microwear and clearly plots among the extant browsers (Fig. 2A).

The rhinoceroses, *Stephanorhinus kirchbergensis* and *Stephanorhinus hemitoechus*, have similar mesowear values (Fig. 1) but

Table 1
Summary of mesowear and microwear data for the fossil assemblages from Steinheim.

Mesowear				Microwear						
Species		N	MWS	N	NP	NS	%LP	%G	SWS	%XS
Palaeoloxodon antiquus	M	–		15	23.73	10.70	66.67	33.33	1.4	100
	SD				7.50	2.02				
Equus ferus	M	80	3.85	9	19.78	18.50	100.00	55.56	1.1	0
	SD		1.06		5.52	1.44				
Stephanorhinus hemitoechus	M	7	4.14	7	12.93	19.71	71.43	28.57	1.3	100
	SD		0.90		3.07	1.22				
Stephanorhinus kirchbergensis	M	5	4.00	4	13.50	16.13	25.00	0.00	0.8	100
	SD		1.00		1.87	2.50				
Megaloceros giganteus	M	13	1.69	8	22.38	9.69	75.00	62.50	1.5	0
	SD		0.63		6.91	1.60				
Cervus elaphus	M	18	1.33	11	17.32	14.36	100.00	18.18	0.8	0
	SD		0.69		7.96	3.57				
Dama dama	M	9	1.67	8	17.38	10.00	75.00	75.00	1.4	0
	SD		0.50		5.83	1.65				
Bos/Bison	M	25	2.28	11	16.55	15.41	36.36	9.09	1.2	36.4
	SD		0.61		5.09	2.76				

AbbreviationsN = Number of specimens; MWS = Mesowear score; NP = Average number of pits; NS = Average number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = Scratch width score; %XS = Percentage of specimens with cross scratches; M = mean; SD = standard deviation.

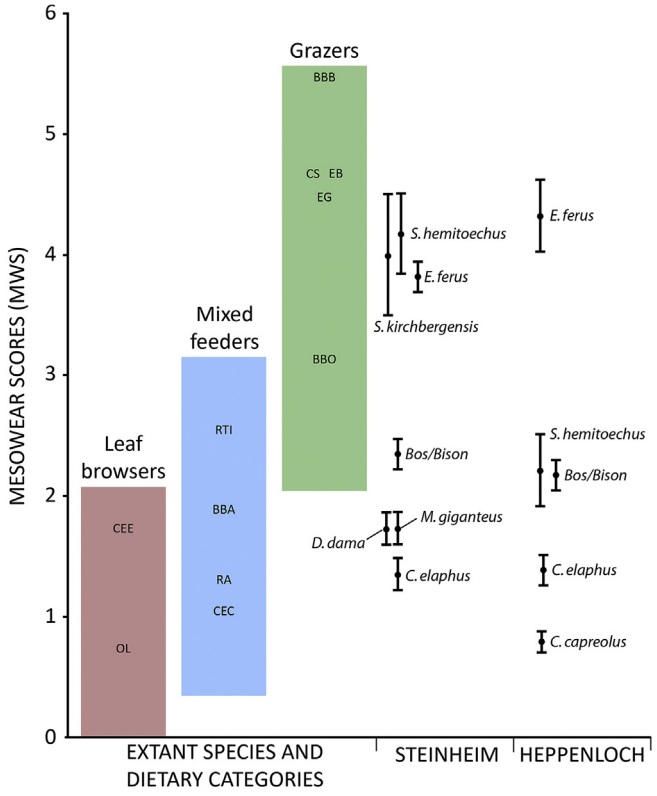

Fig. 1. Mesowear scores of the fossil samples from Steinheim and Heppenloch in comparison to extant browsers, mixed feeders and grazers (data from Fortelius and Solounias (2000) and Rivals et al. (2010, 2013, 2014, 2015b)).

slightly different microwear patterns (same numbers of pits but different numbers of scratches). The two species plot in between the two ecospaces for the extant browsers and grazers, but *Stephanorhinus kirchbergensis* with lower numbers of scratches indicates a browse-dominated diet at the time of death, while *Stephanorhinus hemitoechus*, with higher numbers of scratches, suggests a grass dominated diet (Fig. 2A).

The horse, *Equus ferus*, has a mesowear score that plots among the extant grazers, and that overlaps with the two rhinoceroses (Fig. 1). The microwear pattern suggests a mixed feeding diet (Fig. 2A). The average number of scratches plots in between the two rhinoceroses, supporting the result from the mesowear analysis.

The three cervids, *Megaloceros giganteus*, *Cervus elaphus* and *Dama dama*, have mesowear values that fall among the extant browsers and browse-dominated mixed feeders (Fig. 1). The microwear analysis provide the same result as the three species have microwear patterns typical of browsers (Fig. 2A). It is interesting to note that *Megaloceros giganteus* and *Dama dama* have mesowear and microwear values that overlap, but these two species do not overlap with *Cervus elaphus*, neither in mesowear (Fig. 1) nor microwear (Fig. 2A).

The bovids are represented by the bison and the aurochs. As the two species could not be differentiated on the basis of tooth morphology, we grouped them as *Bos/Bison*. These taxa have a mesowear value that plots among the grass-dominated mixed feeders (Fig. 1), while the microwear pattern indicates browsing or browse-dominated mixed feeding (Fig. 2A). The mixed feeding result could be an artefact of lumping together two species with different diets. The difference between microwear and mesowear could be due to a bias in sampling as all teeth are not suitable for mesowear and microwear.

For most species, the two proxies provide similar results, however for the horse, we observed a discrepancy between mesowear and microwear. The mesowear suggests grazing, while microwear tends toward mixed feeding.

3.2. Heppenloch

At Heppenloch, five species were available for sampling, *Stephanorhinus hemitoechus*, *Equus ferus, Bos/Bison*, *Cervus elaphus* and *Capreolus capreolus*.

Stephanorhinus hemitoechus has a mesowear pattern significantly lower at Heppenloch (MWS = 2.21) than at Steinheim (MWS = 4.14) (Fig. 1). At Heppenloch, *S. hemitoechus* plots among the grass-dominated mixed feeders, very close to the limit value for the browsers. The microwear pattern (Fig. 2B) is also indicative of a grass-dominated mixed feeding diet.

The horse, *Equus ferus*, has a high mesowear value and plots among the extant grazers (Fig. 1). However, in terms of microwear, the horse plots in between the confidence ellipses for the browsers and the grazers but tending more towards the browsers (Fig. 2B).

Bos/Bison has a mesowear score very similar to that of

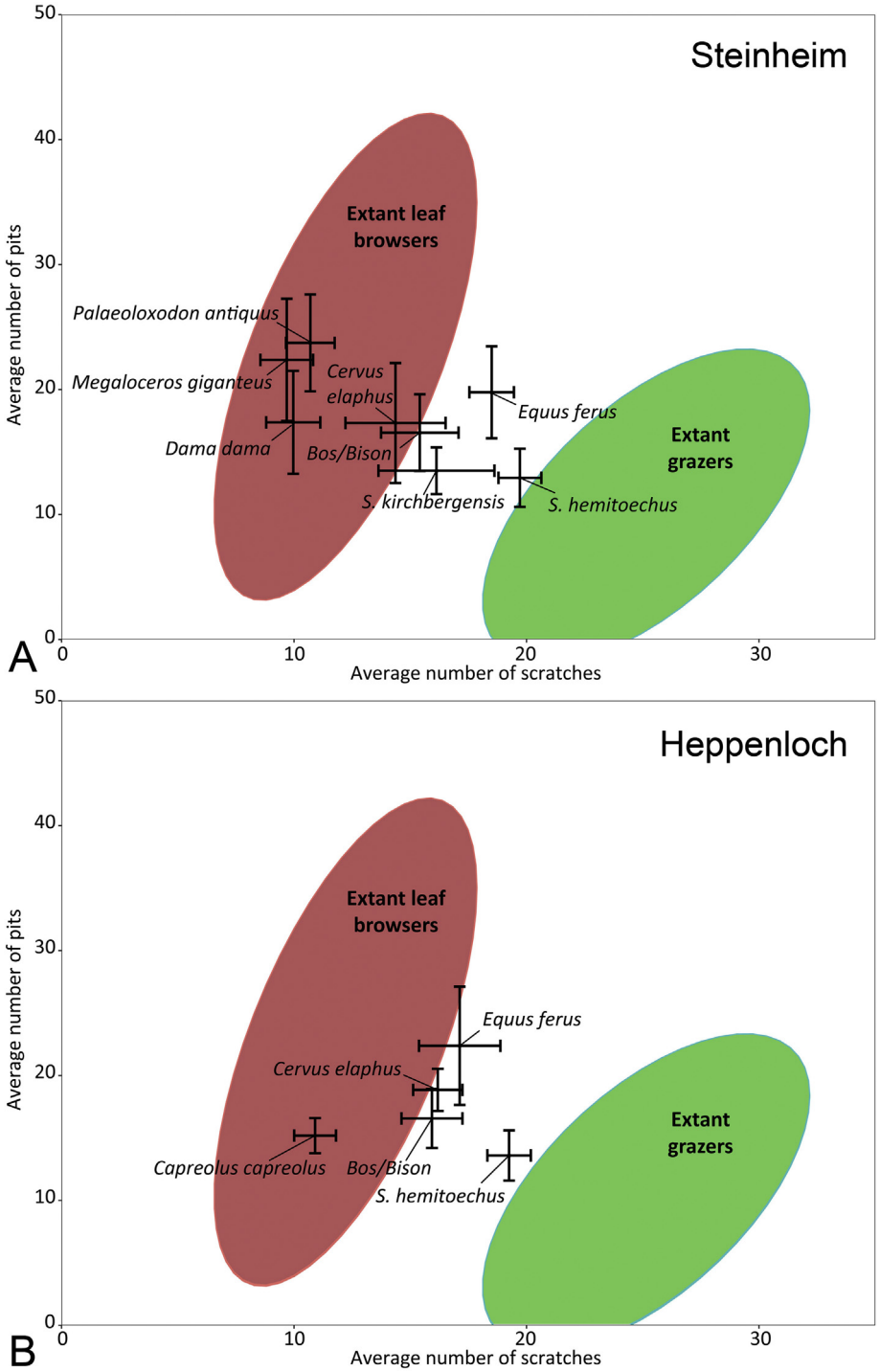

Fig. 2. Bivariate plots of the average numbers of pits and scratches for the ungulates from Steinheim (A) and Heppenloch (B). Bars correspond to standard error of the mean (SEM) for the fossil samples. Grey areas correspond to the Gaussian confidence ellipses ($p = 0.95$) on the centroid for the modern leaf browsers and grazers based data from Solounias and Semprebon (2002) and Rivals et al. (2010, 2013, 2014, 2015b).

S. hemitoechus indicating mixed feeding habits (Fig. 1). Mesowear is consistent with the microwear pattern that also suggests mixed feeding.

The red deer, *Cervus elaphus*, shows a low mesowear score similar to modern leaf browsers or browse-dominated mixed feeders (Fig. 1). The microwear pattern is consistent with the previous result, suggesting also mixed feeding (Fig. 2B).

The roe deer, *Capreolus capreolus*, has the lowest mesowear score for this locality (Fig. 1), indicating leaf browsing. This dietary signal is also observed through microwear analysis with a pattern characterized by low numbers of scratches (Table 2, Fig. 2B).

Similarly to Steinheim, the horse shows some discrepancy between the results from mesowear and microwear but the rhinoceroses, bovids and cervids show consistency in the results from the two proxies.

Table 2
Summary of mesowear and microwear data for the fossil assemblages from Heppenloch.

Mesowear				Microwear						
Species		N	MWS	N	NP	NS	%LP	%G	SWS	%XS
Equus ferus	M	7	4.29	4	22.38	17.13	50	25	1.25	0
	SD		0.76		4.73	1.75				
Stephanorhinus hemitoechus	M	19	2.21	16	13.59	19.25	43.75	12.5	0.94	0
	SD		1.11		2.12	2.36				
Bos/Bison	M	18	2.17	13	16.54	15.96	38.46	7.69	1.08	38.46
	SD		0.62		4.27	2.30				
Cervus elaphus	M	24	1.38	16	18.82	16.21	82.35	29.41	0.88	0
	SD		0.58		3.48	2.12				
Capreolus capreolus	M	6	0.83	6	15.17	11.08	66.67	33.33	0.67	16.67
	SD		0.41		1.72	1.07				

Abbreviations: N = Number of specimens; MWS = Mesowear score; NP = Average number of pits; NS = Average number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = Scratch width score; %XS = Percentage of specimens with cross scratches; M = mean; SD = standard deviation.

4. Discussion

4.1. Dietary traits and habitats

At Steinheim, the dietary traits of the 8 species of large mammals analysed through tooth mesowear cover all categories, from leaf browsers to grazers. This result suggests the availability of a large array of resources for these herbivores on an annual average. Tooth microwear, which reflects more immediate (short-time) behaviour at the ecological scale, indicates browsing and browse-dominated mixed feeding at the time of death for most of the species. Dietary interpretations derived from tooth wear analyses cannot be directly correlated with the type of habitat. However, the availability of closed forested environments at Steinheim is supported by stable isotopes on the assemblages from the Holsteinian interglacial (Pushkina et al., 2014). At Heppenloch, the number of species sampled is lower (N = 5) but the identification of mixed feeders suggests more open habitats than at Steinheim. The interpretation fits with the composition of the assemblage, which seems to be similar, but is lacking *Megaloceros giganteus* and *Stephanorhinus kirchbergensis*. The Heppenloch cave is situated on the Swabian Alb, a karstic plateau with shortage of water. The mammalian assemblage suggests more open conditions than at Steinheim and trees were limited to the valleys (Adam, 1975; Kahlke et al., 2011).

The straight-tusked elephant, *Palaeoloxodon antiquus*, from Steinheim is indicative of the use of browse, and perhaps the use of wooded habitats. In comparison to other assemblages, mesowear and microwear analyses also reported browsing habits for the MIS 11 assemblage from Clacton (Rivals and Lister, 2016; Saarinen and Lister, 2016), however at Swanscombe, the straight-tusked elephants show mixed feeding dietary traits (grass-dominated mixed feeding from microwear and browse-dominated mixed feeding from mesowear) (Rivals and Lister, 2016; Saarinen and Lister, 2016). Among the variability of feeding traits reported for that species (Rivals et al., 2012; Rivals and Lister, 2016), the population from Steinheim is definitely on the browsing-end of the spectrum.

The horse, both at Steinheim and Heppenloch, shows grazing traits through mesowear but mesowear indicates browse-dominated mixed feeding habits. At Steinheim, this result is supported by stable isotopes suggesting relatively humid habitats with dense vegetation (Pushkina et al., 2014) and by ecomorphology (van Asperen, 2010). Similarly to the analysis of stable isotopes, tooth wear suggests that the horse was present in the same habitat and using similar resources than the two rhinoceroses, *Stephanorhinus kirchbergensis* and *Stephanorhinus hemitoechus*. The use of woodland habitats for the horse could be unexpected during the Middle Pleistocene, but such browsing behaviour is not unusual. Horses with a browse-dominated diet were also observed at Schöningen 13 II-4 during the MIS 9 (Rivals et al., 2015a). During the MIS 11, assemblages from the UK such as Clacton, Hoxne, and Swanscombe show clear grazing behaviour for the horse (Rivals and Lister, 2016; Saarinen et al., 2016). At these localities, the two rhinoceroses are also present and show more definite diets, *Stephanorhinus kirchbergensis* having preferences for browse and *Stephanorhinus hemitoechus* for grass. At the localities from the UK, the horse and the rhinoceroses have dietary traits which agree with the diet expected from their morphology (i.e., *Stephanorhinus kirchbergensis* inhabiting woodland habitats while *Stephanorhinus hemitoechus* and *Equus ferus* favouring open grasslands). At Steinheim and Heppenloch, these three species have quite similar diets, but all exhibiting more mixed-feeders than expected.

The cervids from Steinheim, *Megaloceros giganteus*, *Cervus elaphus* and *Dama dama* were browsers. At Heppenloch, *Capreolus capreolus* was also browsing but *Cervus elaphus* was a browse-dominated mixed feeder. The dietary traits identified through tooth wear are in agreement with the diet that would be expected from the brachydont teeth of these three cervids. Similar results were observed in the British sites correlated with MIS 11, such as *Cervus elaphus* at Hoxne and *Dama dama* from Clacton (Rivals and Lister, 2016; Saarinen et al., 2016). The two proxies used in this study are in total agreement and show the use of very similar resources for *Megaloceros giganteus* and *Dama dama* with overlapping values indicating similar diets. *Cervus elaphus*, also a browser, probably had access to slightly different resources.

The bovids from Steinheim and Heppenloch were found to be mixed feeders. Mesowear indicates preferences toward grass, while microwear tends toward browse at the two localities. However, we have to take into account that our sample includes *Bos primigenius* as well as *Bison priscus*. The two species certainly might differ in their diet to avoid competition for resources. We could not confirm the diet of the two species, but previous results from Middle Pleistocene localities show that *Bos primigenius* populations tend toward browse, while *Bison priscus* shows preferences for grass (Rivals, 2012; Rivals and Lister, 2016). *Bos primigenius* from Clacton, for example, shows clear browsing traits while *Bison schoetensacki* from Hundsheim and Deutsch-Altenburg indicates more grazing traits.

The comparison of the dietary traits identified for the large herbivores from Steinheim and Heppenloch were compared to those published for Clacton, Hoxne, and Swanscombe (Rivals and Lister, 2016), three localities correlated with MIS 11. The dietary traits identified in the Steinheim *antiquus*-assemblage are very similar to those reported for Clacton with a dominance of browsers or browse-dominated mixed feeders. Such similarities reported on a biochronological point of view (Schreve, 2001; Schreve and

Bridgland, 2002) are also found at the dietary level, reflecting the presence of similar resources. The Heppenloch assemblage seems to be quite similar, but the fauna is composed mostly of mixed feeders suggesting a more open context than at Steinheim. Our data support an earlier interpretation which reported the absence of *Megaloceros giganteus* and *Stephanorhinus kirchbergensis* and suggested the existence of more open habitats at Heppenloch (Kahlke et al., 2011).

4.2. Low resolution contexts and identification of seasonality

In archaeological sites with high-resolution stratigraphic records, the combined use of tooth mesowear and microwear permitted the identification of seasonality in the accumulation of remains. The time-frame recorded by each proxy is different and discrepancies in the results from the two proxies indicates changes in diets related to seasonal variations in the availability of resources (Davis and Pineda Munoz, 2016; Sánchez-Hernández et al., 2016). The integration of the two techniques successfully identified seasonality in Late Pleistocene sites like Teixoneres Cave (Sánchez-Hernández et al., 2016) and Abric Romaní (Bargalló et al., 2016). In the two localities we analysed, Steinheim and Heppenloch, most of the results obtained through tooth microwear and mesowear are in agreement. The low temporal resolution of the deposits is most likely inducing a time-averaging of the microwear data which does not differ significantly from the mesowear signal. The combination of high resolution proxies such as mesowear and microwear is a powerful technique in fossil sites with high temporal resolution, but it does not seem appropriate to detect seasonality when the deposits may have been accumulated over a long period of time.

5. Conclusion

In assemblages where the temporal resolution is relatively low (compared to some Late Pleistocene assemblages), the interpretations obtained from tooth mesowear and microwear tend to be in agreement due to time averaging. The integration of the two techniques cannot be used to detect seasonality in low-resolution stratigraphic contexts, but both mesowear and microwear, together or independently, are good proxies for inferring paleodiets and reconstructing habitats in Middle Pleistocene sites, such as Steinheim and Heppenloch.

The faunal composition and the dietary traits of the large herbivores from Steinheim indicate predominantly wooded habitats and mixed habitats at Heppenloch. The dietary traits identified at the two localities are similar to those from the British localities which are attributed to the Hoxnian/Holsteinian interglacial and correlated with MIS 11.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2018.03.026.

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